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ORIGINAL ARTICLE

Seasonal quantitative dynamics and ecology of pelagic rotifers in an acidified boreal lake

Svein Birger WÆRVÅGEN,[1]* Tom ANDERSEN[2]

[1]Department of Natural Sciences and Technology, Inland Norway University of Applied Sciences, Campus Hamar, 2318 Hamar;
[2]Department of Biosciences, University of Oslo, Blindernvn 31, 0371 Oslo, Norway
*Corresponding author: svein.warvagen@inn.no

ABSTRACT

Lake Gjerstadvann is a dimictic, oligotrophic, slightly acidified boreal lake in southern Norway (northwest Europe). The planktonic rotifer community of this lake was studied quantitatively during one year in order to investigate the impacts of the local environment and biotic interactions on seasonal succession and habitat selection. Pure suspension feeders (mainly *Keratella* spp., *Conochilus* spp., and *Kellicottia longispina*) together with raptorial graspers or specialised feeders (mainly *Polyarthra* spp. and *Collotheca* spp.) dominated the rotifer community over prolonged periods, whereas carnivorous/omnivorous species (mainly *Asplanchna priodonta*) were extremely uncommon. Low bicarbonate buffering capacity resulted in a distinctive seasonal oscillating pH between 5.0 and 5.6, defining a special acid-transition lake category. The pH values were highest in the productive period during summer, and lowest during ice break-up coinciding with the peak reactive aluminium concentrations of 250-300 µg L^{-1}. As in typical Norwegian boreal perch lakes, the most abundant cladoceran was *Bosmina longispina* due to perch predation on the genus *Daphnia*. Rotifer community structure was significantly related to temperature and oxygen ($P=0.001$ and $P=0.022$), illustrating the important effects of the seasonal cycle and vertical density stratification. The most significant competition indicator species were *B. longispina* and *Eudiaptomus gracilis* (both with $P=0.001$). A variance partitioning indicated that 14% of the total community composition variance could only be explained by biotic interactions, while 19% of the variance could be attributed to environmental gradients. Of the variance, 23% could not be resolved between biotic interactions and environmental gradients, while a residual of 44% was not explainable by any of the variables. Acid conditions alone cannot account for all the observed changes in the rotifer community of this lake with low humic content, since resource limitation and food competition are also important factors shaping rotifer population dynamics and the community structure.

Key words: Rotifera; autecology; food limitation; seasonal succession; boreal perch lake; acidification.

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INTRODUCTION

Pelagic rotifers in North Europe and Northern America are affected to various degrees by anthropogenic acidification processes, which include several abiotic and biotic ecosystem changes (Stenson *et al.*, 1993; Keller *et al.*, 1999; Svensson and Stenson, 2002; Vandysh, 2002; Wærvågen and Nilssen, 2003). The majority of biotic studies in the pelagial of acidified lakes during the last decades has been devoted to pelagic cladocerans, while much less effort has been addressed to pelagic copepods and rotifers. In medium and strongly acidified lakes the major planktonic rotifer species are *Kellicottia longispina*, *Polyarthra* spp., *Keratella taurocephala*, and some more rare species are *Keratella cochlearis*, *Collotheca* spp., *Ascomorpha* spp., and *Keratella serrulata* (Skadovsky, 1926, 1933; Yan and Geiling, 1985; Bērziņš and Pejler, 1987; Morling and Pejler, 1990; Siegfried, 1991; Svensson and Stenson, 2002; Wærvågen and Nilssen, 2003). Most studies focus on non-acidic lakes (Ruttner, 1930; Nauwerck, 1963; Larsson, 1971, 1978; Zimmermann, 1974; Makarewicz and Likens, 1975; Armengol-Díaz *et al.*, 1993; Armengol *et al.*, 1998; Bartumeus and Catalan, 2008; Obertegger *et al.*, 2008), while less is known about acidic lakes. Few studies on rotifer community alterations during acidification are published (Roff and Kwiatkowski, 1977; Hobæk and Raddum, 1980; Mac Isaac *et al.*, 1987; Frost *et al.*, 1998), whereas quantitative seasonal and vertical distribution during acidification is less well known.

Individual species of rotifers display different embryonic development times based on food threshold concentrations influencing interspecific competition (Herzig, 1983; Stemberger and Gilbert, 1985, 1987a, 1987b; Walz, 1995), and consequently affect community species composition during acidification (Wærvågen and Nilssen, 2003). Rotifers often have higher threshold food concentrations than many filter-feeding cladocerans (Duncan, 1989), which makes them inferior competitors at lower food abundance levels. Therefore, when cladocerans dominate, raptorial rotifers feed selectively on larger food items (Obertegger *et al.*, 2011). Rotifer community alternations are often caused by changes in ecosystem productivity driven by eutrophication or acidification (Duncan, 1989; Walz, 1995; Stelzer, 2005). Rotifers are usually more productive under eutrophic conditions whereas food limitation is more probable under oligotrophic conditions (Walz, 1995). Nutrient-rich environments therefore support much higher rotifer abundance, characterized by rotifer species with smaller egg sizes and faster development (Herzig, 1983; Orcutt and Pace, 1984; Walz, 1993). Most rotifers produce resting eggs with typical egg-bank characteristics (Nipkow, 1961), and are known for their rapid re-appearance after water chemistry recovery following prolonged acidification (Raddum *et al.*, 1986; Svensson and Stenson, 2002; Wærvågen and Nilssen, 2003).

