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Freshwater ciliates as ecophysiological model organisms – lessons from *Daphnia*, major achievements, and future perspectives

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With 6 figures and 1 table

Abstract: Similar to *Daphnia*, many planktonic ciliates are algivores that occur in virtually every natural lake and reproduce primarily asexually. Due to their larger population size and shorter generation time, their significance as algal consumers and secondary producers may exceed that of *Daphnia* during algal blooms and when averaged over the season. The high reproduction rate, the ease of culturing, the accessibility to experimental manipulation, and the potential to apply sophisticated measuring techniques such as flow cytometry render some ciliate species ideal candidates for ecophysiological laboratory experiments. This paper summarizes recent research in which ciliates have been used as model organisms for investigating the effect of environmental key parameters on planktonic organisms. Special attention is given to the (combined) effect of temperature, food, pH and predators. Niche partitioning has been studied at the level of genus, species and clone. Open questions and emerging perspectives of ciliate research for issues of general ecological relevance will be discussed at the end of each section.

Key words: ciliates, ecophysiology, temperature, food, *Daphnia.*

Introduction

Ecology seeks to understand the processes that determine the distribution and abundance of organisms in their natural habitats. Since it is impossible to study all potentially relevant ecological factors with every creature in every environment, ecological research is mainly confined to the study of primary processes in selected ecosystems, focusing on the major players in the food web. There are surprisingly few model organisms in aquatic ecological research in general, and in limnology in particular. Thanks to the work by WIN-

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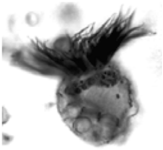
FRIED LAMPERT and his numerous colleagues worldwide, *Daphnia* has become a model organism of international freshwater ecology (LARSSON & WEIDER 1995, LAMPERT 2006). Several main reasons for this success story are listed in Table 1 (see also LAMPERT 2006).

Most of the statements hold true, with some modifications, for planktonic freshwater ciliates (Table 1). Obviously, the unicellular ciliates do not carry eggs, but the equivalent of *Daphnia*'s resting eggs are the ciliate cysts. A major difference between *Daphia* and freshwater ciliates is that the former consist of a well defined crustacean genus, while the latter comprise organisms belonging to different genera, families, and even classes. Oligotrich and prostomatid ciliates are the dominant taxa among the planktonic freshwater ci-

Table 1. Comparison of the significance of *Daphnia* and ciliates in freshwater food webs and as model organisms in various biological disciplines.

Parameter or process	***Daphnia*** 	**Ciliates** 
Central role in pelagic food webs, (at times) most important algivores	yes	yes
Prey for	planktivorous fish, carnivorous cladocerans, *Chaoborus* larvae	Cladocerans, copepods, and rotifers
Reproduction primarily asexual	by cyclic or obligate parthenogenesis	by cell division
Easy to culture and handle	yes	yes, but more difficult to manipulate individually
Model organism for morphological and ecophysiological studies	yes	yes
Eggs and embryos carried by mothers, ideal object for studies of population dynamics	yes	no
High phenotypic plasticity and large intraspecific variation	yes	yes
Produce resting stages	yes, resting eggs	yes, cysts

liates in most natural fresh water lakes, reservoirs, rivers, and ponds (LAYBOURN-PARRY 1992, WEISSE & MÜLLER 1998, WEISSE 2003). Accordingly, if there are model organisms among planktonic freshwater ciliates, they should belong to the oligotrichs and prostomatids to fulfil the first of the criteria listed in Table 1.

The use of ciliates as model organisms has a long tradition, dating back to the seminal papers by GAUSE (1934) in population ecology and SONNEBORN (1937, 1957) on reproduction and inheritance, and the detection of cryptic species. More recently, the unicellular ciliates have been applied as model organisms for the more complex metazoa in cell biology, physiology and other biological disciplines (HAUSMANN & BRADBURY 1996). In aquatic ecology, little use has been made of the specific advantages that ciliates offer, in particular for experimental work.

This paper presents a synopsis of the ciliate research conducted at the Limnological Institute, University of Konstanz, Germany, at the Max-Planck Institute for Limnology, Plön, Germany, and at the Institute for Limnology of the Austrian Academy of Sciences, Mondsee, Austria, over the past 20 years. These three laboratories used freshwater ciliates to study questions of general ecological or ecophysiological relevance under comparable experimental conditions. A significant part of this work was inspired by previous and contemporary research of WINFRIED LAMPERT and his colleagues working with *Daphnia* at Konstanz and Plön. I will therefore use the above list describing the significance of *Daphnia* as a template to illustrate the potential of freshwater ciliates as (future) model organisms. The major goals of this paper are to (1) draw the reader's attention to the enormous potential ciliates offer for ecophysiological studies and (2) to suggest some perspectives for current problems and future work.

Methods

Results presented in this paper are mainly based on results and methods that have been published earlier in a different context. Ciliate sampling, counting and sizing were described in detail by MÜLLER (1989), MÜLLER et al. (1991) and WEISSE et al. (1990). In situ growth rates of ciliates were measured in 4-l diffusion chambers at the mid-lake station (water depth 147 m) in the northwestern part of Upper Lake Constance (MÜLLER & WEISSE 1994, WEISSE 1997, WEISSE & MÜLLER 1998).

All protist species investigated in this study have been reared in the laboratory as non-axenic batch cultures. Most of the experimental studies referred to in this paper used non-clonal ciliate cultures. For details of the experimental design, consult MÜLLER & SCHLEGEL (1999), JÜRGENS & ŠIMEK (2000), WEISSE et al. (2001), WEISSE et al. (2002), WEISSE (2004), and WEISSE & STADLER (2006).

Results and discussion

Central roles of *Daphnia* and ciliates in pelagic food webs – evidence from field studies

The central role that *Daphnia* play in pelagic food webs of temperate and arctic lakes and ponds has been documented in many studies carried out mainly in Europe and North America (Lampert 1985, Sterner 1989, Larsson & Weider 1995, Lampert 2006). Prealpine Lake Constance (in German: Bodensee) is one of the lakes where the ecophysiology of *Daphnia* has been studied in great detail (summarized by Gaedke & Straile 1998, Straile & Geller 1998, Lampert 2006). This lake served as reference ecosystem for the description of the seasonal succession of plankton (Sommer et al. 1986, Sommer 1989), in which the significance of *Daphnia* as algal consumers and fish food was portrayed. In particular, the finding that excessive grazing by *Daphnia* causes the 'clear-water' phase in meso-eutrophic lakes was made in Lake Constance (Lampert 1978 b, Lampert & Schober 1978). The discussions of the Plankton Ecology Group (PEG), a working group affiliated to The International Association of Theoretical and Applied Limnology (Societas Internationalis Limnologiae, SIL) and The International Society for Ecology (INTECOL), began in 1976 (Sommer et al. 1986, Sommer 1989), at the end of the International Biological Programme, i. e. well before the significance of ciliates and other protozoa in aquatic food webs was detected and studied in detail. It is therefore not surprising that protozoa received little attention in the PEG model. The empirical and theoretical investigation of the ecological role of heterotrophic protists in Lake Constance began within the Special Collaborative Programme "Cycling of Matter in Lake Constance" (1986–1997, Bäuerle & Gaedke 1998), funded by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation). An early investigation demonstrated that ciliates are the most important consumers of primary production during the spring phytoplankton peak (Weisse et al. 1990). As in other lakes, the ciliate community in Lake Constance is, both numerically and in terms of biomass, dominated by oligotrich and prostome species (Müller 1989, Müller et al. 1991, Weisse & Müller 1998, Weisse 2003). The overall significance of ciliates as the primary herbivores in this lake became obvious when experimental results were combined with various theoretical modelling analyses (Geller et al. 1991, Gaedke & Straile 1994, Gaedke et al. 1995, Straile 1998). Resulting from those joint efforts, it is now clear that ciliates contribute, on the annual average, more to the total consumption of algal biomass than *Daphnia* (Straile 1995, 1998, Gaedke & Straile 1998).

The importance of *Daphnia* for controlling seasonal plankton dynamics was reinforced at the turn of the last century when the response of lakes to meteorological forcing associated with the North Atlantic Oscillation was studied (Straile 2000, Straile & Adrian 2000, Scheffer et al. 2001). Based upon a refined recent analysis it now appears that, on the long term average, ciliates and rotifers may be of equal importance as *Daphnia* even for the onset of the clear-water phase in Lake Constance (Tirok & Gaedke 2006). There are some years where *Daphnia* clearly dominate in the plankton in late spring and early summer, and there are other years in which ciliates and rotifers are the more important algal grazers during this period. In conclusion, with respect to the mechanisms that control the seasonal succession of phytoplankton in Lake Constance the attention has shifted from *Daphnia* to ciliates. There is no doubt that *Daphnia* play a major role as algal predators, but their overall significance is second to that of ciliates.

The joint investigation on Lake Constance and some other studies revealed that ciliates are not only the most important algal grazers, but that they are also the primary consumers of the heterotrophic nanoflagellates (HNF; Güde 1988, Šimek et al. 1990, Sanders & Porter 1990, Weisse 1991, Cleven 1996, Weisse 1997). When their populations peak, *Daphnia* can decimate the standing stock of HNF within a few days, but their control of HNF dynamics is restricted to a relatively short period (Weisse 1991, Jürgens 1994, Gaedke & Straile 1998, Wickham 1998).

In most natural lakes, both *Daphnia* and ciliates are generally more important as herbivores than as bacterivores. There is no doubt that small HNF are the primary bacterivores, exerting a strong top-down pressure on the bacterial community, particularly in oligotrophic to moderately eutrophic lakes (Sanders et al. 1989, Weisse 1990, Jürgens & Güde 1991, Vaqué & Pace 1992, Weisse & McIsaac 2000, Weisse 2003). In Lake Constance different estimates of the HNF grazing impact on bacteria consistently yielded that HNF remove 40 to 60 % of bacterial production (Weisse 1991, Jürgens & Güde 1991, Straile 1995, Simon et al. 1998). Similar to total herbivory, ciliates are, on the seasonal average, more important than *Daphnia* as bacterial grazers, cropping another 10 to 20 % of bacterial production (Straile 1995, Simon et al. 1998). Specialized bacterivorous ciliates can be major consumers of autotrophic and heterotrophic picoplankton (Sanders et al. 1989, Šimek et al. 1996, 1997, 2000). Highly efficient fine suspension feeding ciliates such as *Strobilidium hexakinetum, Halteria* spp. and several *Vorticella* species may ingest several thousand bacterial cells or several hundred picocyanobacteria ciliate^{-1} h^{-1} (Šimek et al. 1996, 1997, 2000). The uptake and clearance rates of *Halteria* feeding on bacteria are approximately two orders of magnitude higher than the respective rates of typical freshwater HNF (Šimek et al. 2000) and three orders of magnitude lower than typical clearance rates of bacteria eating *Daphnia* (Güde 1988, Jürgens 1994). Accordingly, oligotrich ciliates can become the dominant bacterivores in freshwater systems when their abun-

