Winter decrease of zooplankton abundance and biomass in subalpine oligotrophic Lake Atnsjøen (SE Norway)

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ABSTRACT

Despite the rapidly changing winter conditions in temperate ecosystems, little attention has been devoted to the effects of these changes on lake ecology. Few studies on the seasonal changes in abundance and biomass of the major groups of the metazooplankton community (*i.e,*. rotifers, cladocerans and copepods) in northern oligotrophic lakes include data from the ice-covered winter months. This study reports monthly variation in zooplankton abundance and biomass from June 2010 to October 2011, including winter, in an oligotrophic, subalpine lake in southeastern Norway (Lake Atnsjøen). Changes in rotifer, cladoceran, copepod, and total zooplankton abundances and biomass were related to seasonal variation in water temperature and phytoplankton biomass by means of ordination analysis. The zooplankton abundance and biomass were much lower in winter than during the open water season. However, an under-ice phytoplankton bloom occurred during the final winter months, when snow cover and ice thickness were reduced and (presumably) light penetration increased, leading to an increase in abundance of copepod nauplii. Winter zooplankton abundance was dominated by copepods and rotifers, while winter zooplankton biomass was dominated by copepods and cladocerans. Both phytoplankton and zooplankton had two biomass peaks in 2010 and one peak in 2011. Rotifers dominated zooplankton abundance with a peak in August and total zooplankton abundance followed a similar pattern. In contrast, cladocerans dominated zooplankton biomass with a peak in July and total zooplankton biomass also peaked at this time. Rotifer and total zooplankton abundance and rotifer biomass were most closely correlated to water temperature. However, cladoceran biomass and total biomass were most closely correlated with phytoplankton biomass, but also appeared to be dependent on other carbon sources. Estimates of non-phytoplankton particulate organic carbon indicated that this part of the carbon pool could be an additional food source for zooplankton particularly in early and mid-winter. The longer growing season in 2011 than in 2010, owing to earlier ice-off in 2011, may have contributed to higher phytoplankton and zooplankton biomass in 2011. With climate warming, this is an expected change in temperate lake ecosystems.

INTRODUCTION

Plankton communities in high latitude lakes exhibit significant seasonality because of large seasonal fluctuations of irradiance and temperature (Sommer *et al.*, 1986; Winder and Cloern, 2010). The seasonal succession of the plankton community is one of the most well studied phenomena in freshwater ecology and well described in the PEG-model (Sommer *et al.*, 1986). Initially, the model did not much consider the winter period (Sommer *et al.*,

1986). However, this period is of key importance for the seasonal dynamics of plankton communities (Post *et al.*, 2009), and is not only an inactive period of dormancy (Salonen *et al.*, 2009; Bertilsson *et al.*, 2013; Hampton *et al.*, 2015), as once believed. Thus, the PEG-model was revised and acknowledges the necessity of addressing the winter conditions for plankton dynamics (Sommer *et al.*, 2012). For example, winter conditions may affect plankton dynamics the following year through cross-seasonal cascades (Hampton *et al.*, 2017).

Zooplankton are an important part of aquatic food webs and also play an important role for the biochemical cycling of nutrients. Zooplankton are transferring organic carbon (hereafter C) and energy to higher trophic levels by grazing on phytoplankton, heterotrophic protists, and dead particulate organic matter. In the PEG-model the seasonality of the zooplankton is driven by a combination of changes in temperature, food availability, and predation. Temperature and food availability affect zooplankton directly via effects on growth rates and behavior (Urabe, 1991; Lampert and Trubetskova, 1996), and indirectly through thermally driven seasonal changes (e.g. stratification, Loose and Dawidowicz, 1994). In particular, zooplankton dynamics depend on lake trophic states (Sommer *et al.*, 1986). For example, a generalized temperate eutrophic lake has two (or more) zooplankton peaks during the growing season. The first succeeds the phytoplankton spring bloom and the second trails the

summer/autumn phytoplankton bloom. A generalized temperate oligotrophic lake has one zooplankton peak during the growing season, following the phytoplankton spring bloom (Sommer *et al.*, 1986). However, there is considerable inter- and intra-lake variation in these patterns. The number of zooplankton peaks may change from year to year in the same lake (Halvorsen *et al.*, 2004), likely reflecting annual variability in environmental conditions, demographic stochasticity, or fluctuating food-web interactions. Despite the seasonal variability in zooplankton abundance, there are relatively few investigations reporting on the occurrence of zooplankton under winter ice, as compared to the growing season (Noges *et al.*, 1998; Virro *et al.*, 2009). In addition, winter studies are often limited to brief observations in studies dealing with other issues (Steinhart and Wurtsbaugh, 2003). There are almost no studies describing the seasonal changes in the zooplankton community of high latitude, oligotrophic lakes (Larsson, 1978).

There are major differences in life history strategies, food requirements, and predation resistance between rotifers, cladocerans, and copepods (Brooks and Dodson, 1965; Allan, 1976; Zaret, 1980; Andersen, 1997; Saksgård and Hesthagen, 2004; Hart and Bychek, 2011). Accordingly, the environmental factors that control the seasonal change in abundance and biomass of rotifers, cladocerans, and copepods may differ. There are increasing concerns about effects of climate warming on temperate and arctic lakes. The winter period is expected to be particularly impacted by climate change in ice-covered lakes, as many lakes are experiencing reduced periods of ice coverage (Benson *et al.*, 2012). A longer growing season can affect the phenology of the plankton community, may lead to higher phytoplankton and zooplankton abundance in temperate oligotrophic lakes (De Senerpont Domis *et al.*, 2012; Weyhenmeyer *et al.*, 2013), and could change the predation regime because of changes in activity and metabolic requirements of fishes (Watz *et al.*, 2015). In Greenland lakes, higher water temperatures linked to earlier ice-off was associated with higher biomass of phytoplankton and higher abundances of copepods and *Daphnia*. However, abundance of rotifers was lower in years with earlier ice-off (Christoffersen *et al.*, 2008).

The present study examined seasonal changes in zooplankton abundance and biomass in an oligotrophic, subalpine lake, across the growing season (growing season and open water period are used interchangeably to refer to the ice-free period) and winter season (the ice-covered period). Seasonal changes in zooplankton abundance and biomass were related to changes in temperature and food availability. It was hypothesized that different zooplankton groups respond differently to temperature changes and resource availability.

METHODS

Study site

The study was conducted in Lake Atnsjøen (61° 52'51 N, 10° 09'55 E, Fig. 1). The lake is located in a mountainous area in southeastern Norway at 701 m asl. With a surface area of 4.8 km^2, it is the largest lake in the River Atna watershed. Maximum and mean depth of the lake is 80 m and 35.4 m, respectively. The retention time of the lake is about 6 months. 85 % of the catchment of the lake (457 km^2) is above the tree line, which is at approximately 1000 m asl. The catchment consists mainly of feldspar quartzite, with large deposits of quaternary and fluvial materials in some areas. There are no glaciers in the catchment, but during cold summers patches of snow remain and affect the temperature of the lake. The Atna watershed and Lake Atnsjøen are little affected by human activities. The area where Lake Atnsjøen is located has a continental climate. The 1961–1990 mean annual temperature and precipitation were 0.7°C and 524 mm, respectively. Normally, snow cover lasts from November to early May, and ice cover on the lake lasts from late November to late May. The lake is weakly stratified in summer, with a thermocline usually situated at about 10 m depth (Halvorsen, 2004).

