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# Large biomass of small feeders: ciliates may dominate herbivory in eutrophic lakes

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The importance of ciliates as herbivores and in biogeochemical cycles is increasingly recognized. An opportunity to observe the potential consequences of zooplankton dominated by ciliates arose when winter fish kills resulted in strong suppression of crustaceans by young planktivorous fish in two shallow lakes. On an annual average, ciliates made up 38–76% of the total zooplankton biomass in both lakes during two subsequent years. Consequently, ciliate biomass and their estimated grazing potential were extremely high compared with other lakes of various trophic states and depths. Grazing estimates based on abundance and size suggest that ciliates should have cleared the water column of small ($<5$ μm) and intermediate (5–50 μm) sized phytoplankton more than once a day. Especially, small feeders within the ciliates were important, likely exerting a strong top-down control on small phytoplankton. Particle-attached bacteria were presumably strongly suppressed by intermediate-sized ciliate feeders. In contrast to other lakes, large phytoplankton was proportionately very abundant. The phytoplankton community had a high evenness, which may be attributed to the feeding by numerous fast growing and selective ciliate species. Our study highlights ciliates as an important trophic link and adds to the growing awareness of the role of winter processes for plankton dynamics.

KEYWORDS: phytoplankton; crustaceans; rotifers; filtration rate; winter fish kill

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# INTRODUCTION

Ciliates have been known to be important components of zooplankton communities for more than two decades (Beaver and Crisman, 1989). Nevertheless, trophic cascade studies still focus mainly on the classical food chain: phytoplankton, crustaceans and fish. However, ciliates and rotifers may also be highly relevant for trophic cascades, in that ciliates are known to be often the most important grazers in spring (Weisse *et al.*, 1990; Gaedke and Straile, 1994) and an important food source for large zooplankton (Sanders and Wickham, 1993; Adrian and Schneider-Olt, 1999) and in general their biomass increases with the trophic state (Beaver and Crisman, 1982). The updated version of the Plankton Ecology Group Model explicitly considers ciliates as important grazers of bacteria and small phytoplankton, influencing the phytoplankton composition but less the seasonal patterns (Sommer *et al.*, 2012). Ciliates have short generation times and thus may, in contrast to crustaceans, track phytoplankton developments within 1–2 weeks even at low temperatures (Tirok and Gaedke, 2007b) or even without a time lag (Berninger *et al.*, 1993). Among freshwater zooplankton, they have the highest weight-specific grazing rates (Hansen *et al.*, 1997), which may lead to a strong top-down control of their prey if ciliates become important in terms of biomass. As cyclopoid copepods and cladocerans can exert strong top-down control on ciliates (Wickham and Gilbert, 1993; Wickham, 1998), ciliates often contribute little to the total zooplankton biomass of lakes. They may gain in importance within the pelagic zooplankton community when their predators or competitors fail to build up large biomass and hence to control ciliate development.

Cyclopoids and cladocerans themselves are typically influenced by the abundance of their predators, which are usually fish. Especially in shallow lakes, a long period of ice cover and snow may reduce oxygen concentrations up to the point of anoxia, resulting in a winter fish kill (Tonn *et al.*, 1990), with consequences for the whole food web during the following years. Such a loss of planktivorous fish was observed to reduce the predation pressure on metazooplankton which may increase metazooplankton biomass, mean species size and individual body mass of crustaceans (Balayla *et al.*, 2010; Iglesias *et al.*, 2011) at least on a short time scale (Ruuhijärvi *et al.*, 2010).

Concurrent with reduced biomass in planktivorous fish, winter fish kills can result in young of the year (YOY) fish gaining in importance and exerting a strong predation pressure on metazooplankton (Ruuhijärvi *et al.*, 2010). YOY fish have been observed to graze strongly on cladocerans, typically reducing grazing on phytoplankton and often resulting in more turbid lakes (Romare *et al.*, 1999). Various studies reported the structuring effect of YOY fish in lake food webs (Mills and Forney, 1983; Cryer *et al.*, 1986): In years with strong fish recruitment, cladocerans were less abundant (Mills and Forney, 1983) and rotifers and copepods dominated the zooplankton community (Cryer *et al.*, 1986). These early studies focused on effects on crustaceans and rotifers. However, ciliates may contribute substantially to the top-down control on phytoplankton and bacteria as well as the transfer efficiency of organic matter and energy within the planktonic food web (Sanders and Wickham, 1993; Gaedke *et al.*, 2002). Cascading effects of a winter fish kill, as described for crustaceans and rotifers, are very likely to also affect the protozoan zooplankton; however, knowledge about such specific effects is still rather limited.

We observed a low biomass of adult fish due to partial winter fish kills in two well-studied, small, temperate, shallow lakes (Attermeyer *et al.*, 2013; Brothers *et al.*, 2013; Scharnweber *et al.*, 2014a, b) in two consequent winters (Hilt *et al.*, 2015) and a high abundance of YOY fish particular during the second year. We investigated the zooplankton and phytoplankton communities to unravel their regulation in these lakes and hypothesize that crustaceans and, in particular the large forms, were under severe grazing pressure by YOY fish. In turn, low crustacean biomass was expected to favor ciliates and rotifers. We further hypothesize that ciliates with their high weight-specific grazing rates exert a strong grazing pressure on specific phytoplankton species, promoting a species-specific density dependence of loss rates and thus a diverse phytoplankton community. The emerging strong top-down control by ciliates may result in low phytoplankton and bacterial biomass. This was evaluated by calculating the potential grazing pressure by ciliates based on abundance and size of ciliates and comparing it with measured production rates of phytoplankton and bacteria. We expected that these cascading effects would be more pronounced in the second year, given the second partial winter fish kill in a row. The results were further related to measurements from selected lakes of differing trophic states and depths.

Our results reveal that crustaceans were under severe predation pressure as indicated by a low biomass and the dominance of nauplii and copepodites. Ciliates benefited enormously from the reduced top-down control. They dominated the zooplankton community in terms of biomass, which exceeded values reported from various lakes. The calculated estimates of the grazing rates suggest that ciliates exerted a strong predation pressure on small phytoplankton and particle-attached bacteria. Consequently large, grazing-resistant, slow-growing species accumulated within the phytoplankton community.

# METHOD

## Study site

Field observations were conducted in two very similar small, shallow eutrophic lakes in the North-Eastern part of Germany differing mainly in their composition of primary producers (Table I). The Schulzensee (SS, 53°14′N, 13°16′E) has a well-developed submerged macrophyte community (predominantly *Ceratophyllum submersum*), whereas submerged macrophytes are absent in the Kleiner Gollinsee (GS, 53°01′N, 13°35′E) (Brothers *et al.*, 2013). Both lakes are surrounded by a reed belt. Samples for zooplankton, phytoplankton and bacteria were taken every 4 weeks at nearly the same sampling dates in both lakes in 2010 and 2011, whereby the actual sampling period differed between the plankton groups (see below). In autumn 2010, both lakes were divided by a plastic curtain to conduct an experiment on the fate of terrestrial organic carbon in the food web (Attermeyer *et al.*, 2013; Scharnweber *et al.*, 2014a, b). Thus, in 2011, we analyzed only the samples of the reference half of both lakes.