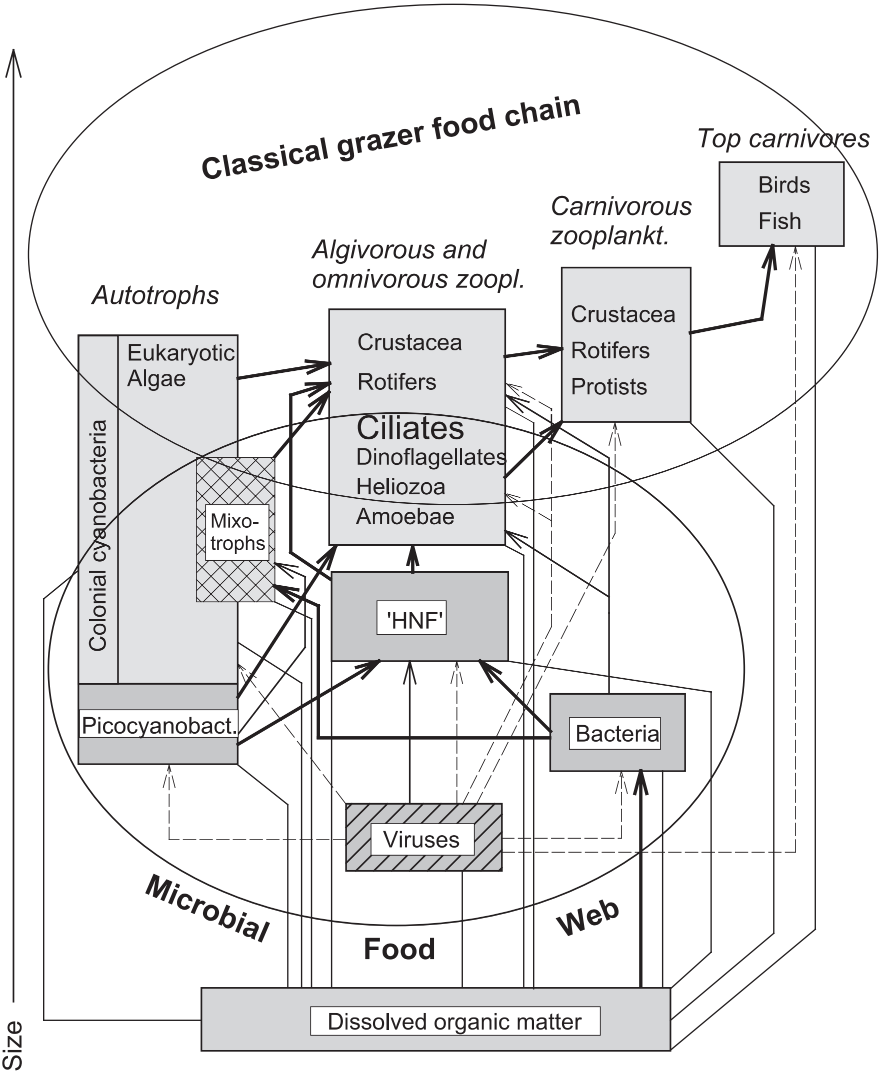


Fig. 1. Trophic interactions and the central position of ciliates in the planktonic food web in lakes. Feeding interactions and bacterial substrate uptake are indicated by solid lines and arrow heads. Viruses attack several components of the planktonic food web (broken lines and arrows). The pool of dissolved organic matter is replenished by various release processes (excretion, exudation, cell lysis, 'sloppy' feeding) and used as substrate by bacteria. There is no strict separation between the classical grazer food chain and the microbial food web, and ciliates and some other protozoa are at the interface of the two aspects of the pelagic food web. 'HNF' denotes the taxonomically diverse functional guild of heterotrophic nanoflagellates, the primary bacterivores (modified after Weisse 2003).

dance reaches approximately 10 cells ml^{-1} (Jürgens et al. 1999, Šimek et al. 2000), i. e. when their cell numbers exceed the abundance of *Daphnia* approximately 1000×. Compared to *Daphnia*, it is an important difference that bactivorous ciliates ingest bacteria smaller than 1 µm, i. e. that they affect the dominant picoplankton size class. The bactivorous ciliates functionally belong to the microbial food web, the algivorous and omnivorous ciliates compete with rotifers, cladocerans and calanoid copeods for the same protist food, namely small (5 – 20 µm), well edible algae such as cryptophytes and chrysomonads. Accordingly, the position of (prostome and oligotrich) ciliates is central in the pelagic food web (Fig. 1).

The release of nutrients and DOC is ultimately linked to the grazing activity of planktonic filter feeders (Fig. 1). The significance of 'sloppy feeding' by *Daphnia* for nutrient regeneration was first demonstrated in Lake Constance (Lampert 1978 a). Quantification of the contribution of the various zooplankters to nutrient regeneration is an even more difficult endeavour than estimating their relative grazing impact (Hochstädter 1997, Güde & Gries 1998). It is clear that both *Daphnia* and ciliates contribute substantially to the release of nutrients and DOC in the epilimnion, but a direct comparison of their respective contribution requires too many assumptions to allow any firm conclusions (Güde & Gries 1998).

The discussion above considered indirect interactions between *Daphnia* and ciliates, such as competition for the same algal and bacterial food. There is, however, also a direct link, because *Daphnia* feed upon most small and common planktonic ciliates and may thus control their population dynamics (Gilbert 1989, Müller et al. 1991, Wickham & Gilbert 1991, Jack & Gilbert 1993, 1997, Jürgens 1994, Pace & Vaqué 1994). In contrast to daphnids, most ciliates are too small and too transparent to fall victim to visually hunting fish species. The top-down control of ciliates and daphnids is therefore clearly different, with the latter being major predators of the former (Table 1).

To summarize this section, many aspects on the trophic role of *Daphnia*, which were discovered mainly in the 1970 s, were confirmed in a surprisingly similar manner for ciliates in the 1980 s and 1990 s. Until recently, our view of the pelagic food web was biased towards *Daphnia*; it now appears that ciliates are quantitatively the more important players in many aquatic ecosystems.

Populations of daphnids and ciliates have clonal genetic structures – they are ideal objects for studies on gene flow, microevolution and local adaptation

Of the major algivorous freshwater taxa, only (calanoid) copepods reproduce exclusively sexually. *Daphnia* and rotifers are cyclic or obligate parthenogenics (De Meester et al. 2006). Similarly, most planktonic freshwater ciliates reproduce asexually by cell division during the growing season. The outcome of asexual reproduction is, however, different between daphnids and planktonic ciliates. In the latter, cell division results in two new daughter cells, thus doubling the population number. In the former, the clutch size, i. e. the number of eggs in the brood chamber of the female *Daphnia*, may vary widely in response to the environmental conditions. The environmental impact on the clutch size was, for instance, investigated in seven alpine lakes in Portugal, which differed with respect to their food levels, predation pressure by fish on neonate and adult *Daphnia* and invertebrate predation on their eggs (Gliwicz & Boavida 1996). The mean number of eggs per clutch of the dominant cladoceran, *D. pulicaria*, ranged from 1.7 to 4.8; several females carried > 15 eggs in their brood pouch. The large clutch size, relative to rotifers, enable *Daphnia* to increase their population numbers rapidly and to colonize new environments, such as many ponds and pools, efficiently. Note that, if the mean number of *Daphnia* offspring is 3, ciliates would have to divide twice in the same time period to increase their population size at the same rate.

The asexual reproduction is an adaptation to stable, favourable environmental conditions, under which a high food supply allows for a fast increase in population numbers. The clonal genetic structures of natural populations, which can be studied with population genetic methods, renders daphnids, rotifers, and ciliates ideal objects for studies on gene flow, microevolution and local adaptation. Stimulated by the pioneering work of Hebert (e. g. Hebert 1974 a, b) extensive use has been made of this advantage in *Daphnia*, and, to a lesser extent, in rotifers (reviewed by De Meester 1996). *Daphnia* populations living in intermittent habitats with a regular phase of sexual reproduction are usually characterized by high genetic diversity and relatively stable genotype frequencies that are close to the Hardy-Weinberg equilibrium. In contrast, permanent populations show low genotypic diversity, rapid seasonal shifts in the genotypic diversity, and gross deviations from the Hardy-Weinberg equilibrium (summarized in De Meester 1996, De Meester et al. 2006). Clonal selection leads to pronounced intraspecific genetic differences in *Daphnia* populations, both temporally and spatially. The general hypothesis, that asexual taxa possess more broadly adapted genotypes (“general purpose genotypes”) was tested, and not supported, with obligate parthenogenetic clones of *D. pulex* (Weider 1993). Analysis of the mitochondrial (mt) DNA variation of the same species provided evidence for both long-distance dispersal of some clones, over thousands of kilometers, and smaller scale biogeographic differences of other clones (Weider et al. 1996 and references therein). Local adaptation of *Daphnia* populations, i. e. genetic differentiation resulting from an adaptive response to local selective forces, was demonstrated for several ecologically relevant traits (De Meester 1996). A recent investigation revealed shifts to cyanobacterial resistance from clones of *D. galeata* in Lake Constance during the period of approximately 40 years of its eutrophication and re-oligotrophication (HAIRSTON et al. 1999). The clones were hatched from dormant eggs that were buried in the lake sediments. In conclusion, it appears that "generalist" *Daphnia* genotypes coexist with "specialists" in many environments, and that the local genetic differentiation in ecologically relevant traits is more pronounced in *Daphnia* than in other zooplankton taxa (DE MEESTER 1996).

Analysis of the genetic population structure of aquatic ciliates, in contrast, is still in its infancy. This is not only for historic grounds, because ciliates have been overlooked in aquatic food web studies until recently, but also because they are smaller and more delicate to handle than the larger metazoan plankters. Moreover, the nuclear dimorphism of ciliates, with a micronucleus responsible for generative functions and a macronucleus with somatic functions, and the unique modes of their DNA evolution (PRESCOTT 2000) complicate the comparative analysis of their genetic population structure. During macronuclear development, over 95 % of its genome may be destroyed, while the copy number of the rRNA gene may exceed 100,000 in some ciliates (BLEYMAN 1996).

Ciliate genetics has been studied in great detail, but this was restricted mainly to the genera *Paramecium, Tetrahymena, Euplotes, Oxytricha* and *Stylonichia* ("the chosen few", NANNEY 1980), which are less common or do not occur at all in the plankton of freshwater lakes. Isoenzyme electrophoretic patterns have been applied as diagnostic tools for the detection of cryptic ciliate species and to study questions of ciliate biogeography, but this could be done after cultivation only (NANNEY et al. 1989, AMMERMANN et al. 1989). More recently, the advent of molecular fingerprinting techniques such as random amplified polymorphic DNA (RAPD; KUSCH & HECKMANN 1996, KUSCH 1998, KUSCH et al. 2000, STOECK & SCHMIDT 1998, STOECK et al. 2000) and analysis of the mitochondrial DNA (BARTH et al. 2006) confirmed the high intraspecific genetic variation in *Paramecium, Euplotes, Stentor* and some other species. The study by BARTH et al. (2006) revealed a high interspecific divergence in the mitochondrial cytochrome c oxidase I (COI) sequences, while the non-coding, nuclear internal transcribed spacer (ITS) regions 1 and 2 were highly conserved. If the knowledge that has been gained with the heterotrich (*Stentor*), hypotrich (*Euplotes*), stichotrich (*Oxytricha*), hymenostome (*Tetrahymena*) and peniculid (*Paramecium*) ciliates is representative for the common oligotrich and prostome ciliates, the freshwater ciliate fauna should have a clonal population structure with potentially high genetic divergence among cosmopolitan species.

Ecophysiological laboratory investigations already demonstrated clonal divergence not only for strains from geographically distant lakes, but also for sympatric clones among common oligotrich and prostome ciliates (Weisse 2002, Weisse & Lettner 2002, Weisse & Rammer 2006). These findings are similar to results obtained with some *Daphnia* populations, where genetic and ecological differentiation were recorded in spite of morphological stasis (Schwenk et al. 2004). It is now clear that the morphospecies concept may dramatically underestimate the biological diversity of freshwater ciliates (Weisse & Rammer 2006).

If microevolution and local adaptation play a role in freshwater ciliates is a matter of considerable debate (reviewed by Weisse 2006). This issue is related to the significance of dispersal and the mode of reproduction. If the gene pool of each population is being swamped by new immigrants, (clone-specific) local adaptation to specific habitats and allopatric speciation should be of minor importance among free-living protists. Similar to the open question of the magnitude of gene flow between different metapopulations, the frequency and significance of sexual reproduction in the field is virtually unknown for most ecologically relevant ciliate species. Isoenzyme analysis provided diagnostic traits for the detection of sexual and asexual strains within a given (morpho)species (Nanney et al. 1980, reviewed by Dini & Nyberg 1993, Lynn 1996). It is clear that amicronucleate ciliates, which do not possess a micronucleus that controls conjugation in ciliates, cannot perform sexual reproduction. The vast majority of micronucleate ciliates will undergo sexual reproduction occasionally, and it is generally assumed that sexual reproduction in ciliates is induced by deteriorating environmental conditions (Dini & Nyberg 1993). However, the proximate factors that trigger sexual reproduction have not yet been studied with common planktonic species.