Sampling

Zooplankton was sampled in the deepest part of Lake Atnsjøen monthly from June 2010 to October 2011, except for March 2011 due to very low temperatures (Fig. 1). Water transparency was measured with a Secchi disk, and temperature was measured with an YSI ProODO™ instrument. Sampling and counting of phytoplankton and zooplankton followed procedures for the long term monitoring program in Lake Atnsjøen, described in detail by Brettum and Halvorsen (2004) and Halvorsen *et al.* (2004). Phytoplankton were analyzed from integrated samples over the top 0 to 10 m of the water column. The integrated water sample was obtained by sampling consecutive water layers (0 to 2 m, 2 to 4 m, 4 to 6 m, 6 to 8 m, and 8 to 10 m) with a two-meter tube sampler (diameter 5.2 cm) and mixing the water samples in a clean container. The phytoplankton samples were fixed with Lugol's solution. Phytoplankton biovolume were converted to C using the formula: C biomass = 0.12 biovolume$^{1.05}$ (Rocha and Duncan, 1985). The concentration of total organic carbon (TOC) was measured from the integrated 0-10 m water samples, according to standard procedures (Standards Norway, 1987). The particulate organic carbon (POC) constitutes 11% of the TOC pool in Lake Atnsjøen (Woszczyk and Jensen, *personal communication*). The concentration of non-phytoplankton and non-zooplankton particulate dead organic matter was estimated using this percentage and subtracting the phyto-

plankton and zooplankton fraction of the POC pool. Quantitative zooplankton samples where obtained using a 14-liter Schindler water sampler at 0, 1, 2, 4, 6, 8, 10, 15, 20, 30 and 50 m depth, with five replicates per depth stratum. These samples were filtered through a 45 µm mesh. The quantitative zooplankton samples were supplemented with zooplankton net hauls (diameter 30 cm, length 1 meter, mesh size 45 µm) for length measurements. Zooplankton samples were preserved with Lugol's solution. Enumeration of zooplankton samples is described by Halvorsen *et al.* (2004).

Zooplankton abundance (ind. L^{-1}) was calculated from the quantitative samples and adjusted for the relative contribution of the volume of each depth layer of the lake, taking into account the bathymetry of the lake (Halvorsen *et al.*, 2004). Dry masses of each taxa were calculated, following Bottrell *et al.* (1976) and Dumont *et al.* (1975), using fixed mean masses for rotifer species and copepod nauplii and species-specific length-dry mass regressions for cladocerans and copepodites/adult copepods. Length measurements were collected on a representative subsample of 20 individuals of each species from each sampling date. The zooplankton biomass was then calculated by multiplying the zooplankton abundances with the individual dry masses. Zooplankton biomasses, as dry mass, were converted to C assuming a C content of 46% (Andersen and Hessen, 1991). The phytoplankton:zooplankton biomass ratio were calculated for each sampling date as the ratio between the epilimnetic phytoplankton biomass (by volume) and the whole water-column zooplankton biomass (by volume). This approach likely biased the data towards higher ratios than if the entire water column was considered for phytoplankton, because phytoplankton would be less abundant at greater depths.

Data analysis

Gridded (1 km²) monthly temperature and precipitation data interpolated from surrounding weather stations provided by the Norwegian Meteorological Institute (Mohr, 2008, 2009) were compared qualitatively with the 1961–1990 averages for the respective monthly means (Nordli and Grimenes, 2004). Ice data was obtained from the Norwegian Water Resources and Energy Directorate. Ice-on and ice-off dates were taken as the dates when the whole lake was ice-covered or ice-free. Correlation analysis (Pearson's correlation, r) was used to evaluate relationships between environmental variables. For seasonal studies, a time lag between variables is common. Hence, for environmental variables (daylength, water temperature, Secchi depth and phytoplankton biomass) measurements at the previous census point (t-1) were included in the correlation matrix.
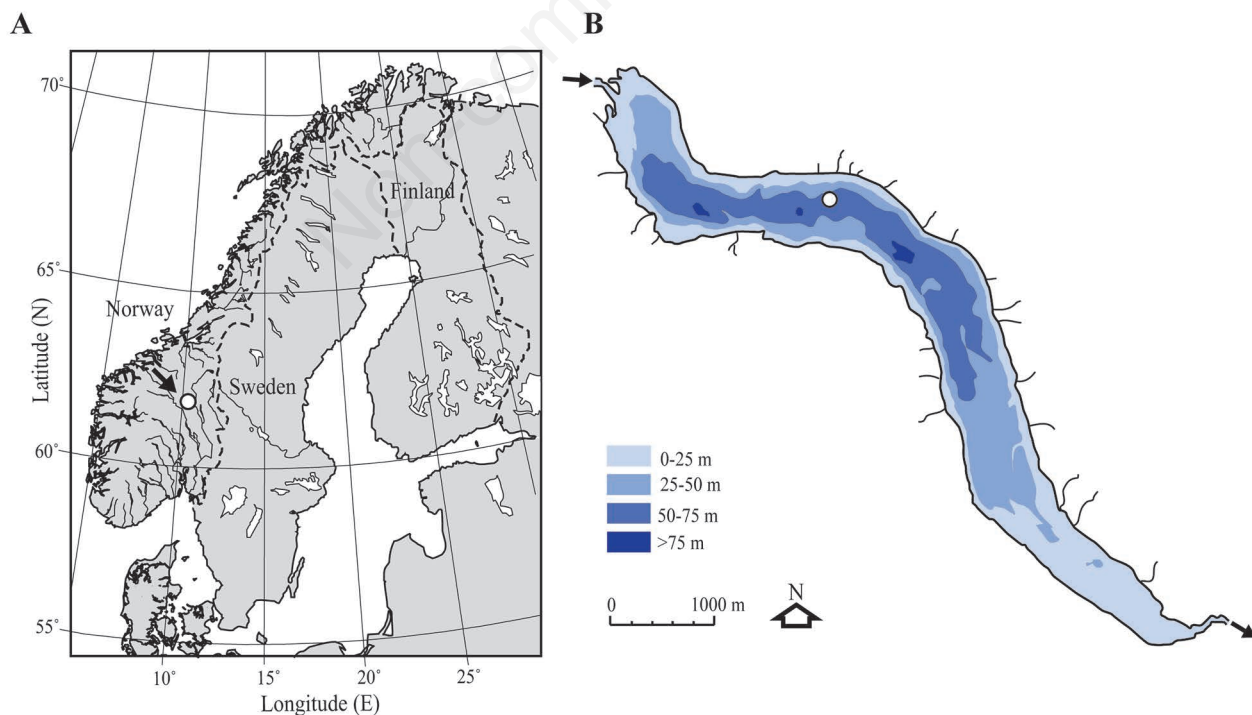

Fig. 1. Map of Scandinavia with the location of Lake Atnsjøen (A, white circle) indicated. Map of Lake Atnsjøen with sampling site indicated (B, white circle). Also indicated is inlet and outlet river (black arrows), and depth contours (blue shading).

Holm Bonferroni correction were used to adjust for multiple comparisons (Holm, 1979). The mean weighted average water temperature of the water column was used in the statistical analysis. Visual inspection of the residuals of the environmental variables confirmed normal distributions. Differences in biological responses between the growing seasons of 2010 and 2011 and the ice-covered period were visualized by boxplots grouped by season.

The relationships between water temperature and phytoplankton biomass and zooplankton abundance and biomass in Lake Atnsjøen were analyzed using unconstrained and constrained ordination techniques. Initially, principal components analysis (PCA) was used to explore the variation in zooplankton abundance and biomass and to estimate gradient length. To identify possible relationships between zooplankton abundance and biomass and water temperature and phytoplankton biomass (at t1 and t-1) the constrained ordination technique redundancy analysis (RDA, ch. Økland, 1990) were applied due to short gradients. A "minimal adequate model" was developed by forward selection of environmental variables with a Monte Carlo test (499 permutations). Only variables that made significant independent contributions to zooplankton abundance/biomass ($\alpha = 0.05$ level) were included in the model. Multicollinearity of the environmental variables was assessed by checking their Variance Inflation Factors (VIF) using a limit of VIF >10 to exclude variables (Borcard et al., 2018). All environmental variables had VIFs below this limit and were thus included in the

analysis. To address the unique and shared effects of water temperature and phytoplankton biomass on zooplankton abundance and biomass, respectively, two variance partitioning analysis' (VPA) were conducted using partial redundancy analysis (Borcard et al., 1992). This technique may be used to divide variation in ecological data sets between environmental variables (or groups of environmental variables, Liu, 1997). The water temperature at t and t-1 were grouped together in the analysis. The same was done for phytoplankton biomass. In VPA, the total variation and the unique contribution of the variables and their joint effects are obtained in several steps. For further description of this method, see for example Liu (1997). Environmental variables were kept untransformed in the correlation analysis, as well as in the ordination analysis. Rotifer, cladoceran and copepod abundance and biomass were transformed ($\log10(x+1)$) for the analysis. Statistical analyses were conducted in SPSS Statistics 24 (IBM, 2017) and CANOCO 5.0 (Ter Braak and Šmilauer, 2012).