## Zooplankton

Zooplankton samples were taken from April to October 2010 and from February to December 2011 from littoral and pelagic locations in each lake. An epilimnetic mixed water sample of 40 L was taken and 50 mL of it was fixed with acidified Lugol's solution (Hoehn *et al.*, 1998). Ciliate samples were quantitatively analyzed with inverted microscopy (Hund Labovert, >100 cells per species and sample counted) as in Müller (Müller, 1989) and Gaedke and Wickham (Gaedke and Wickham, 2004). They were identified to the genus or species level (Curds, 1982; Foissner, 1991; Foissner *et al.*, 1999; Lynn and Small, 2002). Note, that the identification of ciliates below the genus level is possible only for a few species in Lugol-preserved samples. Length and width of 10–20 individuals of each species were measured to calculate the species-specific cell volume (Barthelmeß, 1995; Boit and Gaedke, 2014 and literature cited therein; Tittel, 1997). We used linear regressions to calculate the individual carbon content based on cell volume using the specific conversion factors for ciliates (Müller and Geller, 1993).

*Table I: Characteristics of Gollinsee and Schulzensee*

| | Gollinsee | Schulzensee |
|---|---|---|
| Surface area ($m^2$) | 33 200 | 39 130 |
| $Z_{mean}$ (m) | 1.8 | 2.2 |
| $Z_{max}$ (m) | 2.9 | 4.2 |
| Secchi depth (m) | 1.3 ± 0.4 ($n = 19$) | 1.8 ± 0.3 ($n = 18$) |
| Chlorophyll ($\mu g\ L^{-1}$) | 25.3 ± 16.1 ($n = 17$) | 14.6 ± 8.3 ($n = 17$) |
| TP ($\mu mol\ L^{-1}$) | 1.2 ± 0.3 ($n = 19$) | 1.0 ± 0.2 ($n = 19$) |
| SRP ($\mu mol\ L^{-1}$)[a] | 0.11 ± 0.05 ($n = 19$) | 0.10 ± 0.06 ($n = 19$) |
| Surface area covered by submerged macrophytes | 0% | 20–25% |

For Secchi depth, chlorophyll, total phosphorous (TP) and soluble reactive phosphorous (SRP) monthly mean values (±SD) for the years 2010 and 2011 are shown. TP, SRP and chlorophyll are mean values from samples taken in pelagic and littoral habitats. The number of samples is indicated by *n*.

[a] SRP values below the detection limit were set to half the detection limit (0.01 $\mu mol\ L^{-1}$).

The remaining water was filtered through a 55 µm mesh, and these rotifer and crustacean samples were fixed with 4% sugar formalin (Haney and Hall, 1973). Rotifers and crustaceans were quantitatively analyzed and length and width for rotifers and length for crustaceans were measured. We used power regressions to calculate the individual carbon content based on the volume of rotifers (Telesh *et al.*, 1998) and the length of crustaceans (Dumont *et al.*, 1975). A carbon content of 50% dry weight was assumed (Gaedke, 1992 and references therein). In close cooperation, the zooplankton samples were quantified at the LimSa Gewässerbüro (Constance, Germany, by Dr S. Schmidt-Halewicz) after the detailed descriptions by Schmidt-Halewicz *et al.* (Schmidt-Halewicz *et al.*, 2012).

## Phytoplankton

Littoral and pelagic water samples were taken from April to November 2010 and from January to December 2011. Pelagic samples included equal portions of water from 0.5, 1 and 2 m depth at the middle of the lake, while littoral samples of subsurface water ($z = 0.5$ m) were pooled from three locations within the reed belt. Samples were stored in 500 mL glass jars and fixed with an acidified Lugol's solution. The jars were stored in the dark until laboratory analysis. The samples were analyzed with inverted microscopy distinguishing 70 different morphotypes. The size of at least 20 cells from each morphotype was measured. The average width and length of the cells were used to calculate the morphotype-specific cell volume allowing for the respective shape (Hillebrand *et al.*, 1999) which was converted into the cell-specific individual carbon content (Menden-Deuer and Lessard, 2000). Phytoplankton gross primary production was estimated from monthly Phyto-PAM and HPLC measurements as described by Brothers *et al.* (Brothers *et al.*, 2013) and was converted to net primary production assuming 40% respiration of gross primary production (Platt *et al.*, 1991).

## Bacteria

From June to November 2010 and April to December 2011, pelagic and littoral samples were taken and separated by filtration through 5 µm polycarbonate membranes (Nuclepore) for particle-attached bacteria ($>5$ µm) and free-living bacteria ($<5$ µm; $>2$ µm). Bacteria were SYBR gold-stained and counted with an epifluorescence microscope. The volume of ~100 cells was measured and converted to biomass (Simon and Azam, 1989). Bacterial production of both bacterial fractions was measured by incorporating L-$^{14}$C-leucine (Attermeyer *et al.*, 2013).

## Data analysis

The pelagic and littoral locations of the phytoplankton, zooplankton and bacteria samples were $<50$ m apart from each other. Comparing the species composition, we concluded that these small lakes had horizontally well-mixed water bodies as species biomass and composition were similar in the pelagic and littoral and thus we arithmetically averaged the samples from both habitats.

Phytoplankton diversity was calculated using the Shannon−Wiener Index (H):

$$H = -\sum_{i=1}^{n} \frac{b_i}{b} \ln \frac{b_i}{b},$$

where $b_i$ is the biomass of the $i$th morphotype, $b$ the total phytoplankton biomass and $n$ the number of all morphotypes. The diversity was calculated per sampling day and averaged over each sampling year. The evenness was determined as diversity ($H$) divided by the maximum diversity of the respective community [$\ln(n)$].

To estimate the consumption of bacteria and phytoplankton by ciliates, ciliates were grouped according to their known feeding preferences from the literature (Sanders, 1988; Kivi and Setälä, 1995; Simek *et al.*, 1995) and phytoplankton according to their longest linear dimension into the groups small ($<5$ µm), intermediate (5−50 µm) and large ($>50$ µm). Free-living bacteria were allocated to the small plankton and particle-attached bacteria to the intermediate plankton. We calculated estimates of the grazing pressure by ciliates based on their abundance and biovolume. The potential filtering rate for each ciliate group was estimated using regressions of specific filtering rates against ciliate cell size for each species, corrected for the ambient temperature using a $Q_{10}$ value of 2.8, then summing the rates for all individuals in each feeding group (Hansen *et al.*, 1997). In a second approach, estimates of the maximum ingestion rates were calculated similarly, using both the ciliate cell size and the median prey size within each ciliate feeding group (Hansen *et al.*, 1997). Ultimately, we calculated the proportion of the total available prey which was consumed by each ciliate group per day, given our estimates of grazing rates. This potential loss rate by predation was related to the measured growth rate of the prey group given as the production to biomass ratio.