What is urgently needed is a rigorous test of local adaptation among globally occurring freshwater protozoa. The gene flow from new immigrants should be estimated and related to the frequency of sexual reproduction within a given ciliate population. The current challenge is to find markers and methods to adequately assess the gene flow and rate of adaptive mutations within common ciliate populations.

Ciliates as ecophysiological model organism – advantages and drawbacks, relative to *Daphnia*

The literature on the ecophysiology of *Daphnia* is immense, and this is the primary reason why *Daphnia* has become a model organism for aquatic ecology. The feeding ecology, swimming behaviour including diel vertical migration, respiration, excretion, reproduction, competition, and defence strategies against vertebrate and invertebrate predators have all been studied in great detail with various *Daphnia* species (reviewed by Larsson & Weider 1995, Gliwicz 2003 a, Lampert 2006). The temperature reaction norm, the numerical response (growth rate vs. food concentration), and the functional response (ingestion rate vs. food concentration) have been characterized for most common daphnid species. In comparison, similar investigations are available for only a handful of ciliate species (discussed below).

Ciliates are considerably smaller than *Daphnia*, and this is beneficial or disadvantageous for the researcher, depending on the research topic addressed. Most dominant freshwater ciliates cannot be identified easily and handled individually, due to their tiny cell size. The more difficult detection and identification, often requiring sophisticated staining techniques (FOISSNER et al. 1999), and the taxonomic experience needed render it more difficult to isolate new strains and to establish ciliate cultures than to establish cultures of most daphnids, copepods, or rotifers. Once isolation was successful, many ciliate species can be kept in the laboratory for long periods. Although it is relatively easy for a skilled experimenter to pipette individual cells of 20 or 30 µm length out of a suspension under a stereo microscope, the current methods used in ecophysiological experiments are usually not sensitive enough to allow analysis at the single cell level. Experimental results are therefore assessed at the population level, i. e. the experimental outcome is averaged over the population. This is an advantage because, due to the usually large ciliate cell numbers used in ecophysiogical experiments, the results may be more representative for a species than when a few individual organisms are investigated. An important exception from this rule is the analysis of clonal cultures; in this case, all cells are genetically identical in short term experiments, and the measured experimental mean is comparable to results obtained for individual *Daphnia*. A drawback of the 'population approach' is that the individual variation is neglected. From a conceptual point of view, this approach is unsatisfactory, because natural selection does not select for the mean (WEISSE 2002).

Sophisticated optical techniques are now available to analyse protists at the single cell level (reviewed by WEISSE 2002, 2003). Video microscopy has been applied to measure the feeding process of individual protozoans (BOENIGK & ARNDT 2000 a, b, BOENIGK et al. 2001). This technique revealed a large individual variability among heterotrophic flagellate populations (BOENIGK 2002, BOENIGK & ARNDT 2002). Flow cytometry combines the advantages of the large population size with the analysis of individual cells. With this technique, it is possible to measure cell size, surface properties and various cellular constituents of several thousands of protist cells individually within one minute (RECKERMANN & COLIJN 2000, SHAPIRO 2000, LINDSTRÖM et al. 2002, MARIE et al. 2005). In combination with cell sorting, live cells can be sorted out of a suspension; this method has been applied successfully to establish clonal cultures of freshwater ciliates (LINDSTRÖM et al. 2003). When flow cytometry was applied to measure the uptake of algae by herbivorous protists due to the increase of algal induced autofluorescence, a high individual variability became apparent (reviewed by WEISSE 2002).

Drawbacks of the optical techniques in general, and flow cytometric cell sorting, in particular, are their high costs and the advanced expertise needed. Although modern video microscopy devices and flow cytometers are relatively easy to operate, a deeper understanding of the techniques is a prerequisite to obtain unbiased results and to condense and analyze the immense information stored electronically in a meaningful manner. Clearly, all this is a disadvantage compared to *Daphnia* and copepods which can be identified and manipulated more easily. A corollary of these facts is that at present many more researchers work with *Daphnia* than with freshwater ciliates.

Ecophysiology – The temperature response of freshwater ciliates and *Daphnia*

The temperature response of prostome and oligotrich ciliates has been studied in considerable detail. Growth rates of planktonic freshwater ciliates vary widely and show species-specific adaptations (Fig. 2). Maximum growth rates reported are close to 3 d^{-1} (Fig. 2 A), equivalent to approximately 4 cell divisions d^{-1}. The temperature where growth rates peak can differ by as much as 12–15 °C within closely related species (compare *Urotricha farcta*, Fig. 2 A, with *U. castalia*, Fig. 2 C). In spite of their different temperature optima, both species, like most of the others investigated thus far, are tolerant to a relatively wide range of temperatures. Indications for warm water and cold water species are rare among common freshwater ciliates. The prostome species *Balanion planctonicum* from subalpine lakes in central Europe did not tolerate temperatures >22 °C (Fig. 2 D), and the oligotrich *Meseres corlissi* isolated from the Dominican Republic did not grow at temperatures < 15 °C (Fig. 2 G). Fast growing species such as *U. farcta* (Fig. 2 A) and *Rimostrombidium lacustris* (Fig. 2 H) coexist in many lakes with slowly growing species such as *Coleps spetai* or the scuticociliate *Histiobalantium* sp. (MÜLLER & WEISSE 1994), which was later identified as *H. bodanicum* (KRAINER & MÜLLER 1995). Under food-replete conditions, most freshwater ciliates divide once or twice per day when they are close to their temperature optimum. Fig. 2 illustrates that there are not only obvious species-specific differences, but that the temperature response may also vary within a given species. The intraspecific differences may be relatively minor (Fig. 2 D, H), but they can also reach similar magnitude as interspecific differences (Fig. 2 B). Fig. 2 E shows growth rates only of the fastest growing of four clones of *C. spetai* that have been investigated in parallel; the temperature response of this species was clone-specific (WEISSE & RAMMER 2006). This study and similar investigations revealed significant differences in clonal growth rates among prostome and oligotrich ci-

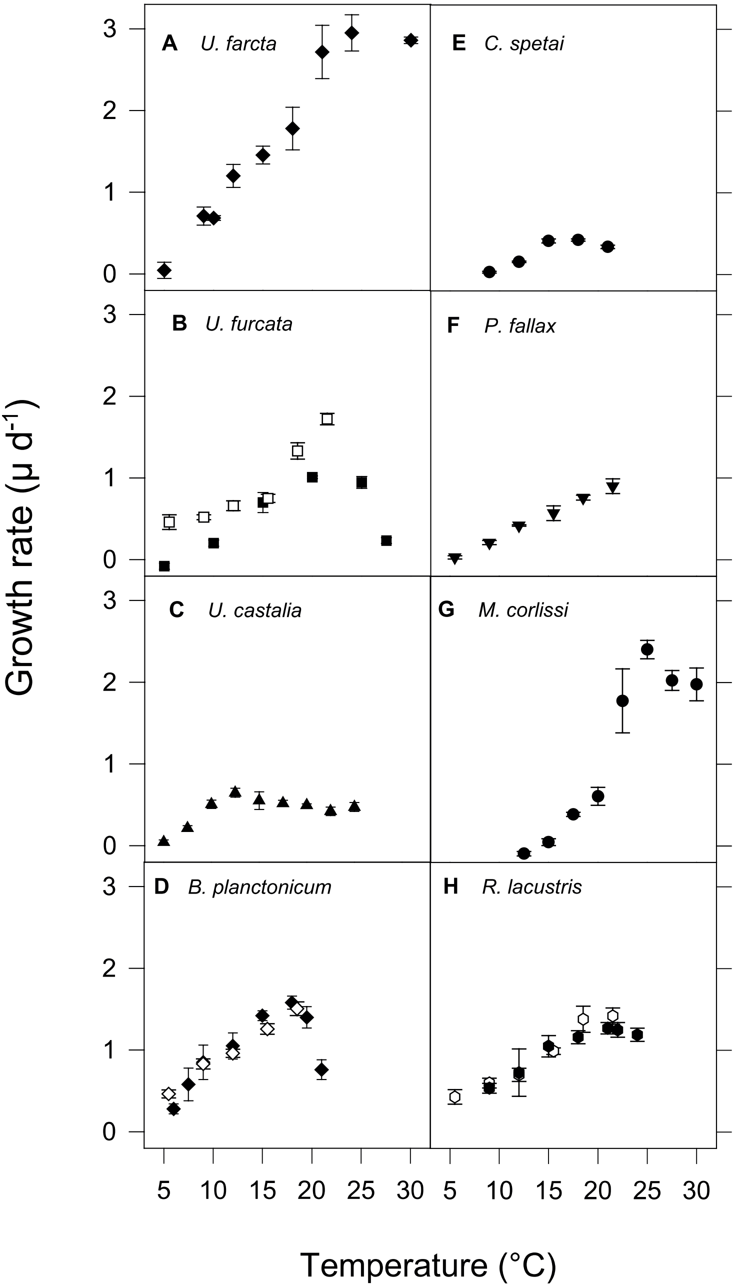


Fig. 2. Population growth rates of prostome **(A–E)** and oligotrich **(F–H)** ciliate species. Symbols denote mean values of several replicates, error bars 1 SD. Sources: WEISSE et al. 2001, WEISSE et al. 2002 (A–D, solid symbols); WEISSE & RAMMER 2006 (E); MÜLLER 1991, MÜLLER & GELLER 1993 (F, open symbols in B, D and H); WEISSE 2004 (G).

liates (reviewed by WEISSE 2002). The consequences of seemingly minor differences in growth rates of exponentially growing ciliates have been demonstrated recently (WEISSE & RAMMER 2006); if there is a clone that contributes initially 1 % to total population cell numbers and this clone grows at a rate 10 % faster than the average cells of this population, the fast growing clone may reach 50 % of the total abundance within two weeks.

In *Daphnia*, individual and population growth are closely coupled. Under saturating food conditions in the laboratory, maximum somatic growth rates of temperate *Daphnia* clones are close to $0.7\,d^{-1}$ and peak between 23 and 26 °C (MITCHELL & LAMPERT 2000). This study revealed relative clonal differences in the temperature response of *D. magna* that are comparable to the results obtained for ciliates. Intrinsic rates of (population) increase (r) of several *Daphnia* species measured in the laboratory at temperatures ≥ 20 °C vary widely, ranging from < 0.1 to $0.44\,d^{-1}$ (reviewed by LENNON et al. 2001). Enclosure experiments in McDaniel Lake, Missouri, revealed maximum r of $0.47\,d^{-1}$ for the native *D. parvula* and $0.53\,d^{-1}$ for the exotic *D. lumholtzi*, respectively, in the temperature range 24–27 °C (LENNON et al. 2001). Such high intrinsic growth rates are rarely reached in situ, because most daphnid populations appear to be food limited in natural lakes during the better time of the year (BOERSMA & VIJVERBERG 1994, MÜLLER-NAVARRA & LAMPERT 1996, SAUNDERS et al. 1999).