RESULTS

Weather conditions

The daylength at Lake Atnsjøen varies between approx. 5 hours in December and 19.5 hours in June (Tab. 1). Average air temperatures at the lake ranged from -18.0°C (Fig. 2, December 2010) to 13.6°C (July 2010). The temperature stayed above 0°C from June 2010–October 2010, and again during April 2011–October 2011. The air temperature dur-

Tab. 1. Daylength (Dayl), ice cover and snow cover, average weighted water temperature of the water column (0 to 80 m), and total carbon concentration (TOC, incomplete for four sampling dates), on the different sampling days.

Date	Day	Dayl (hours)	Ice cover (cm)	Snow cover (cm)	Water temp (°C)	TOC (mg C L⁻¹)
11.06.2010	162	19.50	-	-	5.0	-
06.07.2010	187	19.28	-	-	6.2	2.0
17.08.2010	229	15.78	-	-	7.0	-
08.09.2010	251	13.65	-	-	6.6	1.5
15.10.2010	288	10.07	-	-	5.4	-
03.11.2010	307	8.23	-	-	4.0	-
14.12.2010	348	5.30	40	10	3.3	3.5
26.01.2011	26	7.07	55	50	3.3	2.2
28.02.2011	59	10.22	65	35	3.3	1.6
12.04.2011	102	14.45	60	5	3.3	1.8
11.05.2011	131	17.26	-	-	4.1	2.1
06.06.2011	157	19.27	-	-	4.9	2
05.07.2011	186	19.35	-	-	6.4	2.7
12.08.2011	224	16.28	-	-	6.9	2.3
06.09.2011	249	13.87	-	-	7.3	1.8
12.10.2011	285	10.38	-	-	6.3	1.7

ing the 2010 and 2011 growing seasons was slightly above the average (1961–1990), whereas winter 2010/2011 was colder than average. Also, April 2011 was warmer than average. Variation in precipitation followed the same pattern as for temperature, with highest precipitation during June–August both in 2010 and 2011 (Fig. 2, reaching 43.9 mm in August 2010 and 55.8 mm in July 2011). Precipitation was below average during the entire study period (Fig. 2). The lake was ice-covered from November 15, 2010. This was relatively early, as average ice-on is November 25 (period 1954–2011). The lake was ice-free again from May 8, 2011. This was also relatively early. Average ice-off is May 24 (period 1954–2011) and in 2010 it was May 22. The ice-covered period lasted for 174 days during the winter 2010/2011. Average ice-covered period was 181 days (period 1954–2011). The date for ice-on in 2011 was relatively late on December 5. Ice thickness in winter 2010/2011 varied between 40 cm in December and 65 cm in February (Tab. 1). The snow cover on the ice was rather patchy at times and varied between 5 (April) and 50 cm (January) at the sampling location (Tab. 1). The temperature data indicated that the winter 2010/2011 was colder than average. However, due to the warm April, spring came early as indicated by the early ice-off date.

Water temperature, Secchi depth and phytoplankton biomass

The relative weak summer temperature stratification of Lake Atnsjøen was apparent in both 2010 and 2011 (Tab. 1, Fig. 3). Warming of the upper water layers started

before the first sampling date (June 11, 2010) and as the summer progressed a weak thermocline developed around 10 m. August 2010 had the highest surface temperatures (14.2°C) measured. Cooling of the epilimnion started in September 2010 and continued in October. The autumn overturn occurred in the beginning of November, when the whole water column had a temperature of 4°C. The minimum surface temperature was measured at the end of February 2011 (0.2°C). Warming of the surface layers started under the ice in March and April, leading to the spring overturn immediately after ice-off in the beginning of May. The surface water temperatures in summer 2011 was lower than in 2010 (maximum in 2011 was 12°C in August), explaining the somewhat weaker thermocline in 2011 (Fig. 3). The autumn overturn in 2011 had not taken place at the last sampling date (October 12). The average water temperature did not differ significantly between the growing season of 2010 and 2011 (t=-0.363, df=10, P=0.724). The Secchi-depth varied between 5.9 m (July 2011) and 8.6 m (December 2010), and was generally lower during the open water period than during winter (Fig. 4). Furthermore, it was lower in late spring/early summer than later in summer/early autumn.

The phytoplankton concentration in Lake Atnsjøen varied 2.1 µg C L^{-1} (end of January 2011) and 36.8 µg C L^{-1} (beginning of June 2011, Fig. 4A). The maximum concentration in both 2010 and 2011 occurred in the beginning of June. In addition to this primary peak, 2010 had a secondary phytoplankton peak in September. The concentration was low during winter, until late March/beginning
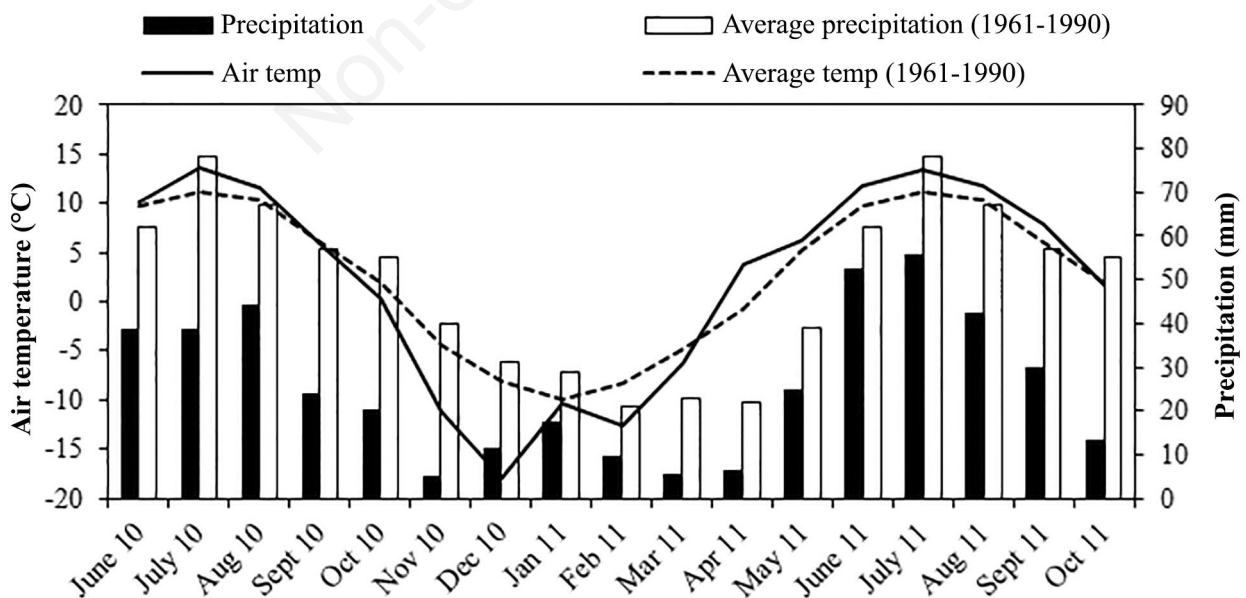

Fig. 2. Monthly average air temperature and precipitation at Lake Atnsjøen in the study period. Also included are the 1961-1990 average taken from Nordli and Grimenes (2004).

of April when the concentration rose and almost reached the level of the preceding growing season.

The average phytoplankton biomass during the open water seasons of 2010 and 2011 were 2.8 and 3.5 times higher, respectively, than during winter (Fig. 5A). Average and maximum biomass during the open water period in 2011 were both 1.4 times higher than in 2010. There was a strong correlation between daylength and phytoplankton biomass, and a somewhat weaker, yet significant, correlation between water temperature$_{t-1}$ and phytoplankton biomass (Tab. 2).

On average, phytoplankton constituted only 10 % of the non-zooplankton POC and from December to February this fraction was much lower (Fig. 4B). The share was highest during the 2011-springbloom in June (20%). The dependency of the seasonal succession of the lake environment on the changes in day length was illustrated by the correlation of water temperature$_{t-1}$, Secchi depth, and phytoplankton biomass with day length (Tab. 2).