To evaluate the size-selective feeding impact by ciliates, we generated biomass size spectra for phytoplankton by summing the biomass of each $\log_2$ size class (based on individual carbon content). As described by Gaedke (Gaedke, 1992), the biomass of each size class was distributed over the adjacent size classes by allocating 25% of the biomass to the upper and lower size class and leaving 50% within the respective size class.

## Data for cross lake comparisons

To evaluate the generality of our findings, we compiled data from lakes of various trophic states and depths (Table II). Cross lake comparisons can be problematic due to differences in sampling procedures, species identification and data processing. To overcome this problem, we used only lakes where the data were gathered and/or processed by the same group of people [GS, SS, the Königssee, Lake Constance, the Arendsee and the Müggelsee (for sampling, see Gaedke *et al.*, 2004)]. We further used zooplankton community measurements averaged across 12 lakes of different trophy and morphometry from North America (Pace, 1986) and rotifer and crustacean data from the Großer Vätersee (Steiner, 2002). We compared the copepod age structure as reflected by the portion of nauplii of the total copepod biomass in GS and SS with those of the Königssee and the Großer Vätersee, for which ratios were

*Table II: Characteristics of the lakes used for comparison*

| Lake | Trophy | Depth (m) Mean | Depth (m) Max | Sampling period | Reference |
|---|---|---|---|---|---|
| Königssee | Oligotroph | 98 | 190 | 1992 (tw) | Barthelmeß (1995) |
| Lake Constance | Mesotroph | 101 | 252 | 1987–1996 (w) | Boit and Gaedke (2014) and literature cited therein |
| Arendsee | Eutroph | 30 | 49.5 | 1994 (w) | Tittel (1997) |
| Müggelsee | Hypertroph | 4.9 | 8 | 1988–1990 (w) | Gaedke *et al.* (2004) and literature cited therein |
| Großer Vätersee[a] | Mesotroph | 5.2 | 11.5 | 1997–1999 (bw) | Steiner (2002) |

Sampling was conducted either twice a week (tw), weekly (w) or biweekly (bw).

[a] For this lake, only rotifer and crustacean data were available.

calculated using the compiled data. For Lake Constance, we calculated the respective ratio from measurements in 1988 (Wölfl, 1989).

## RESULTS

Gollinsee (GS) and Schulzensee (SS) were both characterized by low crustacean biomass, high total phytoplankton biomass and a remarkably high ciliate biomass. Literature estimates of size-specific grazing rates suggest that the enormous ciliate biomass was sufficient to exert strong predation pressure on small phytoplankton and particle-attached bacteria, as described in detail below.

### Metazooplankton biomass and composition

In GS and SS, the volume-specific crustacean community biomass amounted to 33–119 mg C m$^{-3}$ and fell into the range found in deep Lake Constance, the Königssee and the Arendsee (Fig. 1, Supplementary data, Appendix S1). However, it was an order of magnitude lower than in the shallow highly eutrophic Müggelsee and the crustacean biomass per area was much higher in the deep lakes than in the shallow GS and SS. The average crustacean biomass was still lower in both lakes in the second year (Fig. 1, Supplementary data, Appendix S1). Within the community, cladocerans were relevant only in summer 2010 and copepods dominated otherwise (61–83%). In particular, cyclopoid copepodites (mean length 490 μm) and small (mean length 200 μm) and large nauplii (mean length 400 μm) were present, whereas hardly any adult copepods were found. The contribution of nauplii to the copepod biomass was extremely high in both lakes (GS: from 16 to 51%, SS: from 31 to 52%). Predacious metazooplankton such as carnivorous cladocerans and *Chaoborus* sp., which may have reduced the biomass of crustaceans, was not relevant in either lake. The rotifer biomass was lower in 2011 than in 2010 (GS 2010: 72 mg C m$^{-3}$, 2011: 18 mg C m$^{-3}$; SS 2010: 44 mg C m$^{-3}$, 2011: 20 mg C m$^{-3}$; Supplementary data, Appendix S1) and was mainly attributable to biomass peaks in July 2010 which did not develop in 2011. The volume-specific rotifer biomass was in range of those found in the Müggelsee and the Großer Vätersee and about an order of magnitude larger than in lakes Constance, Arendsee and Königssee (Supplementary data, Appendix S1).

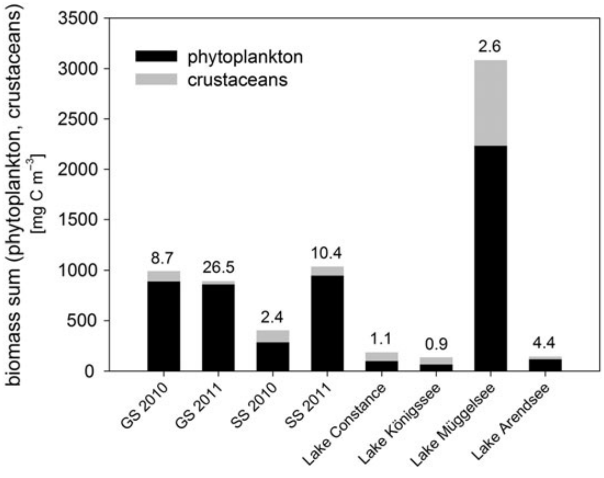

**Fig. 1.** Whole-year arithmetic averaged biomass of phytoplankton and crustaceans for GS and SS in 2010 and 2011. For comparison, measurements from other lakes were included. Numbers on the bars are the average phytoplankton to crustacean biomass ratios.

### Phytoplankton biomass and composition

Along with the low crustacean zooplankton biomass, the volume-specific average phytoplankton biomass was relatively high (Fig. 1, Supplementary data, Appendix S1). In comparison with the deep lakes Constance, Königssee and Arendsee, GS and SS had almost 10 times more phytoplankton biomass and only about 2 times less than the shallow, hypertrophic Müggelsee. The phytoplankton: crustacean biomass ratio was three to four times larger in 2011 than in 2010, and especially in 2011 much higher than in the lakes we used for comparison (Fig. 1). The phytoplankton community was diverse with respect to size (see below and Fig. 2) and composition (Supplementary data, Appendix S3). The Shannon–Wiener Index ranged between 1.8 and 2.2 with 24–34 morphotypes (yearly average, Supplementary data, Appendix S2). The evenness varied between 56 and 65%. Diatoms were often the most important group with respect to biomass, especially in spring but also during other months, whereas cyanobacteria were of minor importance in both lakes.