The temperature reaction norm of freshwater prostomes and oligotrichs (Fig. 2) shows an asymmetric shape, which is similar to the temperature response of *Daphnia* and other ectotherms (HUEY & KINGSOLVER 1989, MITCHELL et al. 2004 and references therein): typically, there is a linear increase from the minimum temperature normally experienced in situ to the maximum growth rates, followed by a narrow or broader plateau and a sudden decline at temperatures beyond the maximum, when key enzymes denature (HUEY & KINGSOLVER 1989, SOMERO et al. 1996, MONTAGNES et al. 2003). The temperature of maximum performance or response (TMR), at which growth rates peak, is considered to represent the temperature optimum (HUEY & KINGSOLVER 1989, MITCHELL et al. 2004). The TMR of *Daphnia* is often high, compared to typically experienced temperature ranges (MITCHELL et al. 2004). As ATKINSON (1996) pointed out, it is misleading to equate the TMR with the temperature optimum, because rates of survival (as a proxy for Darwinian fitness) often decrease considerable at this temperature. Recently, WEISSE (2004) concluded from his study on the temperature response of the oligotrich ciliate *Meseres corlissi* that the peak of the gross growth efficiency (GGE) may represent the temperature optimum. The GGE denotes the efficiency of food convertion, i. e. it is the ratio between production and ingestion (both can be expressed in units of biovolume, dry weight or carbon content). In *M. corlissi*, the GGE was reduced at the temperature extremes. STRAILE (1997) concluded from a literature review that the GGE of ciliates decreases with temperature, but he also pointed to the uncertainty inherently involved in any estimate of the GGE. Food quantity and quality, i. e. the nutritional composition of food and relative predator/prey size, also affect GGE (Gismervik 2005). Obviously, more research is needed with different species to reveal if there is a general relationship between temperature and GGE. The data available for freshwater ciliates (Fig. 2) do not show high TMR, rather, the temperature response of the ciliate species appears to be adapted to the conditions in their natural habitat.

Direct comparisons of temperature dependent maximum growth rates measured in the laboratory with gross population growth rates realised in situ have been reported for *B. planctonicum, U. furcata* and *H. bodamicum* (Müller & Weisse 1994, Weisse & Müller 1998). These studies showed that in situ growth of planktonic ciliates may reach maximum rates, provided that there is plenty of edible food. In mesotrophic and eutrophic temperate lakes such as L. Constance this situation is typical of the spring season, when small edible algae peak (Fig. 3). In this lake, food limitation reduces the in situ growth rates at higher water temperatures in summer (Müller et al. 1991, Weisse & Müller 1998). Due to seasonal shifts in the taxonomic phytoplankton composition, the summer chlorophyll peak contained a higher percentage of larger algae that were inedible for most planktonic ciliates. For temperature sensitive species such as *B. planctonicum* (Fig. 2 D) and *H. bodamicum* nega-

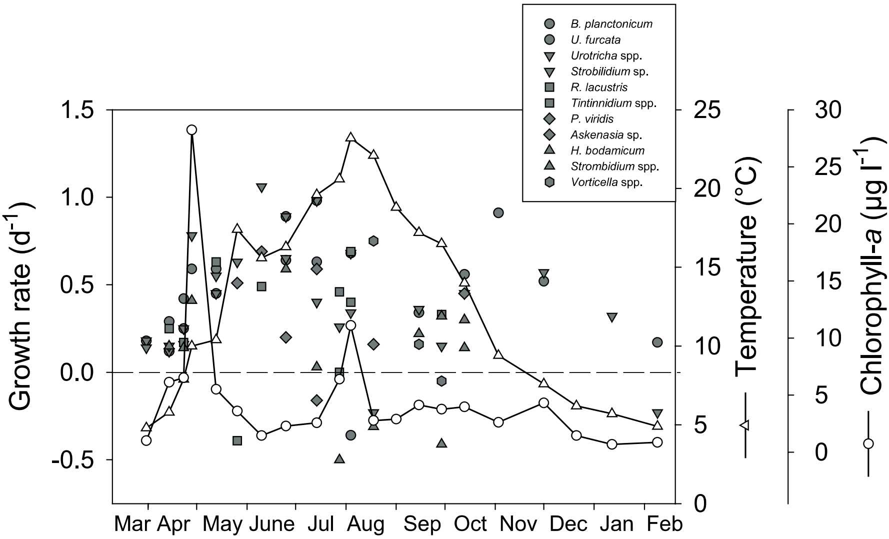


Fig. 3. In situ population growth rates of dominant ciliate taxa in Lake Constance during 1992–1993 in relation to surface temperature and chlorphyll-a concentration (T. Weisse, unpubl. original).

tive population growth rates were measured repeatedly in summer (Fig. 3). Near maximum growth rates of freshwater ciliates have been reported from highly eutrophic lakes and ponds (ARNDT & NIXDORF 1991, JÜRGENS et al. 1999). In most natural freshwater systems it is, at present, not possible to accurately predict the population growth rates of ciliates from laboratory derived maximum growth rates, but it appears safe to conclude that ciliates are food limited in most natural environments. The same conclusion holds true for *Daphnia*; averaged over the year, the estimated biomass turnover time (B/P ratio) of daphnids in Lake Constance is approximately four times longer than that of ciliates (GELLER et al. 1991, GAEDKE & STRAILE 1994).

The interactive effect of temperature and food concentration on ciliate growth rates was studied with *U. farcta* in the laboratory (WEISSE et al. 2002). The numerical response, the cell volume and the cell production rates were all significantly affected by the interaction between temperature and food. The threshold food concentration increased at both ends of the temperature range investigated; in particular, it was more than tenfold shifted up at the highest temperatures tested (21 and 24 °C). A combination of high temperature and moderate food levels, therefore, resulted in negative growth and production rates. This study confirmed results from similar experiments with *Daphnia* (ORCUTT & PORTER 1984, ACHENBACH & LAMPERT 1997, GIEBELHAUSEN & LAMPERT 2001) and rotifers (STELZER 1998).

The results reported in Fig. 2 were measured under constant experimental temperatures. This is a simplification which does not represent the field situation in many smaller water bodies, where diel temperature fluctuations are common during the better part of the year. The effect of fluctuating water temperatures on growth and production rates was investigated with *U. farcta* and *U. furcata* (MONTAGNES & WEISSE 2000). Moderately fluctuating temperatures (± 3 °C difference between day and night) stimulated growth and production rates in two of the four strains studied, but there was no universal trend that could be used to predict the temperature response of ciliates under daily changing environmental temperatures.

The direct effect of food

The relative significance of *Daphnia* and other cladocerans, calanoid copepods, ciliates and rotifers as algal consumers depends on the trophic state of lakes (PORTER et al. 1988, WEISSE 2003). Zooplankton biomass is controlled bottom-up because the various zooplankters need different critical food concentrations to thrive; secondly, zooplankton biomass is controlled top-down due to selective grazing pressure by fish and invertebrate predators. The individual threshold is the food concentration at which the energy gain by assimilation compensates for the metabolic losses by respiration (LAMPERT 1977a, b). The same author defined the population threshold as the food concentration above which the population size may grow, i. e. where production compensates for losses due to senescence and predation. Accordingly, the population threshold realized under usually suboptimal conditions in situ is higher than the individual threshold measured under optimal conditions in the laboratory. In protists and rotifers, the approach is slightly different, because, in most species, threshold levels cannot be assessed with individuals. The threshold food concentration for ciliates and rotifers is determined experimentally as the food concentration which results in a positive population growth rate (e. g., STEMBERGER & GILBERT 1985 a, WEISSE et al. 2002). The threshold food concentrations of rotifers are highly variable among the different taxa, ranging from 0.03–0.5 mg C l^{-1} (assuming that carbon content is 50 % of dry weight), and increase with rotifer size (STEMBERGER & GILBERT 1985 a, b, 1987, ROTHHAUPT 1990). This is opposite to daphnids, where threshold concentrations decrease with size; GLIWICZ (1990) reported threshold concentrations of 0.16–0.04 mg C l^{-1} for 8 daphnid species over a tenfold range in individual body mass (see also GLIWICZ 2003 b).

The numerical response, i. e. the relation of growth rates versus food concentration, has been studied with several prostome and oligotrich freshwater species under comparable experimental conditions (Fig. 4). Overall, the numerical response of the species investigated thus far are relatively similar; most threshold levels fall into the range of < 0.01–0.1 mg C l^{-1}, and saturation

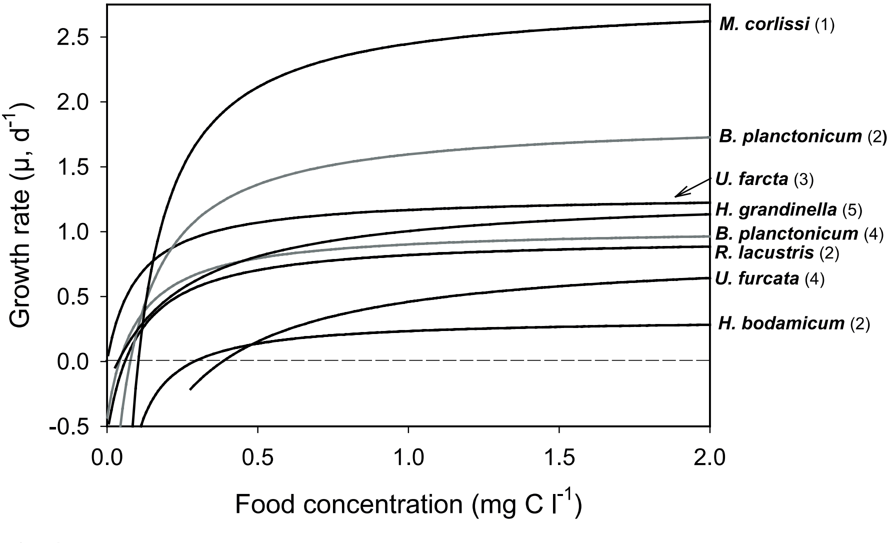


Fig. 4. Numerical response of freshwater ciliate species. Sources: WEISSE 2004 (1), MÜLLER & SCHLEGEL 1999 (2), WEISSE et al. 2002 (3), WEISSE et al. 2001 (4), JÜRGENS & ŠIMEK 2000 (5).

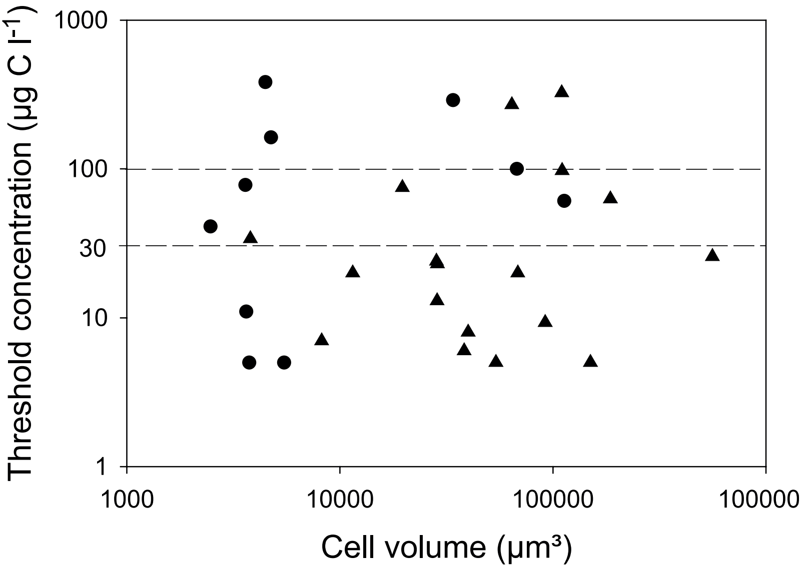


Fig. 5. Threshold food concentrations of freshwater (circles) and marine (triangles) prostome and choreo- and oligotrich ciliates. Sources: Müller & Schlegel 1999, Jürgens & Šimek 2000, Weisse et al. 2001, Weisse et al. 2002 (freshwater species); Jonsson 1986, Montagnes 1996, Montagnes et al. 1996, Montagnes & Lessard 1999, Jeong et al. 1999, Gismervik 2005 (marine species).

is reached in the range of 0.4–0.8 mg C l^{-1} (Fig. 4). The high food threshold reported for *U. furcata* may be an artefact because the majority of cells in this ciliate population stopped feeding when a critical food concentration was reached, but the population did not collapse (Weisse et al. 2001). Similar to the temperature response, the two studies with *B. planctonicum* (Müller & Schlegel 1999, Weisse et al. 2001) shown in Fig. 4 suggest that the numerical response may differ among different strains of the same species.