Zooplankton abundance and biomass

The composition of the zooplankton community was dominated by the cladocerans *Daphnia longispina*, *Bosmina longispina,* and *Holopedium gibberum*, the cyclopoid *Cyclops scutifer* and the calanoid *Arctodiaptomus laticeps. Polyarthra vulgaris*, *P. remata,* and *Kellicottia longispina* dominated the rotifer community. With an average of 11 species the rotifers were the most species rich group. Corresponding values for cladocerans and copepods were 4 and 2 respectively. Rotifer abundance varied between five ind. L^{-1} (February 2011, Fig. 6) and 435 ind. L^{-1} (August 2011), and they constituted the largest part of the total zooplankton abundance. In comparison, rotifers accounted for the smallest part of the zooplankton biomass. The rotifer biomass varied between 16.2 µg C L^{-1} (August 2011) and 0.19 µg C (February 2011). Cladocera

abundance varied between 0.6 ind. L^{-1} (April 2011) and 17 ind. L^{-1} (June 2010, Fig. 6). While they constituted the smallest part of total zooplankton abundance, total zooplankton biomass was dominated by cladocerans. They varied between 1.3 µg C L^{-1} (April 2011) and 49.6 µg C L^{-1} (July 2011). Copepods constituted a larger fraction of the total zooplankton abundance than the cladocerans, and varied between 10 ind. L^{-1} (August 2011) and 40 ind. L^{-1} (April 2011). During the copepod peak in April, they constituted the major part of the total zooplankton abundance. This late winter peak in copepod abundance was caused by an increase in nauplii. The copepod biomass varied be-
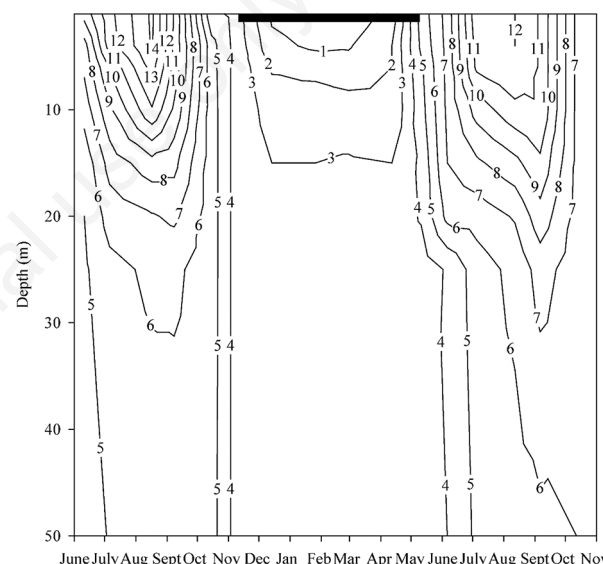

Fig. 3. Isopleth diagrams of water temperatures in Lake Atnsjøen from June 2010–October 2011. The black horizontal bar indicates the winter (ice-covered) period.

Tab. 2. Correlation matrix (r) for environmental variables in Lake Atnsjøen for the period June 2010–October 2011: Daylength, daylength at previous census point (Daylength$_{t-1}$), average water temperature of the water column (Wt), average water temperature of the water column at previous census point (Wt$_{t-1}$), Secchi depth (Secchi), Secchi depth at previous census point (Secchi$_{t-1}$), phytoplankton biomass (Phyto), phytoplankton biomass at previous census point (Phyto$_{t-1}$).

	Daylength	Daylength$_{t-1}$	Wt	Wt$_{t-1}$	Secchi	Secchi$_{t-1}$	Phyto	Phyto$_{t-1}$
Daylength	1							
Daylength$_{t-1}$	0.829*	1						
Wt	0.472	0.836*	1					
Wt$_{t-1}$	0.038	0.530	0.835*	1				
Secchi	-0.793*	-0.754*	-0.461	-0.124	1			
Secchi$_{t-1}$	-0.627	-0.814*	-0.744*	-0.469	0.419	1		
Phyto	0.860*	0.765*	0.487	0.200	-0.675	-0.536	1	
Phyto$_{t-1}$	0.664	0.873*	0.762*	0.502	-0.684	-0.675	0.589	1

Correlation was significant at the 0.05 level (Holm Bonferroni correction for multiple comparisons).

tween 1.9 µg C L⁻¹ (February 2011) and 34.2 µg C L⁻¹ (July 2011). Total zooplankton abundance varied between 19 ind. L⁻¹ (February 2011) and 449 ind. L⁻¹ (August 2011). Minimum total zooplankton biomass was 4.3 µg C L⁻¹ (February 2011) and maximum was 85.9 µg C L⁻¹ (July 2011).

The average abundance and biomass of rotifers were considerable higher during the growing season compared

to winter (Fig. 5 B,F). Rotifer abundances were 4.9 and 13.8 times higher during the 2010 and 2011 open water periods, respectively, than during winter. For rotifer biomass the corresponding values were 5.7 and 13.6. Cladoceran abundance and biomass were also substantially higher during the growing season compared to winter (Fig. 5 C,G). Cladoceran abundances were 5.3 and 4.6 times higher, during the 2010 and 2011 open water peri-
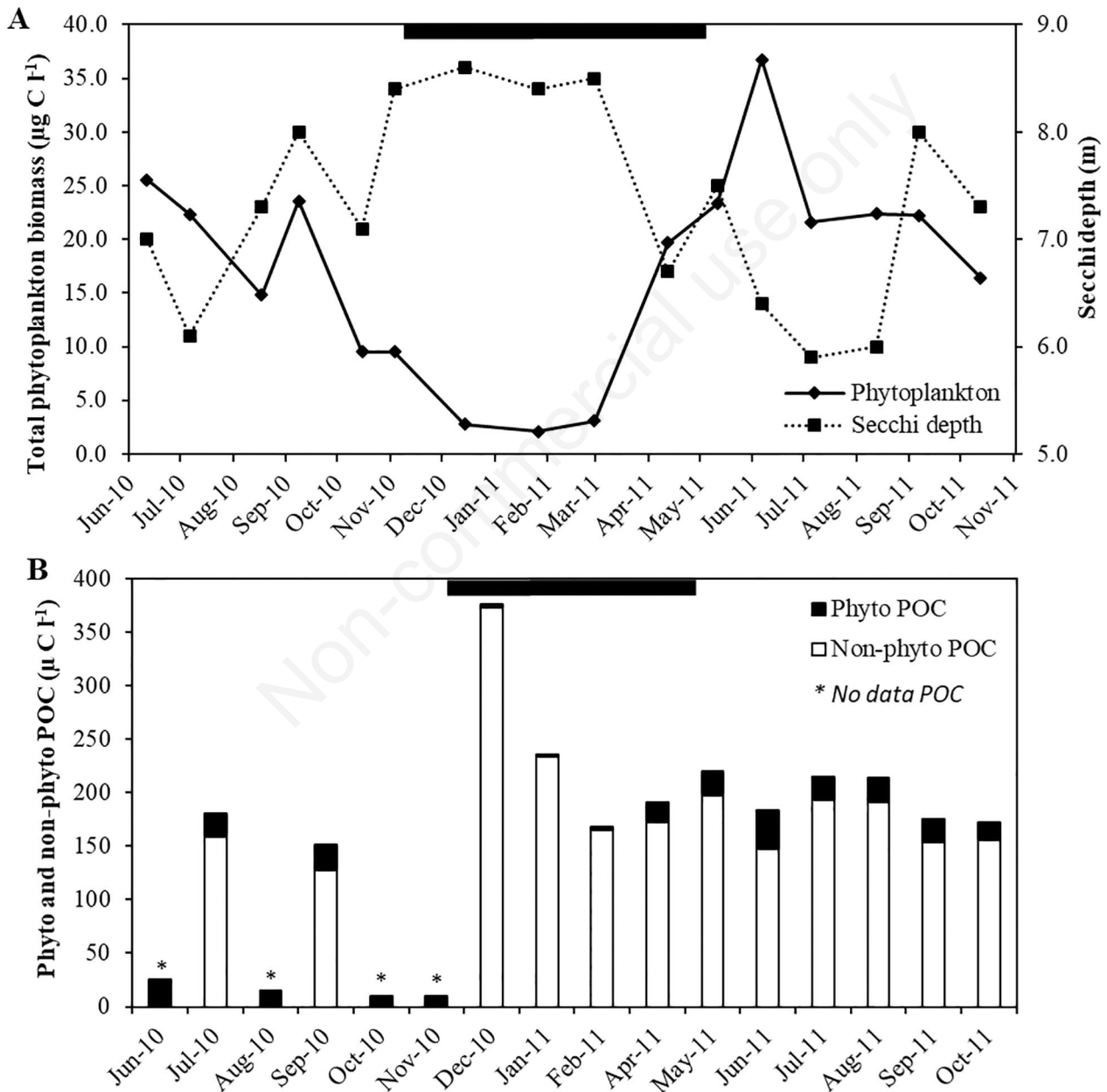