A large part of the phytoplankton biomass accumulated in the intermediate and larger size classes. The highest biomass occurred in the size classes 7–8 (128–256 pg C cell$^{-1}$, 12.0–15.3 μm equivalent spherical diameter) which were dominated by pennate diatoms (Fig. 2, for details on the species composition, see Supplementary data, Appendix S3). In GS and SS, large phytoplankton of the size class 12 (mainly *Peridinium* sp.) contributed high amounts to the total phytoplankton biomass. The relative contribution of very small phytoplankton ($\leq$2 pg C cell$^{-1}$) was low, and the absolute biomass in these size classes was 10–100 mg C m$^{-3}$.

### Ciliate biomass and composition

The very low abundance of adult crustaceans was accompanied by a remarkably high ciliate abundance in 2010 and even higher numbers in 2011 (GS 2010: 42 cells mL$^{-1}$, 2011: 164 cells mL$^{-1}$; SS 2010: 54 cells mL$^{-1}$, 2011: 117 cells mL$^{-1}$). Likewise, ciliates built up extremely high

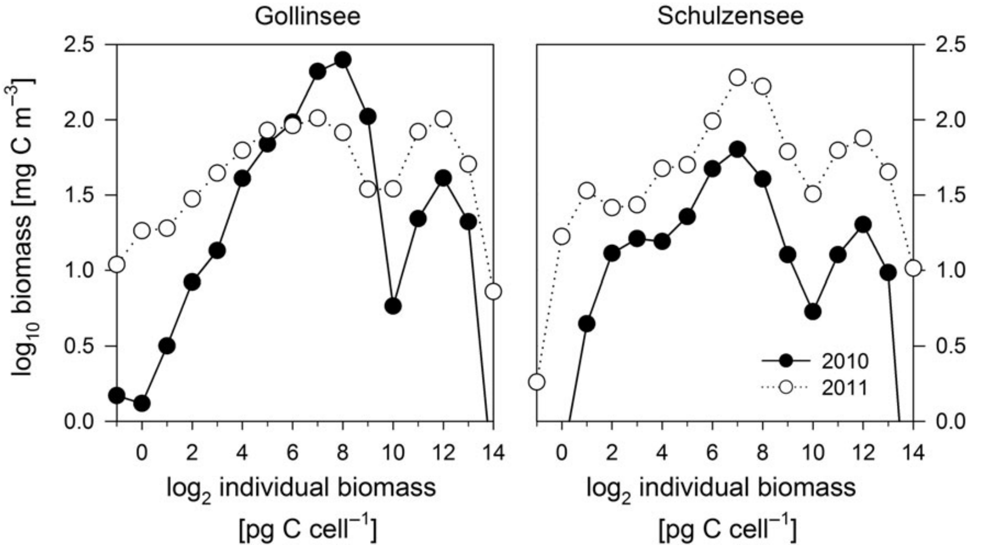

**Fig. 2.** Absolute phytoplankton biomass per size class in GS and SS in 2010 and 2011.

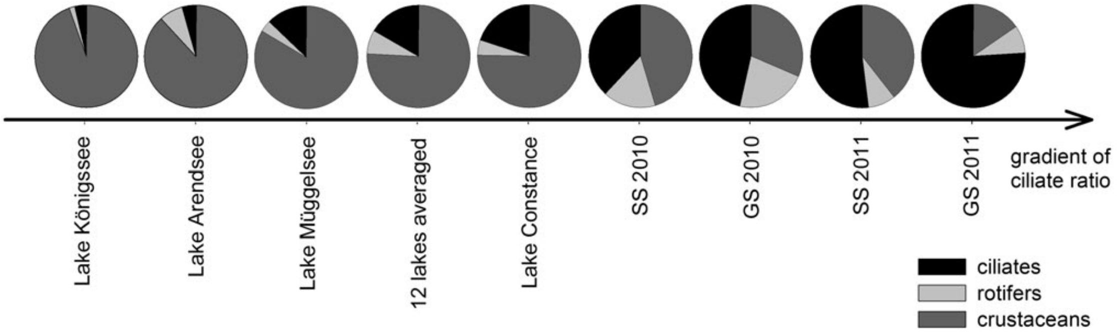

**Fig. 3.** Ratios of arithmetically averaged ciliate, rotifer and crustacean biomasses in GS and SS for 2010 and 2011 and of various lakes for comparison (see Table II for details).

biomass (GS 2010: 151 mg C m$^{-3}$, 2011: 161 mg C m$^{-3}$; SS 2010: 100 mg C m$^{-3}$, 2011: 120 mg C m$^{-3}$, Supplementary data, Appendix S1). Accordingly, ciliates dominated the zooplankton community in terms of biomass in 2010 in GS (47% of total zooplankton biomass) and in both lakes in 2011 (GS: 76%; SS: 52%). Such a relative contribution of ciliates is extremely high in comparison with various lakes of differing trophic state and depths (Fig. 3). In absolute terms, the ciliate biomass was 10−100 times larger than in the deep lakes we used for comparison, and similar to the hypertrophic Müggelsee (Supplementary data, Appendix S1). Ciliate biomass peaked in spring and autumn in both lakes in 2010 and 2011 (Supplementary data, Appendix S4). The ciliate to rotifer biomass ratio was roughly 2 in 2010 and 6−9 in 2011 and thus in 2011 also higher than in the reference lakes.

The ciliate community was composed of an average number of 12−18 different morphotypes per sampling date in both lakes and was rather similar in both lakes. The morphotypes belonged to the taxonomic groups Choreotrichia (36% abundance, 45% biomass), Scuticociliatia (28% abundance, 8% biomass), Prostomatea (21% abundance, 21% biomass) and Peritrichia (1% abundance, 11% biomass). Representatives of the Choreotrichia were typified by members of the genus *Strobilidium*, as were the Scuticociliates by *Cyclidium* and the Prostomatea by *Urotricha* and *Coleps*. The peritrich *Vorticella* is typically epibenthic, as it attaches to a substrate, but when filamentous algae are present, it is also found in the pelagic zone, as was the case in GS and SS. The small *Strobilidium* sp. (individual size: 4500 μm$^3$), the large *Strobilidium* sp. (15 000 μm$^3$) and *Coleps hirtus* (21 000 μm$^3$) were on average the most important ciliate morphotypes in terms of biomass and made up >40−51% of the total ciliate biomass (except GS 2010: 26%). Especially in early spring, large, predatory species as

*Monodinium* sp. (50 000 μm$^3$), *Didinium nasutum* (75 000–200 000 μm$^3$), *Stentor* sp. (980 000 μm$^3$) and *Bursaridium* sp. (370 000–570 000 μm$^3$) gained in importance. Small sized ciliates (cell volume: $10^3$–$10^4$ μm$^3$) made up 30% of the total ciliate biomass on average in 2010 in both lakes and 48% in GS and 43% in SS in 2011. Medium-sized ciliates (cell volume: $10^4$–$10^5$ μm$^3$) contributed on average the largest proportion to the ciliate biomass (48–59%, except for GS 2011 with 40%). Ciliates with a cell volume $>10^5$ μm$^3$ made up the smallest proportion. The largest ciliates were of the same size (in units of carbon) as nauplii and small cladocerans. Thus, ciliates had the potential to graze on the whole size spectrum of phytoplankton.