The data available for planktonic ciliates indicate that there is no obvious relationship of the threshold food concentrations to cell size (Fig. 5). The majority (15 out of 28) of the studies shown in Fig. 5 reported threshold food concentrations of <30 µg C l^{-1}, only 5 studies found threshold food concentrations >100 µg C l^{-1}. Most of the ciliate threshold food concentrations thus fall into the range reported for daphnids and small rotifers. Considering that the results for the various taxa were obtained under laboratory conditions that are not directly comparable (e. g., different food quality and experimental temperature), it may be premature to draw any safe conclusions on the competitive ability of ciliates, relative to that of their metazoan competitors. Direct evidence from field studies is still lacking, but the scarce data available from comprehensive in situ investigations suggests that the population threshold of ciliates may be lower than that of their metazoan competitors, as it has been observed that ciliates appear to dominate secondary production in oligotrophic lakes (WEISSE 2003). It is, however, important to note that the threshold food concept is only one criterion to predict the competitive ability of zooplankton in situ. The ability to withstand starvation, temperature stress, predation pressure or otherwise unfavourable environmental conditions may be equally important in determining the long term persistence of the various species.

The effect of food quality constraints was studied in depth with *Daphnia* (reviewed by GULATI & DEMOTT 1997, STERNER & SCHULTZ 1998, STERNER & ELSER 2002, LAMPERT 2006). Early research focused on the effect of prey cell size in relation to body and filter mesh size of cladocerans, the effect of interfering particles such as filamentous and/or toxic cyanobacteria, the constraints of mineral limitation (e. g. STERNER 1993, DEMOTT et al. 1998, HESSEN et al. 2000), in particular phosphorus limitation (STERNER et al. 1998, STERNER & ELSER 2002, BRETT et al. 2000), and, in recent years, on the effect of limitation by highly unsaturated fatty acids (BRETT & MÜLLER-NAVARRA 1997, VON ELERT 2002, MÜLLER-NAVARRA et al. 2000, MÜLLER-NAVARRA 2006), and the interactions between those two (BECKER & BOERSMA 2003, 2005). The interactive effect of phosphorus limitation and predator-prey interactions has also been studied with *Daphnia* (JEYASINGH & WEIDER 2005).

The PEG model (SOMMER et al. 1986) suggested that *Daphnia* feed efficiently on small cryptophytes and diatoms, but surprisingly little is known on the significance of diatoms in the diet of *Daphnia* (CAROTENUTO & LAMPERT 2004). These authors reported that the green alga *Scenedesmus obliquus* was a better carbon source for *D. pulicaria* than any of their six diatom species tested. Neither the morphological differences of the diatoms nor the presence or absence of polyunsaturated aldehydes had any significant effect on the ingestion rates of *D. pulicaria.* CAROTENUTO & LAMPERT (2004) conclude that the role of diatoms in the diet of *Daphnia* may change seasonally; small, single-celled species typical for the spring peak in temperate lakes will be ingested unselectively together with flagellates such as cryptophytes. The larger, colonial diatoms dominating during summer may be largely prevented from grazing by *Daphnia*.

Compared to *Daphnia*, the various and interacting effects of food quality received hitherto little attention in ciliate research. Laboratory investigations showed that small cryptophytes and chrysophytes are easily ingested and support high growth rates of many freshwater ciliates, while diatoms seem to be inadequate food for most species (SKOGSTAD et al. 1987, MÜLLER & SCHLEGEL 1999). This conclusion is supported by direct experimental evidence and indirect observations from the field (MÜLLER et al. 1991, WEISSE & MÜLLER 1998). The effect of the food stoichiometry and the fatty acid composition of prey on growth and production rates are areas for future research with ciliates, possibly using the models developed by Grover & Chrzanowski (2006).

The formation and significance of cysts in the life cycle of freshwater ciliates

Many *Daphnia*, copepods, rotifers and some other zooplankton taxa form diapausing eggs which are deposited in the lake sediments and may remain viable for several decades (reviewed by Hairston 1996). Diapausing eggs are an important part of the life strategy that enable those taxa to survive unfavourable environmental conditions, e. g. periods of food shortage or when ephemeral water bodies dry up. Similar to those metazoan taxa, many ciliates form resting cysts when environmental conditions become adverse (Foissner et al. 2005). The potential significance of cyst formation for the life strategy of planktonic ciliates was detected only recently. If the knowledge gained with metazooplankton is applied to ciliates, temperature, food, daylength, and predator avoidance are candidates as the main proximate factors controlling their encystment and excystment. While resting cysts are known from several loricate and aloricate oligotrich ciliates, the complete encystment-excystment cycle has been studied in only 5 aquatic species, including *Pelagostrombidium fallax* (Müller 1996, Müller & Wünsch 1999, Müller 2002, Müller et al. 2002) as the only species from freshwater lakes. Two populations of *P. fallax*, in prealpines Lakes Constance (Germany) and Mondsee (Austria), developed distinctly different seasonal patterns of cyst formation in response to the seasonal development of the entire plankton communities of these lakes (Müller et al. 2002). Cyst age was identified as the most important factor controlling excystment of this ciliate (Müller 2002). Cysts older than 3 months excysted spontaneously at 4 °C in the dark, while a temperature stimulus was necessary to trigger excystment of younger cysts. Müller (2002) concluded that the period of dormancy of *Pelagostrombidium* sp. in temperate lake sediments usually does not exceed 6 months. It remains to be seen if other ciliates deposit long-lived resting cysts that may be functionally comparable to the diapausing eggs of *Daphnia*. Similarly, the role of cysts for the long distance dispersal of freshwater ciliates is an area for future research.

Recent observations with the rare oligotrich ciliate *Meseres corlissi*, which occurs in freshwater but is not a typical planktonic species (Weisse 2004), revealed intraspecific differences between tropical and temperate strains in the proximate factors triggering encystment. In the tropical strain, encystment was induced when temperature dropped below 20 °C (Weisse 2004); growth, encystment, excystment and cyst survival of two temperate strains depended strongly on the presence or absence of soil components in the culture medium, while temperature was unimportant (Müller et al. 2006). These differences

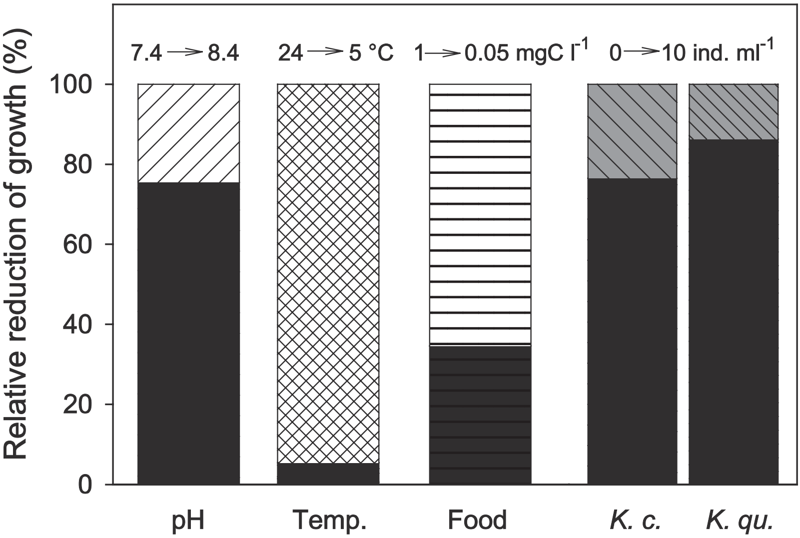


Fig. 6. The relative effect of major environmental parameters of growth rates of small *Urotricha* species (K. c. = *Keratella cochlearis*, K. qu. = *K. quadrata*). The solid bars denote the reduction of maximum population growth rates when the environmental parameters become unfavourable. The seasonal variation of the respective parameters encountered in prealpine lakes is indicated on top of the bars; if, e. g., the pH increases from 7.4 to 8.4, growth rate is reduced to 76 % of its maximum. Similarly, the presence of 10 rotifers ml^{-1} reduced the ciliate growth by 14–24 %. The experiments on the effect of pH, temperature and food were performed with *U. farcta* (Weisse & Stadler 2006 and references therein), the experiments with the rotifers were conducted with *U. furcata* (Weisse & Frahm 2002).

were interpreted as local adaptation of two morphologically and genetically indistinguishable, but geographically distant populations of a cosmopolitan, but rare ciliate species. Due to the unusual ultrastructure and biochemical composition of the resting cysts of *Meseres* that has been studied in detail (Foissner et al. 2005, Foissner 2005), this species may serve as model organism for future studies on the ontogeny of ciliate resting cysts and may also cast new light on ciliate phylogeny.

The relative significance of major environmental parameters for the population dynamics of freshwater ciliates

The various ecophysiological investigations with *Urotricha* spp. reported above have been conducted under similar laboratory conditions, i. e. with similar food, small *Cryptomonas* spp., and at similar temperature (12.5–16 °C) and light (12 : 12 or 14 : 10 L : D cycle, moderate light intensity) conditions. It is thus possible to evaluate the relative significance of each of the major environmental parameters for the population dynamics of the ciliates, assuming realistic seasonal changes in situ for each parameter. Of the factors studied thus far, temperature and food had the strongest impact on the ciliate population growth rates (Fig. 6). The overwhelming importance of temperature and food has been confirmed with several other prostome and oligotrich freshwater species (Figs 2 and 4). Relative to the other environmental factors, the effect of pH on the distribution and ecophysiology of aquatic ciliates has been studied only little. The pH impact on growth rates appears to be minor within a given water body at circumneutral pH, but may restrict the occurrence and distribution of freshwater ciliates in contrasting environments (WEISSE & STADLER 2006).

Both rotifer species reduced the growth rate of *U. furcata* moderately, probably primarily by direct feeding on the ciliates. Note that the rotifer impact was minor on small *Urotricha* spp., but may control the population dynamics of other, similar sized ciliate species (WEISSE & FRAHM 2002). In contrast to interactions between daphnids and rotifers and daphnids and ciliates, the potential feeding relationships between rotifers and ciliates have been studied only slightly. ARNDT (1993), GILBERT & JACK (1993), and STENSON & SVENSSON (1995) investigated feeding of predatory rotifers on some ciliates. GILBERT (1994) demonstrated that some oligotrich ciliates use a jumping behaviour to escape ingestion by rotifers. Indirect interactions such as exploitative competition between rotifers and ciliates have been studied only little (WEISSE & FRAHM 2002).

Conclusions

The dominant prostome and oligotrich freshwater ciliates show, in many respects, astounding similarities to daphnids. Their overall significance in the planktonic food web as consumers of protist prey, as secondary producers and as nutrient remineralizers is similar. While the role of ciliates in the food web has been investigated in some detail, the life strategy, biochemistry and molecular genetics of ciliates are clearly understudied. The life cycle of ciliates, with its sequence of asexual and sexual stages, and the occurrence of resting stages during unfavourable environmental conditions, is also remarkably similar to that of *Daphnia*. The significance of sexual reproduction and cyst formation is, however, poorly understood for planktonic ciliates. Due to their, relative to *Daphnia*, even shorter generation time, larger population numbers and smaller size, ciliates offer some specific advantages that should be explored in future ecophysiological and genetic studies. For instance, since many ciliates divide twice or thrice per day, their adaptive response to changing environmental conditions can be studied experimentally over many (~ 1000) generations within one or two years. There is reason to hope that the long tradition of using ciliates as model organisms will be rejuvenated in aquatic ecology – this contribution is an attempt towards this ambitious goal.