Fig. 4. Phytoplankton biomass and Secchi depth (upper panel) in Lake Atnsjøen from June 2010–October 2011. Non-phytoplankton particulate organic carbon (Non-phyto POC) compared to the phytoplankton fraction of POC (phyto POC, lower panel). See methods for description of calculation of POC. The black horizontal bars indicate the winter (ice-covered) period.

ods, respectively, than during winter. For cladoceran biomass the corresponding values were 5.0 and 6.1. Though, average copepod abundance was slightly lower during the growing season compared to winter (0.8 for open water period in 2010 compared to winter and 0.9 for open water period 2011 compared to winter, Fig. 5D), copepod biomass showed similar pattern as rotifer and cladoceran biomass (2.6 for open water period in 2010 compared to winter and 4.3 for open water period 2011 compared to winter, Fig. 5H). Finally, average total zooplankton abundance and biomass was also considerable higher during the open water period than during winter (Fig. 5 E,I). Total zooplankton abundance were 2.1 and 4.7 times higher during the 2010 and 2011 growing seasons, respec-

tively, than during winter. For total zooplankton biomass the corresponding values were 3.7 and 5.5.

Due to the very high rotifer abundance in august 2011, average and maximum total zooplankton abundance during the open water period of 2011 was 2.2 and 4.8 times higher, respectively, than during the 2010 open water period (Fig. 5E). Average biomass of all zooplankton groups, as well as average total zooplankton biomass, was also slightly higher during the 2011 open water period than during the 2010 open water period (Fig. 5 F-I). The differences were greater for peak zooplankton biomass estimates. The timing of and number of peaks for rotifer and copepod biomass during the growing season were similar for 2010 and 2011 with rotifer maximum in august and
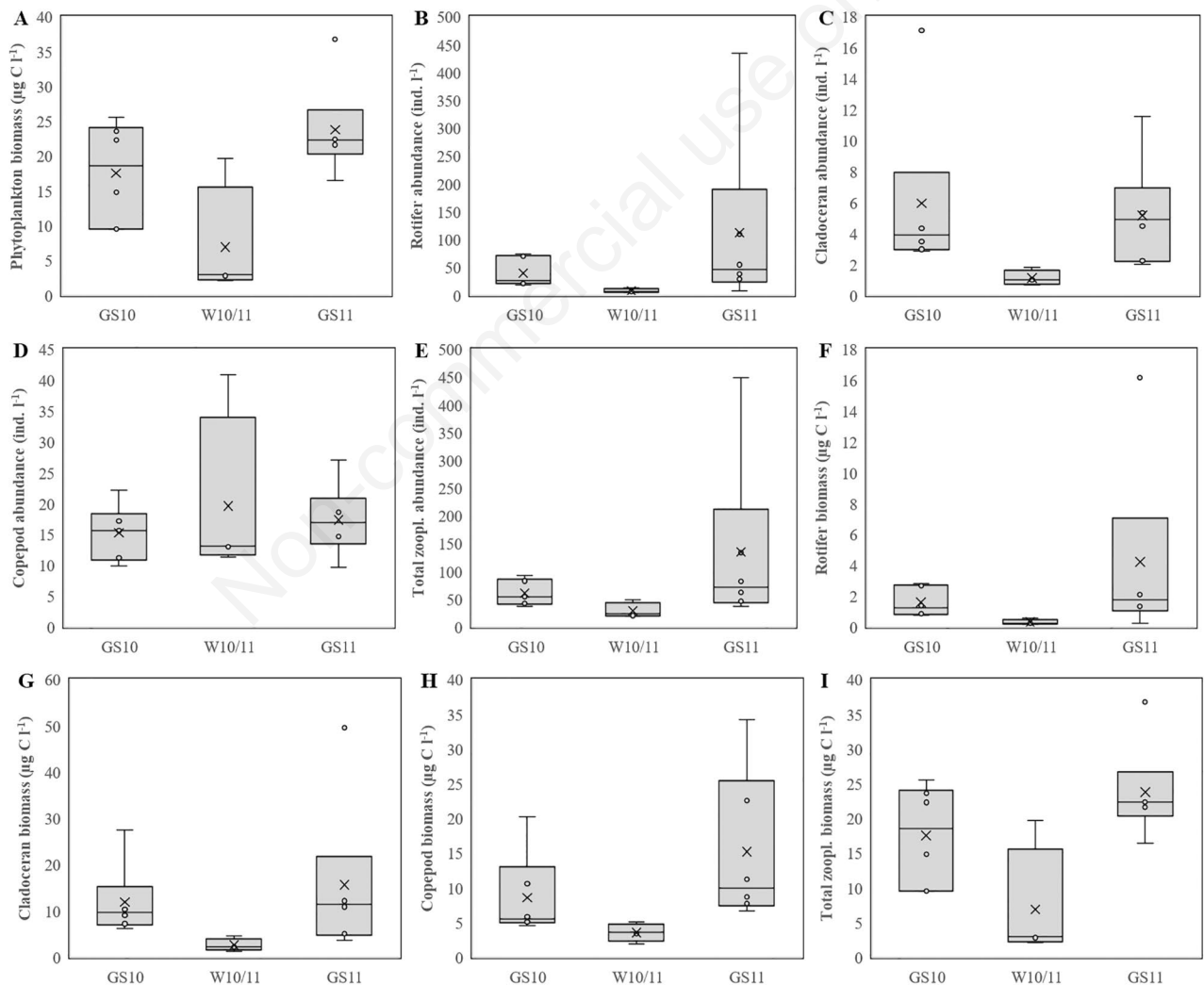

Fig. 5. Boxplots grouped by season (GS10, growing season of 2010; W10/11, ice-covered period 2010/2011; GS11, growing season 2011), showing median, mean, minimum, first quartile, third quartile, maximum, and outliers of phytoplankton biomass (A), rotifer abundance (B), cladoceran abundance (C), copepod abundance (D), total zooplankton abundance (E), rotifer biomass (F), cladoceran biomass (G), copepod biomass (H), and total zooplankton biomass (I). Mean and outliers are indicated by "x" and "o" respectively.

copepod maximum in June (2010)/July (2011). For comparison, the number of cladoceran biomass peaks differed between the two growing seasons. Maximum cladoceran biomass was reached in July both years. However, 2010 had a secondary smaller peak in October. The development of the total zooplankton biomass followed the same pattern as the cladoceran biomass.

The PCA indicated that the seasonal variation in zooplankton abundance was mainly determined by changes in rotifer abundance (Fig. 7A). The first two RDA axes in the constrained ordination of zooplankton abundance