## Bacterial biomass

The total volumetric biomass of bacteria ranged between 60 and 142 mg C m$^{-3}$; thus, the phytoplankton biomass was 5–15 times larger. It was dominated by free-living bacteria (~2–5 times higher than particle-attached bacteria), whereas cell-specific biomasses were higher in the attached fraction compared with the free-living fraction (~2 times). However, as particle-attached bacteria clump, the effective prey size was several times larger.

## Ciliate top-down effects on phytoplankton and bacteria

Ciliates were categorized according to their feeding type into feeders of small, intermediate and large particles, and phytoplankton and bacteria were grouped according to their edibility for these ciliate groups. Small and intermediate feeders had the largest biomass within the ciliates, whereas large feeders were of minor importance (~20% or less, Fig. 4). The pattern was different within the prey. On average, the small prey contributed the least to the prey biomass and the portion of large prey varied strongly between lakes and years (10–71%). Over the course of the years, the biomass ratio prey:ciliates was usually above 1 and declined along with the groups "large", "intermediate" and "small". The average prey: ciliates ratio ranged from 38 to 203 for large particles, from 5 to 24 for the intermediate prey and from 2 to 5 for the small groups.

The estimated proportion of the water column filtered daily by ciliates was calculated based on the abundance and size of ciliates and suggests a huge impact by small feeders. Except for a few dates, the small feeders achieved the highest estimated proportion of the filtered water column, on average 0.8–1.1 times per day in 2010 and 1.9–3.5 times per day in 2011, followed by the intermediate feeders filtering the water 0.7–1.8 times per day for GS and SS. The calculated ingestion rate of phytoplankton and bacteria by ciliates was related to the actual amount of prey to estimate the proportion of prey potentially consumed by ciliates per day (Fig. 5). The median proportion of small phytoplankton grazed by small ciliate feeders is above 1, implying that based on our estimates >100% of the actual biomass could be grazed by the ciliates per day. The median values for intermediate-sized phytoplankton were usually one order of magnitude lower than for small phytoplankton. The production:biomass ratios of the entire phytoplankton were in the range of the calculated consumed proportion of intermediate-sized phytoplankton, suggesting production sufficient to sustain the ingestion rates by intermediate ciliate grazers

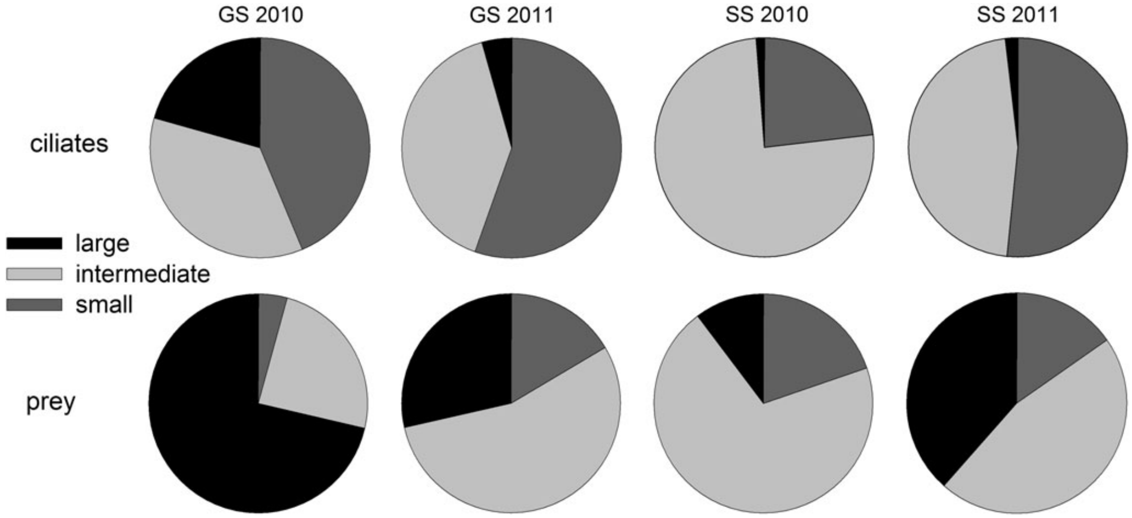

**Fig. 4.** Average biomass ratio of large, intermediate and small feeders within the ciliates and their prey (phytoplankton and bacteria) in GS and SS in 2010 and 2011. Free-living bacteria were allocated to the small plankton and particle-attached bacteria to the intermediate plankton.