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References

ACHENBACH, L. & LAMPERT, W. (1997): Effects of elevated temperatures on threshold food concentrations and possible competitive abilities of differently sized cladoceran species. – Oikos **79:** 469–476.

AMMERMANN, D., SCHLEGEL, M. & HELLMER, K. H. (1989): North American and Eurasian strains of *Stylonychia lemnae* (Ciliophora, Hypotrichida) have a high genetic identity but differ in the nuclear apparatus and in their mating behaviour. – Eur. J. Protistol. **25:** 67–74.

ARNDT, H. (1993): Rotifers as predators on components of the microbial web (bacteria, heterotrophic flagellates, ciliates) – a review. – Hydrobiologia **255/256:** 231–246.

ARNDT, H. & NIXDORF, B. (1991): Spring-clearwater phase in a eutrophic lake: Control by herbivorous zooplankton enhanced by grazing on components of the microbial web. – Verh. Internat. Verein. Limnol. **24:** 879–883.

ATKINSON, D. (1996): Ectotherm life-history responses to developmental temperature. – In: JOHNSTON, I. A. & BENNETT, A. F. (eds): Animals and temperature: phenotypic and evolutionary adaptation – University Press, Cambridge, pp. 183–204.

BARTH, D., KRENEK, S., FOKIN, S. I. & BERENDONK, T. U. (2006): Intraspecific genetic variation in *Paramecium*, revealed by mitochondrial *CO*I sequences. – J. Eukaryot. Microbiol. **53:** 20–25.

BÄUERLE, E. & GAEDKE, U. (eds) (1998): Lake Constance: characterization of an ecosystem in transition. – Arch. Hydrobiol. Spec. Iss. Advanc. Limnol. **53:** 1–610.

BECKER, C. & BOERSMA, M. (2003): Resource quality effects on life histories of *Daphnia*. – Limnol. Oceanogr. **48:** 700–706.

– – (2005): Differential effects of phosphorus and fatty acids on *Daphnia magna* growth and reproduction. – Limnol. Oceanogr. **50:** 388–397.

BLEYMAN, L. K. (1996): Ciliate genetics. – In: HAUSMANN, K. & BRADBURY, P. C. (eds): Ciliates: cells as organisms – G. Fischer, Stuttgart, pp. 291–324.

BOENIGK, J. (2002): Variability of ingestion rates with stage in cell cycle of a heterotrophic nanoflagellate (*Spumella* sp.) measured by an individual-based approach. – Eur. J. Protistol. **38:** 299–306.

BOENIGK, J. & ARNDT, H. (2000 a): Particle handling during interception feeding by four species of heterotrophic nanoflagellates. – J. Eukaryot. Microbiol. **47:** 350–358.

BOENIGK, J. & ARNDT, H. (2000 b): Comparative studies on the feeding behaviour of two heterotrophic nanoflagellates: the filter-feeding choanoflagellate *Monosiga ovata* and the raptorial-feeding kinetoplastid *Rhynchomonas nasuta*. – Aquat. Microb. Ecol. **22:** 243–249.

– – (2002): Bacterivory by heterotrophic flagellates: community structure and feeding strategies. – Antonie van Leeuwenhoek **81:** 465–480.

BOENIGK, J., ARNDT, H. & CLEVEN, E.-J. (2001): The problematic nature of fluorescently labeled bacteria (FLB) in *Spumella* feeding experiments – an explanation by using video microscopy. – Arch. Hydrobiol. **152:** 329–338.

BOERSMA, M. & VIJVERBERG, J. (1994): Seasonal variations in the condition of two *Daphnia* species and their hybrid in a eutrophic lakes: Evidence for food limitation under field conditions. – J. Plankton Res. **16:** 1793–1809.

BRETT, M. T. & MÜLLER-NAVARRA, D. C. (1997): The role of highly unsaturated fatty acids in aquatic food-web processes. – Freshwat. Biol. **38:** 483–499.

BRETT, M. T., MÜLLER-NAVARRA, D. C. & PARK, S.-K. (2000): Empirical analysis of the effect of phosphorus limitation on algal food quality for freshwater zooplankton. – Limnol. Oceanogr. **45:** 1564–1575.

CAROTENUTO, Y. & LAMPERT, W. (2004): Ingestion and incorporation of freshwater diatoms by *Daphnia pulicaria*: do morphology and oxylipin production matter? – J. Plankton Res. **26:** 563–569.

CLEVEN, E.-J. (1996): Indirectly fluorescently labelled flagellates (IFLF): a tool to estimate the predation on free-living heterotrophic flagellates. – J. Plankton Res. **18:** 429–442.

DE MEESTER, L. (1996): Local genetic differentiation and adaptation in freshwater zooplankton populations: patterns and processes. – Ecoscience **3:** 385–399.

DE MEESTER, L., VANOVERBEKE, J., DE GELAS, K., ORTELLS, K. & SPAAK, P. (2006): Genetic structure of cyclic parthenogenetic zooplankton populations – a conceptual framework. – Arch Hydrobiol. **167:** 217–244, this issue.

DEMOTT, W. R., GULATI, R. D. & SIEWERTSEN, K. (1998): Effects of phosphorus-deficient diets on the carbon and phosphorus balance of *Daphnia magna*. – Limnol. Oceanogr. **43:** 1147–1161.

DINI, F. & NYBERG, D. (1993): Sex in ciliates. – In: JONES, J. G. (ed.): Advances in Microb. Ecol., vol. 13 – Plenum Press, New York, London, pp. 129–144.

FOISSNER, W. (2005): The unusual, Lepidosome-coated resting cyst of *Meseres corlissi* (Ciliophora: Oligotrichea): Transmission electron microscopy and phylogeny. – Acta Protozool. **44:** 217–230.

FOISSNER, W., BERGER, H. & SCHAUMBURG, J. (1999): Identification and ecology of limnetic plankton ciliates. – Bayerisches Landesamt für Wasserwirtschaft, Munich, pp. 1–793.

FOISSNER, W., MÜLLER, H. & WEISSE, T. (2005): The unusual, Lepidosome-coated resting cyst of *Meseres corlissi* (Ciliophora: Oligotrichea): Light and scanning electron microscopy, cytochemistry. – Acta Protozool. **44:** 201–215.

GAEDKE, U. & STRAILE, D. (1994): Seasonal changes of the quantitative importance of protozoans in a large lake. An ecosystem approach using mass-balanced carbon flow diagrams. – Mar. Microb. Food Webs **8:** 163–188.

– – (1998): Daphnids: Keystone species for the pelagic food web structure and energy flow. – A body size-related analysis linking seasonal changes at the population and ecosystem levels. – Arch. Hydrobiol. Spec. Iss. Advanc. Limnol. **53:** 587–610.

Gaedke, U., Straile, D. & Pahl-Wostl, C. (1995): Trophic structure and carbon flow dynamics in the pelagic community of a large lake. – In: Polis, G. & Winemiller, K. (eds): Food Webs: Integration of Pattern and Dynamics – Chapman & Hall, New York, pp. 60–71.

Gause, G. J. (1934): The struggle for existence. – Williams and Wilkins Baltimore. Reprinted edition, Hafner, New York, 1964, pp. 1–163.

Geller, W., Berberovic, U., Gaedke, U., Müller, H., Pauli, H.-R., Tilzer, M. M. & Weisse, T. (1991): Relations among the components of autotrophic and heterotrophic plankton during the seasonal cycle 1987 in Lake Constance. – Verh. Internat. Verein. Limnol. **24:** 831–836.

Giebelhausen, B. & Lampert, W. (2001): Temperature reaction norms of *Daphnia magna*: the effect of food concentration. – Freshwat. Biol. **46:** 281–289.

Gilbert, J. J. (1989): The effect of *Daphnia* interference on a natural rotifer and ciliate community: Short-term bottle experiments. – Limnol. Oceanogr. **34:** 606–617.

– (1994): Jumping behavior in the oligotrich ciliates *Strobilidium velox* and *Halteria grandinella* and its significance as a defense against rotifers. – Microb. Ecol. **27:** 189–200.

Gilbert, J. J. & Jack, J. D. (1993): Rotifers as predators on small ciliates. – Hydrobiologia **255/256:** 247–253.

Gismervik, I. (2005): Numerical and functional responses of choreo- and oligotrich planktonic ciliates. – Aquat. Microb. Ecol. **40:** 163–173.

Gliwicz, Z. M. (1990): Food threshold and body size in cladocerans. – Nature **343:** 638–640.

– (2003 a): Between hazards of starvation and risk of predation: The ecology of offshore animals.– Excellence in ecology, Book 12, International Ecology Institute, Oldendorf/Luhe, pp. 1–379.

– (2003 b): Zooplankton. – In: O'Sullivan, P. & Reynolds, C. S. (eds): The lakes handbook, vol. 1. – Blackwell Science Ltd, Oxford, pp. 461–516.

Gliwicz, Z. M. & Boavida, M. J. (1996): Clutch size and body size at first reproduction in *Daphnia pulicaria* at different levels of food and predation. – J. Plankton Res. **18:** 863–880.

Grover, J. P. & Chrzanowski, T. H. (2006): Stoichiometry and growth kinetics in the "smallest zooplankton" – phagotrophic flagellates. – Arch Hydrobiol. **167:** 467–487, this issue.

Güde, H. (1988): Direct and indirect influences of crustacean zooplankton on bacterioplankton of Lake Constance. – Hydrobiologia **159:** 63–73.

Güde, H. & Gries, T. (1998): Phosphorus fluxes in Lake Constance. – Arch. Hydrobiol. Spec. Iss. Advanc. Limnol. **53:** 505–544.

Gulati, R. D. & DeMott, W. R. (1997): The role of food quality for zooplankton: Remarks on the state-of-the-art, perspectives and priorities. – Freshwat. Biol. **38:** 753–768.

Hairston, N. G. J. (1996): Zooplankton egg banks as biotic reservoirs in changing environments. – Limnol. Oceanogr. **41:** 1087–1092.

Hairston, N. G. J., Lampert, W., Caceres, C. E., Holtmeier, C. L., Weider, L. J., Gaedke, U., Fischer, J. M., Fox, J. A. & Post, D. M. (1999): Rapid evolution revealed by dormant eggs. – Nature **401:** 446.

Hausmann, K. & Bradbury, P. C. (eds) (1996): Ciliates: cells as organisms – G. Fischer, Stuttgart, pp. 1–485.

Hebert, P. D. N. (1974 a): Enzyme variability in natural populations of *Daphnia magna*. II. Genotypic frequencies in permanent populations. – Genetics **77:** 323–334.

– (1974 b): Ecological differences between genotypes in natural populations of *Daphnia magna*. – Heredity **33:** 327–337.

Hessen, D. O., Alstad, N. E. W. & Skardal, L. (2000): Ca limitation in *Daphnia magna*. – J. Plankton Res. **22:** 553–568.

Hochstädter, S. (1997): Erstellung und Analyse von Phosphornahrungsnetzen im pelagischen Kreislaufs des Bodensees. – Hartung-Gorre Verlag, Konstanz, pp. 1–158.

Huey, R. B. & Kingsolver, J. G. (1989): Evolution of thermal sensitivity of ectotherm performance. – Trends Ecol. Evol. **4:** 131–135.

Jack, J. D. & Gilbert, J. J. (1993): Susceptibilities of different-sized ciliates to direct suppression by small and large cladocerans. – Freshwat. Biol. **29:** 19–29.

– – (1997): Effects of metazoan predators on ciliates in freshwater plankton communities. – J. Euk. Microbiol. **44:** 194–199.

Jeong, H. J., Shim, J. H., Lee, C. W., Kim, J. S. & Koh, S. M. (1999): Growth and grazing rates of the marine planktonic ciliate *Strombidinopsis* sp. on red-tide and toxic dinoflagellates. – J. Eukaryot. Microbiol. **46:** 69–76.

Jeyasingh, P. D. & Weider, L. J. (2005): Phosphorus availability mediates plasticity in life-history traits and predator-prey interactions in *Daphnia*. – Ecol. Lett. **8:** 1021–1028.