had eigenvalues of 0.641 and 0.071, respectively (Fig. 7B). The environmental variables accounted for 72.6% of the variation in zooplankton abundance (adjusted explained variation 61.6%). There was a significant relationship between the set of environmental variables and zooplankton abundance (*i.e.* all canonical axes, F-ratio =6.6, P=0.002). The "minimal adequate model" included the explanatory variables water temperature$_t$ and phytoplankton biomass$_{t-1}$ (water temperature$_t$ pseudo-F =22.7, P=0.002; phytoplankton biomass$_{t-1}$ pseudo-F =2.9, P=0.042). Rotifer abundance was most strongly corre-
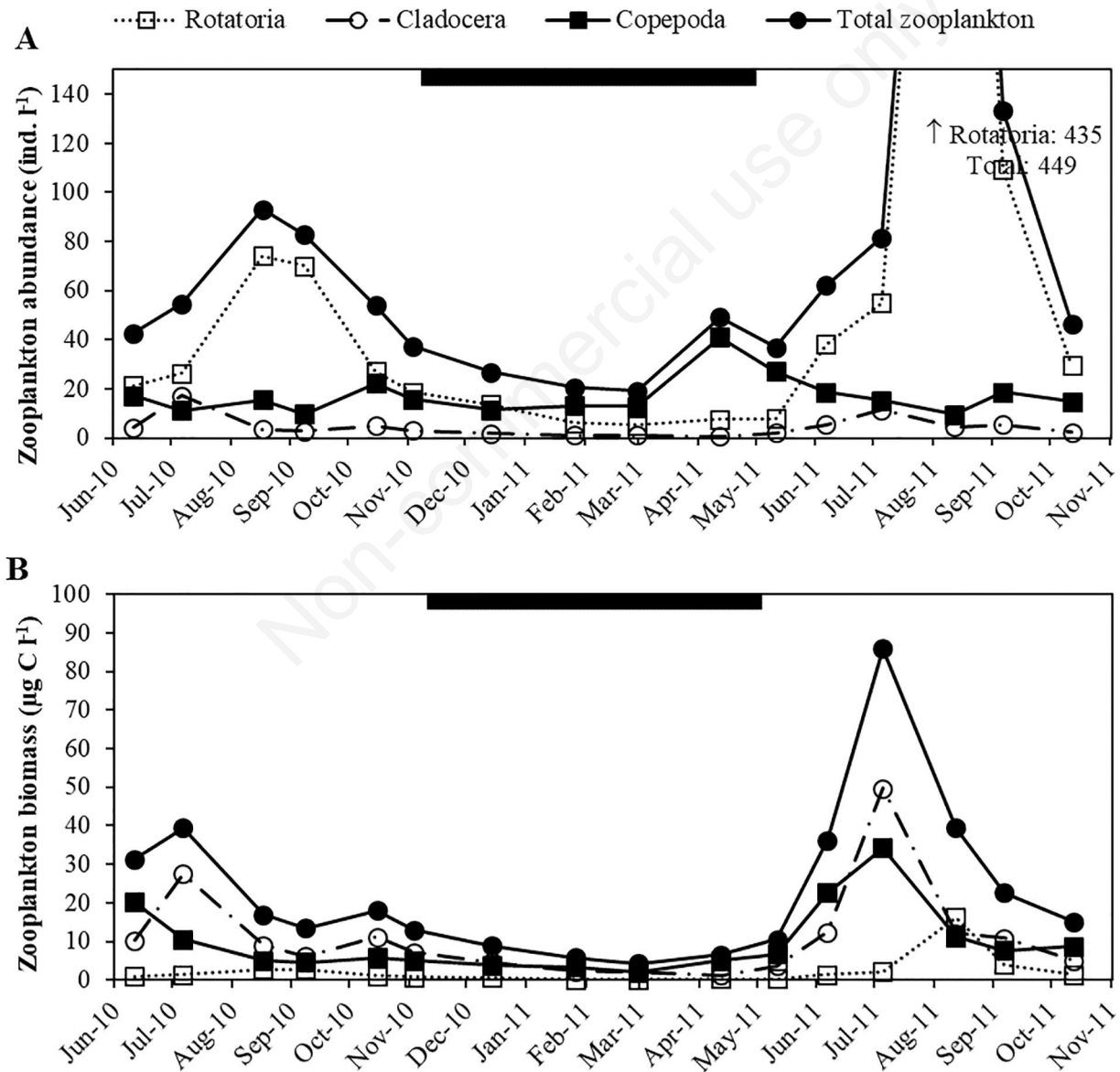

Fig. 6. Zooplankton abundance (A) and biomass (B) in Lake Atnsjøen from June 2010–October 2011. The black horizontal bars indicate the winter (ice-covered) period.

lated with water temperature, while cladoceran abundance was more closely related to phytoplankton biomass. The seasonal variation in zooplankton biomass was mainly due to changes in cladoceran and copepod biomass (Fig. 7C). In the constrained RDA of zooplankton biomass the first two axes had eigenvalues of 0.615 and

0.133, respectively (Fig. 7D). The environmental variables accounted for 77.6% of the variation in zooplankton biomass (adjusted explained variation 68.6%). There was a significant relationship between the set of environmental variables and zooplankton biomass (*i.e.*, all canonical axes, F-ratio =8.6, P=0.002). The same ex-
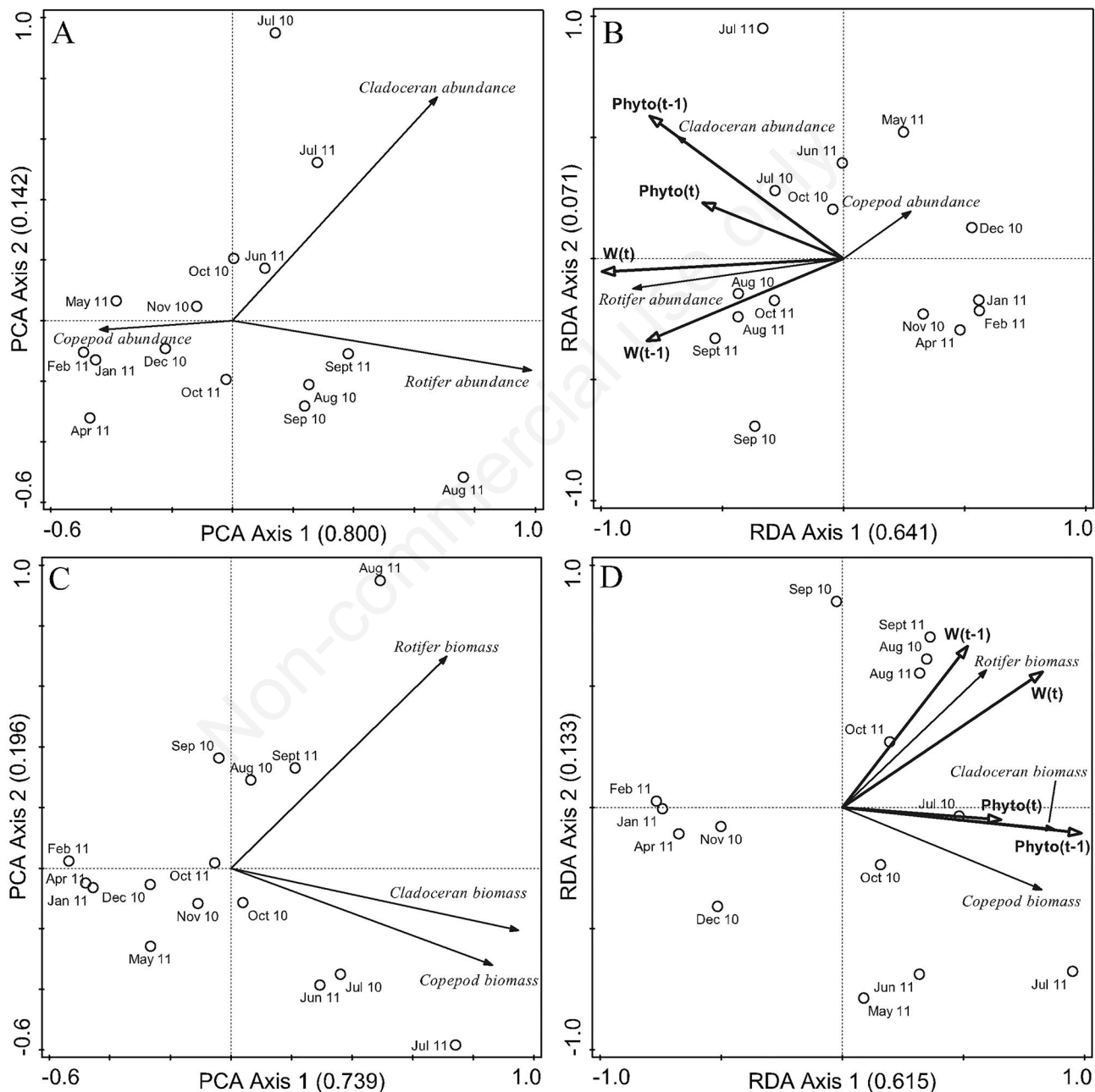