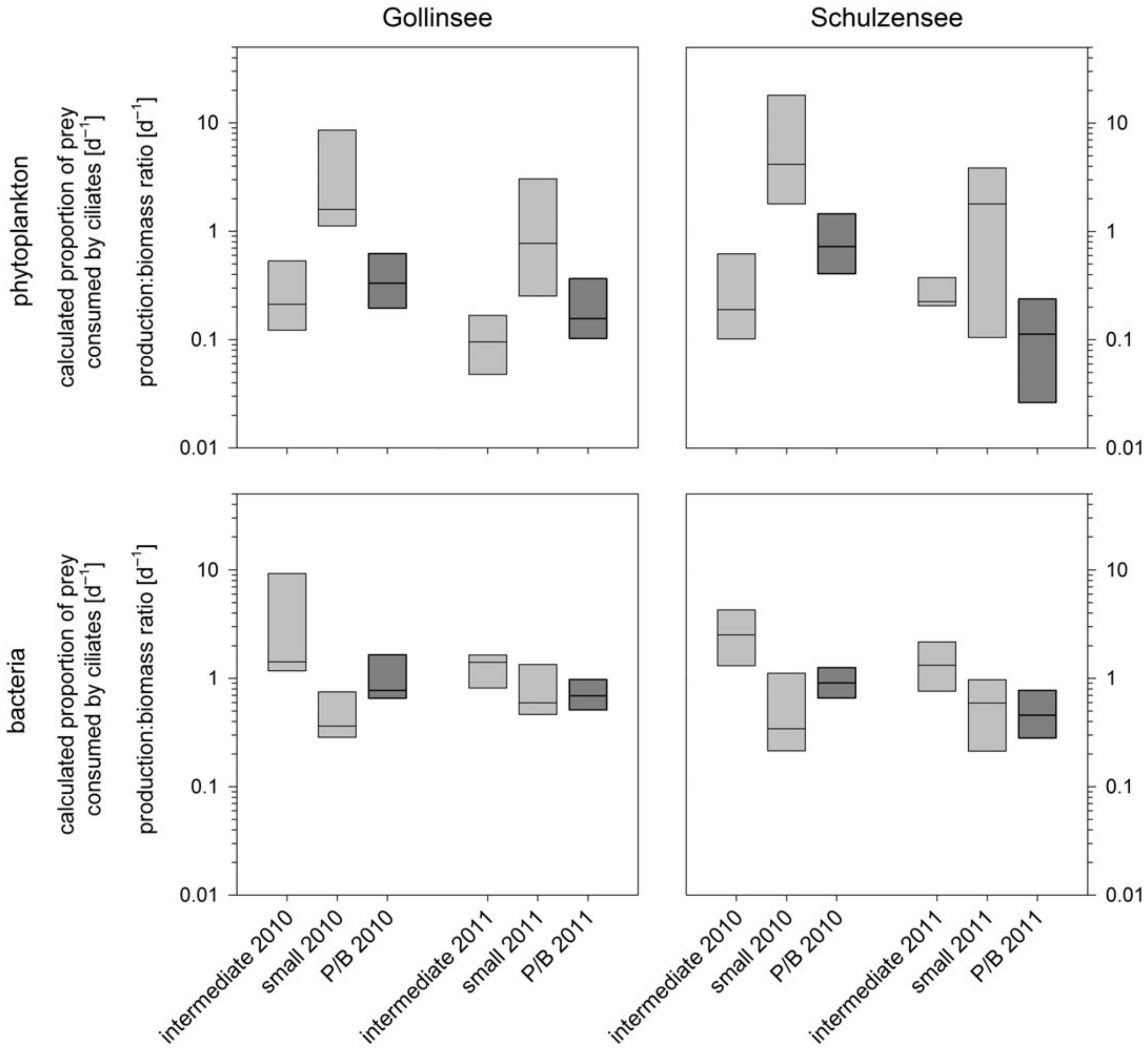

**Fig. 5.** Calculated proportion of potentially ingested prey (phytoplankton: upper panels; bacteria: lower panels) by ciliates of feeding type intermediate and small in GS and SS in 2010 and 2011. P/B indicates the production to biomass ratio of the entire phytoplankton or bacteria community and allow a comparison between phytoplankton growth and potential grazing losses. Intermediate ciliate feeders graze on particle-attached bacteria and small ciliate feeders graze on free-living bacteria. The median is given as line within each box which represents the middle 50% of the values of the respective year.

(Fig. 5). However, the average phytoplankton production:biomass ratios were too low to maintain constant phytoplankton biomass when taking the large calculated ingestion rates by small feeders into account. The opposite pattern was found for bacteria (Fig. 5). According to the calculated estimates of the grazing rates, the proportion of particle-attached bacteria consumed by intermediate feeders was much larger than the proportion of free-living bacteria consumed by the respective ciliates. The bacterial production:biomass ratio was in the range of the calculated proportion of bacterial biomass consumed by small feeders and much lower than for intermediate feeders. Thus, the growth rate of the prey (indicated by the production to biomass ratio) was much lower than the very high ingestion we calculated for small phytoplankton and particle-attached bacteria.

# DISCUSSION

The winter fish kill revealed several important aspects about the role of ciliates in pelagic food webs. First, low biomass of crustaceans, arising through grazing by very high densities of YOY fish, released ciliates from otherwise effective predation pressure. Second, when released from predation pressure, ciliates attained remarkably high

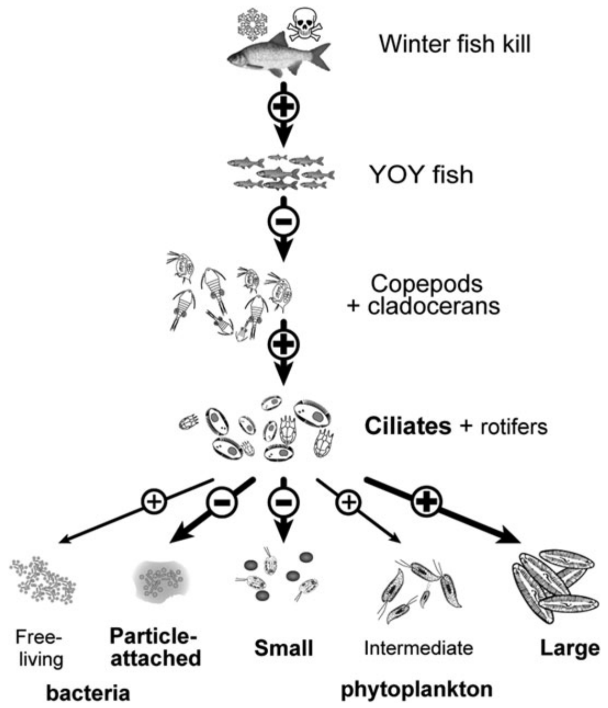

**Fig. 6.** Cascading effects of the winter fish kill for the pelagic food web. + indicates positive effects; − negative effects. Effects were more pronounced within groups highlighted by bold letters and large signs.

biomass, even in moderately eutrophic lakes such as those in our study. We conclude that this high ciliate biomass and the accompanying high estimated grazing pressure on various phytoplankton size classes altered the phytoplankton size structure, but were only partially successful in suppressing phytoplankton (Fig. 6). Finally, the release of ciliates from grazing pressure only moderately changed their community structure, with the same small species typical for many pelagic systems also dominating in the lakes of our study.

## Metazooplankton under severe grazing pressure

Owing to the partial winter fish kills prior to our sampling campaign and in between both years, the adult fish biomass was reduced and YOY fish dominated with respect to abundance, being several times more abundant than before the fish kills (Hilt *et al.*, 2015). A severe top-down control of crustaceans by YOY fish was indicated by low biomass and their composition (Fig. 6). In their review, Mehner and Thiel (Mehner and Thiel, 1999) concluded that in temperate regions, YOY fish have the largest impact on zooplankton in late summer and autumn. This is in line with our observation that in 2011, adult crustaceans were almost absent and nauplii and copepodites dominated the crustacean community during the respective time. The ratio of nauplii to total copepod biomass was unusually high (∼50% in 2011) compared with other lakes (Königssee: 7%, Großer Vätersee: 6%, Lake Constance: 2–7%; Table II) and confirmed the high predation pressure on adult copepods and the potential benefit for nauplii from cannibalistic predator release (Van Den Bosch and Santer, 1993). The cladoceran biomass was reduced even more strongly than the copepod biomass from 2010 to 2011 which can be explained by the fact that copepods are able to escape more efficiently from fish predation (Winfield *et al.*, 1983).