Jonsson, P. R. (1986): Particle size selection, feeding rates and growth dynamics of marine plankton oligotrichous ciliates (Ciliophora: Oligotrichina). – Mar. Ecol. Prog. Ser. **33:** 265–277.

Jürgens, K. (1994): Impact of *Daphnia* on planktonic microbial food webs – A review. – Mar. Microb. Food Webs **8:** 295–324.

Jürgens, K. & Güde, H. (1991): Seasonal changes in the grazing impact of phagotrophic flagellates on bacteria in Lake Constance. – Mar. Microb. Food Webs **5:** 27–37.

Jürgens, K. & Šimek, K. (2000): Functional response and particle size selection of *Halteria* cf. *grandinella*, a common freshwater oligotrichous ciliate. – Aquat. Microb. Ecol. **22:** 57–68.

Jürgens, K., Skibbe, O. & Jeppesen, E. (1999): Impact of metazooplankton on the composition and population dynamics of planktonic ciliates in a shallow, hypertrophic lake. – Aquat. Microb. Ecol. **17:** 61–75.

Krainer, K.-H. & Müller, H. (1995): Morphology, infraciliature and ecology of a new planktonic ciliate, *Histiobalantium bodamicum* n. sp. (Scuticociliatida: Histiobalantiidae). – Eur. J. Protistol. **31:** 389–395.

Kusch, J. (1998): Local and temporal distribution of different genotypes of pond-dwelling *Stentor coeruleus*. – Protist **149:** 147–154.

Kusch, J. & Heckmann, K. (1996): Population structure of *Euplotes* ciliates revealed by RAPD fingerprinting. – Ecoscience **3:** 378–384.

Kusch, J., Welter, H., Stremmel, M. & Schmidt, H. J. (2000): Genetic diversity in populations of a freshwater ciliate. – Hydrobiologia **431:** 185–192.

Lampert, W. (1977a): Studies on the carbon balance of *Daphnia pulex* de Geer as related to environmental conditions. III. Production and production efficiency. – Arch. Hydrobiol. Suppl. **48:** 336–360.

– (1977b): Studies on the carbon balance of *Daphnia pulex* de Geer as related to environmental conditions. IV. Determination of the "threshold" concentration as a factor controlling the abundance of zooplankton species. – Arch. Hydrobiol. Suppl. **48:** 361–368.

– (1978a): Release of dissolved organic carbon by grazing zooplankton. – Limnol. Oceanogr. **23:** 831–834.

– (1978b): Climatic conditions and planktonic interactions as factors controlling the regular succession of spring algal blooms and extremely clear water in Lake Constance. – Verh. Internat. Verein. Limnol. **20:** 969–974.

– (1985): Food limitation and the structure of zooplankton communities. – Arch. Hydrobiol. Spec. Iss. Advanc. Limnol. **21:** 1–497.

– (2006): *Daphnia:* Model herbivore, predator and prey. – In: Gliwicz, Z. M., Mazurkiewicz-Boron, G. & Rouen, K. (eds): Reviewing European Freshwater Sciences, 2005 – Pol. J. Ecol. (in press).

Lampert, W. & Schober, U. (1978): Das regelmäßige Auftreten von Frühjahrsalgen-Maximum und "Klarwasserstadium" im Bodensee als Folge von klimatischen Bedingungen und Wechselwirkungen zwischen Phyto- und Zooplankton. – Arch. Hydrobiol. **82:** 364–386.

Larsson, P. & Weider, L. J. (1995): Cladocera as model organisms in biology. – Dev. Hydrobiol. **107:** 1–307.

Laybourn-Parry, J. (1992): Protozoan plankton ecology. – Chapman & Hall, London, pp. 1–231.

Lennon, J. T., Smith, V. H. & Williams, K. (2001): Influence of temperature on exotic *Daphnia lumholtzi* and implications for invasion success. – J. Plankton Res. **23:** 425–433.

Lindström, E. S., Weisse, T. & Stadler, P. (2002): Enumeration of small ciliates in culture by flow cytometry and nucleic acid staining. – J. Microbiol. Meth. **49:** 173–182.

– – – (2003): Live sorting and survival of unstained and DAPI-stained ciliates by flow cytometry. – Arch. Hydrobiol. **157:** 173–184.

Lynn, D. H. (1996): Systematics of ciliates. – In: Hausmann, K. & Bradbury, P. C. (eds): Ciliates: cells as organisms – G. Fischer, Stuttgart, pp. 51–72.

Marie, D., Simon, N. & Vaulot, D. (2005): Phytoplankton cell counting by flow cytometry. – In: Andersen, R. A. (ed.): Algal culturing techniques – Elsevier/Academic Press, pp. 145–155.

Mitchell, S. E., Halves, J. & Lampert, W. (2004): Coexistence of similar genotypes of *Daphnia magna* in intermittent populations: response to thermal stress. – Oikos **106:** 469–478.

Mitchell, S. E. & Lampert, W. (2000): Temperature adaptation in a geographically widespread zooplankter, *Daphnia magna*. – J. Evol. Biol. **13:** 371–382.

Montagnes, D. J. S. (1996): Growth responses of planktonic ciliates in the genera *Strobilidium* and *Strombidium*. – Mar. Ecol. Progr. Ser. **130:** 241–254.

MONTAGNES, D. J. S., BERGER, J. D. & TAYLOR, F. J. R. (1996): Growth rate of the marine planktonic ciliate *Strombidinopsis cheshiri* Snyder and Ohman as a function of food concentration and interclonal variability. – J. Exp. Mar. Biol. Ecol. **206:** 121–132.

MONTAGNES, D. J. S., KIMMANCE, S. A. & ATKINSON, D. (2003): Using *Q*10: Can growth rates increase linearly with temperature? – Aquat. Microb. Ecol. **32:** 307–313.

MONTAGNES, D. J. S. & LESSARD, E. J. (1999): Population dynamics of the marine planktonic ciliate *Strombidinopsis multiauris*: its potential to control phytoplankton blooms. – Aquat. Microb. Ecol. **20:** 167–181.

MONTAGNES, D. J. S. & WEISSE, T. (2000): Fluctuating temperatures affect growth and production rates of planktonic ciliates. – Aquat. Microb. Ecol. **21:** 97–102.

MÜLLER, H. (1989): The relative importance of different ciliate taxa in the pelagic food web of Lake Constance. – Microb. Ecol. **18:** 261–273.

– (1991): *Pseudobalanion planctonicum* (Ciliophora, Prostomatida): ecological significance of an algivorous nanociliate in a deep meso-eutrophic lake. – J. Plankton Res. **13:** 247–262.

– (1996): Encystment of the freshwater ciliate *Pelagostrombidium fallax* (Ciliophora, Oligotrichida) in laboratory culture. – Aquat. Microb. Ecol. **11:** 289–295.

– (2002): Laboratory study of the life cycle of a freshwater strombidiid ciliate. – Aquat. Microb. Ecol. **29:** 189–197.

MÜLLER, H., FOISSNER, W. & WEISSE, T. (2006): The role of soil in the life cycle of *Meseres corlissi* (Ciliophora: Oligotrichea): experiments with two clonal strains from the type locality, an astatic meadow pond. – Aquat. Microb. Ecol. **42:** 199–208.

MÜLLER, H. & GELLER, W. (1993): Maximum growth rates of aquatic ciliated protozoa: the dependence on body size and temperature reconsidered. – Arch. Hydrobiol. **126:** 315–327.

MÜLLER, H. & SCHLEGEL, A. (1999): Responses of three freshwater planktonic ciliates with different feeding modes to cryptophyte and diatom prey. – Aquat. Microb. Ecol. **17:** 49–60.

MÜLLER, H., SCHÖNE, A., PINTO-COELHO, R. M., SCHWEIZER, A. & WEISSE, T. (1991): Seasonal succession of ciliates in Lake Constance. – Microb. Ecol. **21:** 119–138.

MÜLLER, H., STADLER, P. & WEISSE, T. (2002): Seasonal dynamics of cyst formation of strombidiid ciliates in alpine Lake Mondsee, Austria. – Aquat. Microb. Ecol. **29:** 181–188.

MÜLLER, H. & WEISSE, T. (1994): Laboratory and field observations on the scuticociliate *Histiobalantium* from the pelagic zone of Lake Constance, FRG. – J. Plankton Res. **16:** 391–401.

MÜLLER, H. & WÜNSCH, C. (1999): Seasonal dynamics of cyst formation of pelagic strombidiid ciliates in a deep prealpine lake. – Aquat. Microb. Ecol. **17:** 37–47.

MÜLLER-NAVARRA, D. C. (2006): The nutritional importance of ω-poly unsaturated fatty acids and their use as trophic markers: Does it contradict? – Arch Hydrobiol. **167:** 501–513, this issue.

MÜLLER-NAVARRA, D. C., BRETT, M. T., LISTON, A. M. & GOLDMAN, C. R. (2000): A highly unsaturated fatty acid predicts carbon transfer between primary producers and consumers. – Nature **403:** 74–77.

MÜLLER-NAVARRA, D. C. & LAMPERT, W. (1996): Seasonal patterns of food limitation in *Daphnia galeata*: separating food quantity and food quality effects. – J. Plankton Res. **18:** 1137–1157.

NANNEY, D. L. (1980): Experimental ciliatology. – Wiley, New York, pp. 1–303.

NANNEY, D. L., COOPER, L. E., SIMON, E. M. & WHITT, G. S. (1980): Isozymic characterization of three mating groups of the *Tetrahymena pyriformis* complex. – J. Protozool. **27:** 451–459.

NANNEY, D. L., MEYER, E. B., SIMON, E. M. & PREPARATA, R.-M. (1989): Comparison of ribosomal and isozymic phylogenies of tetrahymenine ciliates. – J. Protozool. **36:** 1–8.

ORCUTT, J. D. & PORTER, K. G. (1984): The synergistic effects of temperature and food concentration on life history parameters of *Daphnia*. – Oecologia **63:** 300–306.

PACE, M. L. & VAQUÉ, D. (1994): The importance of *Daphnia* in determining mortality rates of protozoans and rotifers in lakes. – Limnol. Oceanogr. **39:** 985–996.

PORTER, K. G., PEARL, H., HODSON, R., PACE, M., PRISCU, J., RIEMANN, B., SCAVIA, D. & STOCKNER, J. (1988): Microbial interactions in lake foodwebs. – In: CARPENTER, S. R. (ed.): Complex Interactions in Lake Communities – Springer, Berlin, pp. 234–255.

PRESCOTT, D. M. (2000): Genome gymnastics: unique modes of DNA evolution and processing in ciliates. – Nat. Rev. Genet. **1:** 191–198.

RECKERMANN, M. & COLIJN, F. (eds) (2000): Aquatic flow cytometry: achievements and prospects. – Sci. Mar. **64:** 117–268.

ROTHHAUPT, K. O. (1990): Population growth rates of two closely related rotifer species: effects of food quantity, particle size, and nutritional quality. – Freshwat. Biol. **23:** 561–570.

SANDERS, R. W. & PORTER, K. G. (1990): Bacterivorous flagellates as food resources for the freshwater crustacean zooplankter *Daphnia ambigua*. – Limnol. Oceanogr. **35:** 188–191.

SANDERS, R. W., PORTER, K. G., BENNETT, S. J. & DEBIASE, A. E. (1989): Seasonal patterns of bacterivory by flagellates, ciliates, rotifers, and cladocerans in a freshwater plankton community. – Limnol. Oceanogr. **34:** 673–687.

SAUNDERS, P. A., PORTER, K. G. & TAYLOR, B. E. (1999): Population dynamics of *Daphnia* spp. and implications for trophic interactions in a small, monomictic lake. – J. Plankton Res. **21:** 1823–1845.