Fig. 7. Results from the ordination analysis of zooplankton abundance and biomass in Lake Atnsjøen during the period June 2010–October 2011. PCA biplot of zooplankton abundance (A). RDA triplot of zooplankton abundance (B), environmental variables included are water temperature and phytoplankton biomass at t and t-1, eigenvalues are given in brackets on the axes. PCA biplot of zooplankton biomass (C). RDA triplot of zooplankton biomass (D), environmental variables and eigenvalues as in B.

planatory variables were included in the minimal adequate model for zooplankton biomass (phytoplankton biomass$_{t-1}$ pseudo-F =19.5, P=0.002; water temperature$_t$ pseudo-F =6.3, P=0.002) as for zooplankton abundance. Rotifer biomass was stronger correlated with water temperature, while cladoceran biomass was more correlated to phytoplankton biomass. The variance partitioning analysis indicated that the shared effect of water temperature and phytoplankton biomass explained the largest significant fraction of the total variation in zooplankton abundance, but water temperature alone also had a significant contribution (Tab. 3). Even though the main effect of phytoplankton biomass was not significant it still had to be considered due to the significant shared effect of water temperature and phytoplankton biomass. The

shared effect of water temperature and phytoplankton biomass also explained the largest fraction of the total variation in zooplankton biomass and the effect was significant (Tab. 3). Phytoplankton biomass alone explained a larger fraction than water temperature alone, but both contributions were significant. The significant shared effect of water temperature and phytoplankton biomass on the total variation in zooplankton abundance and biomass could be due to the correlation between water temperature and phytoplankton biomass.

The ratio of phytoplankton to zooplankton biomass varied between 0.25 in July 2011 and 2.98 in April 2011 (Fig. 8). On 11 out of the 16 sampling dates, the ratio was below 1.0 and on half of the sampling dates the ratio was below 0.8. During winter, the ratio was typically below 0.8.

Tab. 3. Results from the variance partitioning analysis of zooplankton abundance and biomass in Lake Atnsjøen. P-values were corrected by the Holm Bonferroni to account for multiple comparisons

| Fraction	Zooplankton abundance			Zooplankton biomass		
	% of explained	% of total	P	% of explained	% of total	P
Water temperature (W$_t$ and W$_{t-1}$)	37.0	26.9	0.032	18.5	14.4	0.024
Phytoplankton biomass (Phyto$_t$ and phyto$_{t-1}$)	9.4	6.8	0.312	30.4	23.6	0.024
Shared effect of water temperature (W$_t$ and W$_{t-1}$) and phytoplankton biomass (Phyto$_t$ and phyto$_{t-1}$)	53.6	38.9	0.006	51.1	39.6	0.006
Total explained variation	100	72.6		100	77.6	
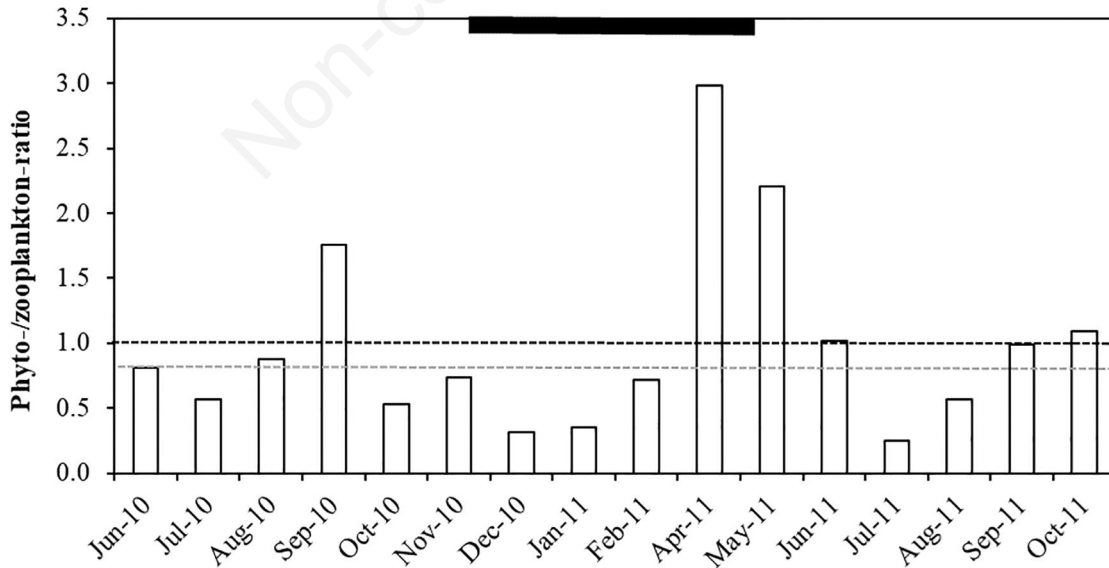
Fig. 8. Phytoplankton:zooplankton biomass ratio (C:C) in in Lake Atnsjøen from June 2010–October 2011. The black dotted horizontal line indicate a phytoplankton:zooplankton biomass ratio of one. The grey dotted horizontal line indicate the primary production to zooplankton biomass ratio of 0.8 needed for zooplankton maintenance estimated by Hessen et al. (2003b). The black horizontal bar indicates the winter (ice-covered) period.

DISCUSSION

Information on abundance of metazoan zooplankton under ice is scarce in the literature. The range of crustacean zooplankton abundances reported by Hampton and colleagues (2017) covers the winter average in Lake Atnsjøen. Typically, winter abundance and biomass increase with lake trophic state (Dokulil and Herzig, 2009). However, by including only one winter, the current study does not shed light over annual variability in winter zooplankton abundance and biomass in Lake Atnsjøen. Dokulil and Herzig (2009) note that winter zooplankton may be quite variable from year to year in the same lake, which is likely also the case in Lake Atnsjøen.

Overall, zooplankton abundance and biomass in Lake Atnsjøen were lower in winter than during the growing season. This accords with findings of Hampton *et al.* (2017). However, average winter copepod abundance did not differ much from average abundances during the open water period, due to the late winter peak in copepod nauplii. As data from other winters are not available for comparison, it is not possible to tell whether this is normal or an outlier occurrence. The revised PEG-model acknowledges the importance of the winter period (Sommer *et al.*, 2012). For example, winter zooplankton populations may exert a substantial grazing pressure on the spring phytoplankton, reducing the spring phytoplankton peak (Sommer *et al.*, 2012). It is becoming increasingly clear that carry-over effects from the winter may affect lake ecology throughout the year and this includes the zooplankton component of the lake ecosystem (Adrian *et al.*, 2006). The 2010/2011 late winter build-up of copepod nauplii concurrent to increasing phytoplankton biomass, kick-started the copepod population and may have contributed to the higher copepod biomass in 2011 compared to 2010. In Lake Atnsjøen, the winter survival of *C. scutifer* may vary from above 60% to as little as 6% (Halvorsen *et al.*, 2004). Such a high variation might be linked to annual variation in ice thickness and snow cover affecting light availability for phytoplankton under the ice as shown in a mountain lake (Obertegger *et al.*, 2017). Variation in winter mortality clearly has consequences for the spring and summer population of *C. scutifer* in the lake.

Seasonal lake studies of metazoan zooplankton that include the ice-covered period are rare (Larsson, 1978; Larsson *et al.*, 1978; Virro *et al.*, 2009). The average total metazoan biomass in Lake Øvre Heimsdalsvatn (southwestern Norway) for months with ice cover in 1972 (January – early June and late October to December) was approx. 14 µg DW l^{-1}, corresponding to approx. 7 µg C L^{-1}, (assuming a carbon content of 46%, Andersen and Hessen, 1991). The winter average in Lake Atnsjøen at 6.4 µg C L^{-1} was similar. The average total metazoan biomass in Øvre Heimdalvatn during the growing season in

1972 (approx. 19 µg C L^{-1}) was somewhat lower than the Lake Atnsjøen 2010 open water average (23.9 µg C L^{-1}) and only half of the 2011 open water average (39.9 µg C L^{-1}). Both lakes are oligotrophic (Kloster, 1978; Halvorsen, 2004). However, due to its higher altitude Lake Øvre Heimdalsvatn has a shorter open-water season than Lake Atnsjøen (Larsson *et al.*, 1978). The summer zooplankton biomass increases with length of the growing season in oligotrophic lakes (Weyhenmeyer *et al.*, 2013). Hence, longer growing season may explain the higher zooplankton biomass in Lake Atnsjøen compared to Lake Øvre Heimsdalsvatn.