## Effects on phytoplankton

Phytoplankton was released from predation pressure by crustaceans and thus built up large biomass compared with the deep lakes. In both study lakes, the phytoplankton:crustacean ratio was even higher than reported from the hypertrophic Müggelsee which is characterized by cyanobacteria blooms. In the Arendsee, however, where planktivorous fish stocking released phytoplankton from its top-down control (Tittel *et al.*, 1998), the phytoplankton:crustacean ratio was closest to those measured in GS and SS, which is consistent with an exceptionally low crustacean biomass in the two lakes (Fig. 1).

The phytoplankton community in GS and SS was as diverse as reported for shallow Danish lakes of similar trophy (Jeppesen *et al.*, 2000). However, phytoplankton diversity in the Danish lakes was driven by a high species number, whereas in GS and SS, the fewer phytoplankton species were more evenly distributed, resulting in a similar Shannon–Wiener Index. In our ciliate-dominated zooplankton communities, consumers were more selective than in communities dominated by, for example, filter feeding *Daphnia*, which likely promoted a relatively even distribution of the biomass across the different morphotypes and size ranges.

Phytoplankton often escapes zooplankton grazing pressure by accumulating in forms which are beyond the preferred size spectra of the consumers. In GS and SS, ciliates potentially grazed on a broad range of phytoplankton sizes classes. However, the shape of phytoplankton size spectra (Fig. 2) did not deviate very much from those in Lake Constance (Gaedke, 1992) and the Müggelsee (Gaedke *et al.*, 2004). A remarkable exception was the high proportion of large phytoplankton species which increased over the study period, especially in GS (Fig. 6). This may be attributed to the strong decrease in crustacean biomass controlled by high YOY fish abundance. The biomass peak of the size spectra was constituted by pennate diatoms. The majority of the ciliates could presumably neither graze on these pennate diatoms nor on other large phytoplankton (mainly *Peridinium* sp.).

## Severe top-down control by ciliate dominance

Ciliates, which are usually suppressed by metazooplankton grazing (Wickham and Gilbert, 1993; Wickham, 1998; Adrian and Schneider-Olt, 1999; Jürgens *et al.*, 1999; Hansen, 2000), dominated the zooplankton community in our study lakes where high abundance of YOY fish released the ciliates from top-down control by crustaceans (Fig. 3). Not only the proportional contribution of ciliates to total zooplankton biomass, but also their absolute biomass was much higher than reported from various other lakes. Ciliate numbers ranged up to 350 cells $mL^{-1}$ and the yearly average ranged between 42 and 164 cells $mL^{-1}$. In another temperate eutrophic lake, the maximum density reached 9 cells $mL^{-1}$ (Laybourn-Parry *et al.*, 1990) and average densities of 56 cells $mL^{-1}$ were reported for eutrophic tropical lakes (Beaver and Crisman, 1982). In shallow eutrophic Lake, Võrtsjärv ciliates also dominated (66% of zooplankton biomass) within the zooplankton community because metazooplankton grazing was inhibited by filamentous algae and strong, continuous resuspension (Zingel and Noges, 2010). Thus, maximum densities reached 285 cells $mL^{-1}$ and yearly average densities were 52 cells $mL^{-1}$. In another study in Lake Võrtsjärv, sampling was conducted for several years during the annual abundance peaks at eight different sites in the lake and ciliate abundances were observed to range between 80 and 123 cells $mL^{-1}$ (Karus *et al.*, 2014a). In our study, the ciliates seemed to benefit exceptionally from the absence of crustaceans, which were fully controlled by YOY fish, exhibiting a positive feedback on ciliates via a trophic cascade. The ciliate abundance in GS and SS was on average 10 times larger than previously observed in an experimental removal of metazooplankton in the Schöhsee (Wickham, 1998), which may be attributed to the higher productivity in GS and SS.

In GS and SS, ciliates rather than rotifers dominated when crustaceans failed to build up. Although the contribution of rotifers to the total zooplankton biomass in GS and SS was larger than in other lakes of various depth and trophic state, the ratio of ciliate to rotifer biomass was still up to 15 times higher in GS and SS than in other lakes. Thus, ciliates benefited proportionally more from crustacean absence than rotifers. Rotifers are competitors and predators of ciliates, but the actual strength of interaction is species-specific (Weisse and Frahm, 2002). The dominant rotifer species, *Keratella cochlearis*, is small and thus more likely a competitor of ciliates, feeding on small and intermediate phytoplankton, rather than preying on ciliates. The egg ratio of *K. cochlearis*, i.e. the number of eggs per female, serves as an indicator of food limitation (Gonzalez and Frost, 1992; Weithoff *et al.*, 2000). It was below 0.2 in early summer and autumn, suggesting severe food limitation for rotifers. Given the large overlap in the feeding niches of small ciliates and rotifers, this suggests that also the small feeders within the ciliates were food limited, at least part of the year.

Interestingly, the release from grazing pressure did not radically change the ciliate species composition. The ciliate community was dominated by Choreotrichia, Scuticociliatia, Prostomatea and Peritrichia, including species typical for the pelagic zone of lakes with crustacean zooplankton present in sizable numbers such as *Halteria*, *Strobilidium* and *Cyclidium* (Foissner *et al.*, 1999; Gaedke and Wickham, 2004 and references therein). Small ciliates dominated along with some large, predatory species potentially feeding on the small ciliates. Some, such as *Stentor* and *Bursaridium*, are capable of ingesting algae, ciliates and small rotifers, while *Didinium* is specialized on other, larger, ciliates (Hewett, 1988; Jiang and Morin, 2005). In an experiment where metazooplankton was removed, predacious ciliates comprised 63% of the total ciliate biomass and a decline in abundance of small ciliates along with an increase in predacious ciliates suggested a strong top-down control (Agasild *et al.*, 2013). In contrast, in SS, the biomass of predacious ciliates can be neglected and in GS, apart from a peak in spring 2010, they contributed on average only 10% of the total ciliate biomass. While the size of predaceous ciliates was large by ciliate standards ($200 \times 10^3 - 800 \times 10^3$ $\mu m^3$), the size was well within the preferred size range of many cyclopoid copepods (Brandl and Fernando, 1975). Cyclopoids are capable of remarkably high ingestion rates on ciliates (Wickham, 1995), and large, unarmored, relatively slow-swimming species such as *Bursaridium* and *Stentor* may represent the preferred prey of the few cyclopoids (adult and copepodites) present in the two study lakes. Thus, the inability of predacious ciliates to fully exploit an open niche may have been due to their only partial release from predation pressure. Overall, for whatever reason, the absolute biomass of predacious ciliates was too low to suppress ciliates and thus predation within ciliates was of minor importance most of the year in both lakes.