SCHEFFER, M., STRAILE, D., VAN NES, E. H. & HOSPER, H. (2001): Climate warming causes regime shifts in lake food webs. – Limnol. Oceanogr. **46:** 1780–1783.

SCHWENK, K., JUNTTILA, P., RAUTIO, M., BASIANSEN, F., KNAPP, J., DOVE, O., BILLIONES, R. & STREIT, B. (2004): Ecological, morphological, and genetic differentiation of *Daphnia* (*Hyalodaphnia*) from the Finnish and Russian subarctic. – Limnol. Oceanogr. **49:** 532–539.

SHAPIRO, H. M. (2000): Microbial analysis at the single-cell level: tasks and techniques. – J. Microbiol. Methods **42:** 3–16.

ŠIMEK, K., HARTMAN, P., NEDOMA, J., PERNTHALER, J., SPRINGMANN, D., VRBA, J. & PSENNER, R. (1997): Community structure, picoplankton grazing and zooplankton control of heterotrophic nanoflagellates in a eutrophic reservoir during the summer phytoplankton maximum. – Aquat. Microb. Ecol. **12:** 49–63.

ŠIMEK, K., JÜRGENS, K., COMERMA, M., ARMENGOL, J. & NEDOMA, J. (2000): Ecological role and bacterial grazing of *Halteria* spp.: small freshwater oligotrichs as dominant pelagic ciliate bacterivores. – Aquat. Microb. Ecol. **22:** 43–56.

ŠIMEK, K., MACEK, M., PERNTHALER, J., STRASKRABOVÁ, V. & PSENNER, R. (1996): Can freshwater planktonic ciliates survive on a diet of picoplankton? – J. Plankton Res. **18:** 597–613.

ŠIMEK, K., MACEK, M., SEDA, J. & VYHNÁLEK, V. (1990): Possible food chain relationships between bacterioplankton, protozoans, and cladocerans in a reservoir. – Internat. Rev. ges. Hydrobiol. **75:** 583–596.

SIMON, M., TILZER, M. M. & MÜLLER, H. (1998): Bacterioplankton dynamics in a large mesotrophic lake: I. Abundance, production and growth control. – Arch. Hydrobiol. **143:** 385–407.

SKOGSTAD, A., GRANSKOG, L. & KLAVENESS, D. (1987): Growth of freshwater ciliates offered planktonic algae as food. – J. Plankton Res. **9:** 503–512.

SOMERO, G. N., DAHLHOFF, E. & LIN, J. J. (1996): Stenotherms and eurytherms: mechanisms establishing thermal optima and tolerance ranges. – In: JOHNSTON, I. A. & BENNETT, A. F. (eds): Animals and temperature: phenotypic and evolutionary adaptation – University Press, Cambridge, pp. 53–78.

SOMMER, U. (ed.) (1989): Plankton ecology: succession in plankton communities. – Brock/Springer series in contemporary bioscience, Springer, Berlin, pp. 1–369.

SOMMER, U., GLIWICZ, Z. M., LAMPERT, W. & DUNCAN, A. (1986): The PEG-model of seasonal succession of planktonic events in fresh waters. – Arch. Hydrobiol. **106:** 433–471.

SONNEBORN, T. M. (1937): Sex, sex inheritance and sex determination in *Paramecium aurelia*. – Proc. Natl. Acad. Sci. USA **23:** 378–385.

– (1957): Breeding systems, reproductive methods, and species problems in protozoa. – In: MAYR, E. (ed.): The species problem – American Association for the Advancement of Science, Washington, pp. 155–324.

STELZER, C.-P. (1998): Population growth in planktonic rotifers. Does temperature shift the competitive advantage for different species? – Hydrobiologia **387/388:** 349–353.

STEMBERGER, R. S. & GILBERT, J. J. (1985 a): Assessment of threshold food levels and population growth in planktonic rotifers. – Arch. Hydrobiol. Beih. Ergebn. Limnol. **21:** 269–275.

– – (1985 b): Body size, food concentration, and population growth in planktonic rotifers. – Ecology **66:** 1151–1159.

– – (1987): Rotifer threshold food concentrations and the size-efficiency hypothesis. – Ecology **68:** 181–187.

STENSON, J. A. E. & SVENSSON, J.-E. (1995): Food quality and population densities in *Asplancha priodonta*. – Limnologica **25:** 43–47.

STERNER, R. W. (1989): The role of grazers in phytoplankton succession. – In: SOMMER, U. (ed.): Plankton Ecology. – Springer, Berlin, pp. 337–364.

– (1993): *Daphnia* growth on varying quality of *Scenedesmus* – mineral limitation of zooplankton. – Ecology **74:** 2351–2360.

STERNER, R. W., CLASEN, J., LAMPERT, W. & WEISSE, T. (1998): Carbon:phosphorus stoichiometry and food chain production. – Ecol. Lett. **1:** 146–150.

STERNER, R. W. & ELSER, J. J. (2002): Ecological stoichiometry. – Princeton University Press, Princeton.

STERNER, R. W. & SCHULTZ, K. L. (1998): Zooplankton nutrition: recent progress and a reality check. – Aquat. Ecol. **32:** 261–279.

STOECK, T. & SCHMIDT, H. J. (1998): Fast and accurate identification of European species of the *Paramecium aurelia* complex by RAPD-fingerprints. – Microb. Ecol. **35:** 311–317.

STOECK, T., WELTER, H., SEITZ-BENDER, D., KUSCH, J. & SCHMIDT, H. J. (2000): ARDRA and RAPD-fingerprinting reject the sibling species concept for the ciliate *Paramecium caudatum* (Ciiophora, Protoctista). – Zool. Scr. **29:** 75–82.

STRAILE, D. (1995): Die saisonale Entwicklung des Kohlenstoffkreislaufes im pelagischen Nahrungsnetz des Bodensees – Eine Analyse von massenbilanzierten Flußdiagrammen mit Hilfe der Netzwerktheorie. – Hartung-Gorre Verlag, Konstanz, pp. 1–143.

– (1997): Gross growth efficiencies of protozoan and metazoan zooplankton and their dependence on food concentration, predator-prey weight ratio, and taxonomic group. – Limnol. Oceanogr. **42:** 1375–1385.

– (1998): Biomass allocation and carbon flow in the pelagic food web of Lake Constance. – Arch. Hydrobiol. Spec. Iss. Advanc. Limnol. **53:** 545–563.

– (2000): Meteorological forcing of plankton dynamics in a large and deep continental European lake. – Oecologia **122:** 44–50.

STRAILE, D. & ADRIAN, R. (2000): The North Atlantic Oscillation and plankton dynamics in two European lakes – two variations on a general theme. – Glob. Change Biol. **6:** 663–670.

STRAILE, D. & GELLER, W. (1998): Crustacean zooplankton in Lake Constance from 1920 to 1995: Response to eutrophication and re-oligotrophication. – Arch. Hydrobiol. Spec. Iss. Advanc. Limnol. **53:** 255–274.

TIROK, K. & GAEDKE, U. (2006): Spring weather determines the relative importance of ciliates, rotifers and crustaceans for the initiation of the clear-water phase in a large, deep lake. – J. Plankton Res. **28:** 361–373.

VAQUÉ, D. & PACE, L. M. (1992): Grazing on bacteria by flagellates and cladocerans in lakes of contrasting food-web structure. – J. Plankton Res. **14:** 307–321.

VON ELERT, E. (2002): Determination of limiting polyunsaturated fatty acids in *Daphnia galeata* using a new method to enrich food algae with single fatty acids. – Limnol. Oceanogr. **47:** 1764–1773.

WEIDER, L. J. (1993): A test of the “general-purpose” genotype hypothesis: Differential tolerance to thermal and salinity stress among *Daphnia* clones. – Evolution **47:** 965–969.

WEIDER, L. J., HOBÆK, A., CREASE, T. J. & STIBOR, H. (1996): Molecular characterization of clonal population structure and biogeography of arctic apomictic *Daphnia* from Greenland and Iceland. – Mol. Ecol. **5:** 107–118.

WEISSE, T. (1990): Trophic interactions among heterotrophic microplankton, nanoplankton and bacteria in Lake Constance. – Hydrobiologia **191:** 111–122.

– (1991): The annual cycle of heterotrophic freshwater nanoflagellates: role of bottom-up versus top-down control. – J. Plankton Res. **13:** 167–185.

– (1997): Growth and production of heterotrophic nanoflagellates in a meso-eutrophic lake. – J. Plankton Res. **19:** 703–722.

WEISSE, T. (2002): The significance of inter- and intraspecific variation in bacterivorous and herbivorous protists. – Antonie van Leeuwenhoek **81:** 327–341.

– (2003): Pelagic microbes – Protozoa and the microbial food web. In: O'SULLIVAN, P. & REYNOLDS, C. S. (eds): The lakes handbook, vol. 1 – Blackwell Science Ltd, Oxford, pp. 417–460.

– (2004): *Meseres corlissi*: a rare oligotrich ciliate adapted to warm water and temporary habitats. – Aquat. Microb. Ecol. **37:** 75–83.

– (2006): Biodiversity of freshwater microorganisms – achievements, problems, and perspectives. – In: GLIWICZ, Z. M., MAZURKIEWICZ-BORON, G. & ROUEN, K. (eds): Reviewing European Freshwater Sciences, 2005 – Pol. J. Ecol. (in press).

WEISSE, T. & FRAHM, A. (2002): Direct and indirect impact of two common rotifer species (*Keratella* spp.) on two abundant ciliate species (*Urotricha furcata, Balanion planctonicum*). – Freshwat. Biol. **47:** 53–64.

WEISSE, T., KARSTENS, N., MEYER, V. C. M., JANKE, L., LETTNER, S. & TEICHGRÄBER, K. (2001): Niche separation in common prostome freshwater ciliates: the effect of food and temperature. – Aquat. Microb. Ecol. **26:** 167–179.

WEISSE, T. & LETTNER, S. (2002): The ecological significance of intraspecific variation among freshwater ciliates. – Verh. Internat. Verein. Limnol. **28:** 1880–1884.

WEISSE, T. & MCISAAC, E. A. (2000): Significance and fate of bacterial production in oligotrophic lakes in British Columbia. – Can. J. Fish. Aquat. Sci. **57:** 96–105.

WEISSE, T. & MÜLLER, H. (1998): Planktonic protozoa and the microbial food web in Lake Constance. – Arch. Hydrobiol. Spec. Issues Advanc. Limnol. **53:** 223–254.

WEISSE, T., MÜLLER, H., PINTO-COELHO, R. M., SCHWEIZER, A., SPRINGMANN, D. & BALDRINGER, G. (1990): Response of the microbial loop to the phytoplankton spring bloom in a large prealpine lake. – Limnol. Oceanogr. **35:** 781–794.

WEISSE, T. & RAMMER, S. (2006): Pronounced ecophysiological clonal differences of two common freshwater ciliates, *Coleps spetai* (Prostomatida) and *Rimostrombidium lacustris* (Oligotrichida), challenge the morphospecies concept. – J. Plankton Res. **27:** 55–63.

WEISSE, T. & STADLER, P. (2006): Effect of pH on growth, cell volume, and production of freshwater ciliates, and implications for their distribution. – Limnol. Oceanogr. **51:** 1708–1715.

WEISSE, T., STADLER, P., LINDSTRÖM, E. S., KIMMANCE, S. A. & MONTAGNES, D. J. S. (2002): Interactive effect of temperature and food concentration on growth rate: A test case using the small freshwater ciliate *Urotricha farcta*. – Limnol. Oceanogr. **47:** 1447–1455.

WICKHAM, S. A. (1998): The direct and indirect impact of *Daphnia* and cyclops on a freshwater microbial food web. – J. Plankton Res. **20:** 739–755.

WICKHAM, S. A. & GILBERT, J. J. (1991): Relative vulnerabilities of natural rotifer and ciliate communities in cladocerans: laboratory and field experiments. – Freshwat. Biol. **26:** 77–86.

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