The importance of temperature *versus* phytoplankton biomass for the different zooplankton groups was clearly different. Rotifer abundance and biomass were most strongly related to temperature, while phytoplankton biomass (at t-1) had a stronger impact on cladoceran abundance and biomass, as well as copepod biomass. This difference is likely related to the life history strategies of the three zooplankton groups. Rotifers and cladocerans mainly reproduce parthenogenetically, while copepods have obligate sexual reproduction. Moreover, rotifers have short generation times (Allan, 1976; Walz, 1995; Andersen, 1997; Gillooly, 2000), as well as lower food concentration thresholds (Stemberger and Gilbert, 1985). This life history strategy confers a strong dependency on temperature (Edmondson, 1965). In comparison, cladocerans have longer generation times and higher food concentration thresholds (Allan, 1976; Andersen, 1997). The cladoceran life history strategy is therefore more dependent on resource availability. Copepods have even longer generation times (Allan, 1976; Andersen, 1997), with a life cycle lasting one or two years in Lake Atnsjøen (Halvorsen *et al.*, 2004). Additionally, fish predation on zooplankton may be high in oligotrophic lakes such as Lake Atnsjøen (Jeppesen *et al.*, 2003). Cladocerans suffer higher mortality from fish predation than rotifers and copepods, at least in summer (Saksgård and Hesthagen, 2004). The dominating fishes in Lake Atnsjøen are arctic char (*Salvelinus alpinus*) and brown trout (*Salmo trutta*). Although both species utilize crustacean zooplankton (largely cladocerans) as food, char is the most important zooplankton predator in the lake. Char shows a strong preference for larger species such as *Daphnia* (Saksgård and Hesthagen 2004; Sandlund O.T. *et al.*, *personal communication*), but also eats some cyclopoid copepods in winter (Nilssen, 1977). Rotifers are not eaten by the fish (Saksgård and Hesthagen, 2004). The fish predation intensity in the pelagic zone in oligotrophic lakes with large char populations typically increases during the summer, peaks in mid/late summer, and declines again in September (Hindar and Jonsson, 1982). Besides resource limitation, increasing fish predation likely also reduced zooplankton biomass after the spring bloom in June.

Low light levels, ice and snow cover, and cold water contributed to a low phytoplankton biomass in Lake Atnsjøen during the early and mid-winter 2010/2011. With increasing daylength and light availability and decreasing snow cover in April, phytoplankton biomass increased towards the end of winter. A relative high under-ice phytoplankton biomass is not an uncommon phenomenon in temperate and arctic lakes, during late winter when light availability increases (Chandler, 1940; Langeland and Reinertsen, 1982; Forsström *et al.*, 2007). In fact, light is more important than temperature in limiting phytoplankton production in lakes (Winder and Sommer, 2012). The average winter phytoplankton biomass in Lake Atnsjøen was in the upper range of that observed in other ice-covered lakes (Hampton *et al.*, 2017). Except for the late winter bloom, phytoplankton availability to zooplankton was much lower during winter than during the growing season. The fraction of non-phytoplankton POC was much higher than that of phytoplankton POC, as is the case in many nutrient poor Norwegian lakes during the growing season (Hessen *et al.*, 2003a). Furthermore, non-phytoplankton POC in early winter was higher than during the growing season, which was also observed by Rautio *et al.* (2011) in an oligotrophic subarctic lake.

The current study indicated the close association between zooplankton and phytoplankton biomass, underlining the importance of phytoplankton as an important food resource for zooplankton (Galloway *et al.*, 2014). However, the phytoplankton/zooplankton ratios in summer, autumn, and winter were below zooplankton maintenance requirements (Hessen *et al.*, 2003b). In addition, the prevailing low phytoplankton biomass in the lake was below the threshold food concentrations of many species even during the spring bloom (Andersen, 1997). These findings indicate that the Lake Atnsjøen zooplankton was also dependent on other C-resources. Zooplankton may also utilize autochthonous or allochthonous derived dead POC, either directly or via DOC fueling the microbial loop (Grey *et al.*, 2001; Galloway *et al.*, 2014). The estimates of non-algal POC in Lake Atnsjøen, which include both autochthonous and allochthonous dead POC as well as the components of the microbial loop, indicate that this part of the C-pool was an important potential additional C-sources for the zooplankton. This could be especially true during early and mid-winter, when algal food is very low (Grey *et al.*, 2001; Rautio *et al.*, 2011). However, C requirements of the zooplankton also decrease at this time, due to lower temperatures and because many species enter a dormant phase during winter (Kibby, 1971; Allan, 1976). Another aspect that should be considered is omnivory, both in a strict sense and from an ontogenetic perspective. For example, some *Daphnia* species are capable of eating smaller zooplankters (Wickham *et al.*, 1993). *Cyclops* has an ontogenetic shift in feeding mode, with the smaller developmental stages being primarily herbivorous, while larger developmental stages are mainly predacious (Zaret, 1980; Santer, 1993). Hence, for species or stages capable of utilizing smaller zooplankton as food, phytoplankton concentration underestimates food availability.

The current study does not contradict the PEG-model (Sommer *et al.*, 1986; Sommer *et al.*, 2012), however, it exemplifies how the plankton dynamics in oligotrophic lakes may be affected by a changing climate (De Senerpont Domis *et al.*, 2012). Like many other ice-covered lakes, Lake Atnsjøen experiences an increase in the ice-free period due to a warmer climate. This is especially caused by a warmer late winter/early spring resulting in an earlier ice-off (Jensen unpublished results). The early ice-off and late ice-on dates in 2011 resulted in an unusually long growing season (ice-free period) of 211 days. This was 26 days longer than the average for the period 1954–2011, and 34 days longer than in 2010. During the period 1954-2011 only two years have seen a longer open water period than 2011. In comparison, 2010 had an open water period shorter than average (1954-2011), mainly due to early ice-on. A longer growing season may lead to higher phytoplankton and zooplankton abundance and biomass in temperate oligotrophic lakes (De Senerpont Domis *et al.*, 2012; Weyhenmeyer *et al.*, 2013). The early onset of the growing season and its long duration in 2011 may have contributed to the somewhat higher phytoplankton biomass and zooplankton abundance/biomass in 2011 than in 2010. For instance, in Müggelsee, Germany, the magnitude of the phytoplankton spring bloom increased with decreasing ice duration (Adrian *et al.*, 1999). Since the current study only represents two open water seasons and the winter period between, it is not possible to draw any conclusion regarding the importance of a prolonged growing season. Lower than average winter precipitation, causing reduced snowpack and potentially greater light penetration in late spring, could also have contributed to kickstart the phytoplankton production resulting in higher phytoplankton and zooplankton biomass during the open water period in 2011. It is intriguing that the difference between the two years in Lake Atnsjøen was larger for zooplankton biomass (and abundance) than for phytoplankton biomass. Phytoplankton productivity may have been higher in 2011 compared to 2010, thus potentially sustaining a higher zooplankton population that kept phytoplankton biomass low. Zooplankton may also have utilized other food sources than phytoplankton, as outlined above. Differences in fish predation regimes on zooplankton between 2010 and 2011 are less likely to explain annual differences in zooplankton biomass, as test fishing in 2010 and 2011 showed very similar fish population size (Hesthagen T. and Saksgård R., *personal communication*).

CONCLUSIONS

In conclusion, the zooplankton abundance and biomass were much lower in winter than during the open water season in oligotrophic subalpine Lake Atnsjøen, with the exception of the final winter months. During the later period snow cover and ice thickness were reduced and (presumably) light penetration increased, leading to an under-ice phytoplankton bloom and an increase in abundance of copepod nauplii. Hence, the study lends support to the view emerging during the last decade, that winter is not only an unimportant period of dormancy (Salonen *et al.*, 2009; Sommer *et al.*, 2012; Bertilsson *et al.*, 2013; Hampton *et al.*, 2015). The somewhat higher phytoplankton and zooplankton abundance and biomasses in 2011, with earlier ice-off and longer growing season compared to 2010, also hint to some of the expected changes of climate change on northern lake ecosystems.

ACKNOWLEDGMENTS

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