A shift towards dominance of ciliates as observed in our study implies an increase in the total grazing pressure by zooplankton, despite an overall constant zooplankton biomass as ciliates consume per unit biomass ~3–4 times more than crustaceans (Tirok and Gaedke, 2006). Species-specific ciliate filtration rates are typically in the range 0.5–10 $\mu L\ h^{-1}$ $cell^{-1}$, at temperatures 10–20°C (Jonsson, 1986; Simek *et al.*, 1995). Simply applying a median literature filtration rate, e.g. 2 $\mu L\ h^{-1}$ $cell^{-1}$, multiplied by the average ciliate abundances for the two lakes studied (42–164 cells $\text{mL}^{-1}$) gives a rough estimate of the potential community filtration rate, e.g. 2 μL $\text{h}^{-1}$ $\text{cell}^{-1}$ × 24 h × 70 cells $\text{mL}^{-1}$ = 3.4 times per day filtering the water volume. Using Hansen *et al.*'s (Hansen *et al.*, 1997) cell-volume-specific formulas, corrected to the ambient temperatures in the lakes, allowed more accurate estimates for each sampling date, delivering yearly average values in the range of 0.7–3.5 $\text{day}^{-1}$ for the community filtration rate. These calculated estimates of the filtration rate by ciliates indicated that small feeders were the most important ciliate group for phytoplankton grazing. This resulted in very high calculated ingestion rates on a restricted size range of the phytoplankton size spectrum, leading to an accumulation of large phytoplankton species (Figs 2 and 4). The phytoplankton to ciliate biomass ratio increased along with the groups of small, intermediate and large feeders, further supporting a large predation pressure by small feeders (Fig. 4). In theory, a certain amount of prey can sustain the same amount of predator biomass if the prey has a substantially higher weight-specific production than the predator (Gaedke *et al.*, 2002; Boit and Gaedke, 2014). Additionally, the actual biomass ratio for the small feeders may be larger as we did not measure autotrophic picoplankton (APP; length <2 μm) as potential prey. In general, the share of APP on phytoplankton decreases with eutrophication. Therefore, we assume a moderate biomass increase in small prey. For example, in the eutrophic Arendsee, the APP contributed a maximum of 4% to the total autotrophic biomass (Tittel, 1997). Adding this overall small amount of prey to the small size classes raises the biomass of the small prey by ~25%. This rough estimate, however, still implies a biomass of small phytoplankton in GS and SS between 10 and 100 mg C $\text{m}^{-3}$, which is considered as the threshold for positive population growth for various ciliate species (Weisse, 2006; Tirok and Gaedke, 2007a). Thus, ciliates were presumably not able to reduce the biomass of small phytoplankton further. In line with that estimate, the calculated ciliate ingestion rates strongly exceeded the growth rates of small phytoplankton, even considering that small phytoplankter are more productive than the average community. Mass-balanced fluxes of the pelagic food web indicate that the phytoplankton and bacteria production was sufficient to maintain the large ciliate biomass, but did not allow for their maximum potential growth rates (unpublished data). Consequently, these calculations deliver further evidence that ciliates were likely bottom-up controlled, as reported for another shallow eutrophic lake where the grazing impact by metazooplankton was low (Zingel and Noges, 2010). However, the monthly sampling restricts the generality of our conclusions as ciliates, but also phytoplankton and bacteria, have generation times on the order of 1 day, and tight coupling between ciliate and algal dynamics has previously been reported (Berninger *et al.*, 1993; for seasonal dynamics, see Supplementary data, Appendix S4). Thus, opposed dynamics might have been overlooked. Nevertheless, by sampling in two lakes for 2 years, we obtained consistent results of four replicates, which lower the chance for undetected opposed effects.

The distinction between free-living and particle-associated bacteria enabled us to also investigate the grazing pressure on both bacteria fractions separately. Accordingly, the highest grazing pressure by ciliates was presumably exerted on particle-attached bacteria, which had a much higher cell-specific biomass than free-living bacteria (Fig. 6). Particle-associated bacteria seem to be easier to ingest by ciliates because of their generally larger size and association with particles which can be more easily ingested by ciliates (Gonzalez *et al.*, 1990). As a consequence, free-living bacteria may were released from ciliate predation (Fig. 5). Omnivorous ciliates as, for example, *Halteria* are generally efficient grazers of suspended bacteria (Simek *et al.*, 1996; Jürgens and Simek, 2000). Unfortunately, the role of heterotrophic nanoflagellates was not considered in our study, but the high grazing pressure of ciliates on nanophytoplankton estimated would imply top-down control by ciliates on heterotrophic nanoflagellates as well. Thus, free-living and smaller bacteria were likely released from flagellate grazing in the lakes studied. This is supported by the observation that ciliates instead of nanoflagellates became the main bacterial grazers after the experimental addition of juvenile planktivorous fish to an otherwise fishless pond (Karus *et al.*, 2014b). It is certain that the observed winter fish kill resulted in a concomitant decrease in crustaceans and increase in ciliates. Therefore, the microbial loop increased in importance for organic matter and nutrient cycling and thus represents an exceptionally significant component in the lake's food web under such environmental conditions.

## CONCLUSIONS

Owing to partial winter fish kills followed by a very high density of YOY fish, the zooplankton community composition deviated significantly from that in other lakes. A ciliate dominance developed with strongly reduced biomass of adult crustaceans, whereas nauplii and copepodites gained in relative importance. According to the estimated grazing pressure, small sized phytoplankton and particle-attached bacteria were likely top-down controlled by the small and intermediate particle feeders within the ciliates (Fig. 6). Ciliates have a narrower feeding niche than an equivalent biomass of crustacean zooplankton, preventing them from controlling the larger phytoplankton size classes, in which biomass accumulated. We emphasize the importance of more detailed measurements of ciliates, as they can be an important trophic link in the pelagic food web, especially, if crustaceans are reduced. Additionally, our measurements add to the recently recognized importance of winter processes for fish and plankton development during subsequent years, which are far beyond a simple reset.

## SUPPLEMENTARY DATA

Supplementary data can be found online at http://plankt.oxfordjournals.org.

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## DATA ARCHIVING

Data will be archived in the research database (based on PostgreSQL) of the Leibniz-Institute of Freshwater Ecology and Inland Fisheries (www.igb-berlin.de) which will be publicly available from 2016 onwards.

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