It is crucial for the understanding of anthropogenic lake acidification and possible trajectories of lake recovery to distinguish between several different categories of acidified lakes (Nilssen and Wærvågen, 2002a; Wærvågen and Nilssen, 2003, 2011), especially chronically acidic lakes and so-called acid-transition lakes (Henriksen, 1979, 1980). In chronically acidic lakes, the bicarbonate buffering capacity is inoperative and pH has stabilised in the low range, usually at 4.4-4.8 (Nilssen, 1982a). Furthermore, all fish species have been eliminated and the new top lake predators are different species of invertebrates, especially pelagic corixids and notonectids (Hemiptera), chaoborids (Diptera), and water beetles (Coleoptera). Acid-transition lakes, including categories between slightly affected and chronically acidified, characterise localities in which the residual bicarbonate buffering capacities are negatively affected with strong pH fluctuations usually between 5.0 and 6.0. In the boreal part of Fennoscandia such lakes were extremely common during the peak acidification period (Henriksen, 1979, 1980), and many organisms, including most fish species, were negatively affected or disappeared altogether (Nyberg *et al.*, 1995). A typical acid-transition lake is dominated by aging fish populations (in southern Norway often Eurasian perch, aged 5-7 years on average), while young stages are missing or produce strong cohorts only in years with favourable spring climatic conditions (Kleiven *et al.,* 1990; Linløkken *et al.,* 1991). In acidic, fish-deficient or fishless ecosystems, competition and invertebrate predation are probably of decisive importance in rotifer ecology (Eriksson *et al.*, 1980; Nyman *et al.*, 1985; Yan *et al.*, 1991). The susceptibility of rotifers to invertebrate predators is fairly well documented in non-acidic lakes, however, except for the voracious chaoborid larvae, such knowledge is sparse for acidified lakes (Nyberg, 1984; Yan *et al.*, 1991).

Aquatic ecosystems have been studied in this region of southern Norway since the early 1970s, including both the anthropogenic acidification of aquatic systems and their subsequent recovery during recent years (Nilssen, 1980, 1984; Nilssen and Sandøy, 1990; Nilssen and Wærvågen, 2002a, 2002b, 2003; Wærvågen and Nilssen, 2003, 2010, 2011). The majority of lakes in this area were, at the time of the present study (1980-81), still strongly affected by acid precipitation from a variety of sources in Europe (Drabløs and Tollan, 1980; Nilssen, 1980, 1982a, 1982b). The investigated boreal Lake Gjerstadvann (Fig. 1) belonged to a typical acid-transition lake category with pH fluctuating between 5.0 and 5.6. The study was part of a research programme in southern Norway (Fig. 1), which comprised lakes with strongly contrasting chemistry and biology. The aim of the present study was to investigate the seasonal and vertical quantitative distribution of pelagic rotifers in order to relate the rotifer community to abiotic and major biotic factors in a typical boreal acidic-transition lake dominated by Eurasian perch. This may improve our general knowledge concerning the process of acidification and ecosystem structures of anthropogenic acidified lakes and their subsequent recovery, including the ecology, life histories and habitat dynamics of pelagic rotifers in northern boreal lakes.

METHODS

Study area

Samples from Lake Gjerstadvann were collected from early February 1980 to mid-March 1981. The lake is situated 31 m above sea level (asl) (58° 53´ N, 9° 02´ E, WGS84 datum) in a region in southern Norway characterised by a mixture of continental and oceanic climates (Fig. 1 a,b). Lake Gjerstadvann is dimictic with bottom temperatures slightly above 4°C in the ice-free period and with a relatively deep mixed layer because of its considerable water through-flow (Figs. 1d and 2). The seasonal changes in water chemistry are mainly due to spring snow-melt and seasonal rainfalls in summer and autumn (Figs. 1d and 2), which are further described in Wærvågen and Nilssen (2010). The lake is situated below the postglacial marine limit (*i.e.* about 100 m asl in this area), but most of the catchment area of the lake is situated above the postglacial marine limit, thus draining more acidified water, measured with mean pH 4.7 in 1980 (Hindar *et al.*, 1984). Lake Gjerstadvann had a mean pH of 5.2 in 1980-81, was oligotrophic (based on total phosphorus; see Results), and oligo- to mesohumic (based on the water colour in mg Pt L^{-1}; see Fig. 2). Mean reactive aluminium (RAl) concentrations were 200-250 µg L^{-1}, and the harmful labile fraction (lAl) at these pH values was about 40-70% of the RAl values (Lydersen, 1998).

Sampling and data collection

Chemical and biological samples were taken simultaneously, approximately at mid-day, every fortnight during the ice-free period, and circa monthly during the rest of the year. Chemical samples were collected using a Ruttner sampler at a fixed station at the deepest point (27 m) of the lake (Fig. 1c), at depths shown in Tab. 1. Water colour expressed as mg Pt L^{-1} was measured on a Lovibond comparator, primarily representing the amount of aquatic humic substances (Fig. 2). Total organic carbon (TOC) content of the water is closely related to Pt (mg L^{-1}), and usually TOC corresponds to one-tenth of the Pt-value in this North European Fennoscandian region (Degerman, 1987). Chemical analyses were performed according to standard analytical methods, see further details in Wærvågen and Nilssen (2010).

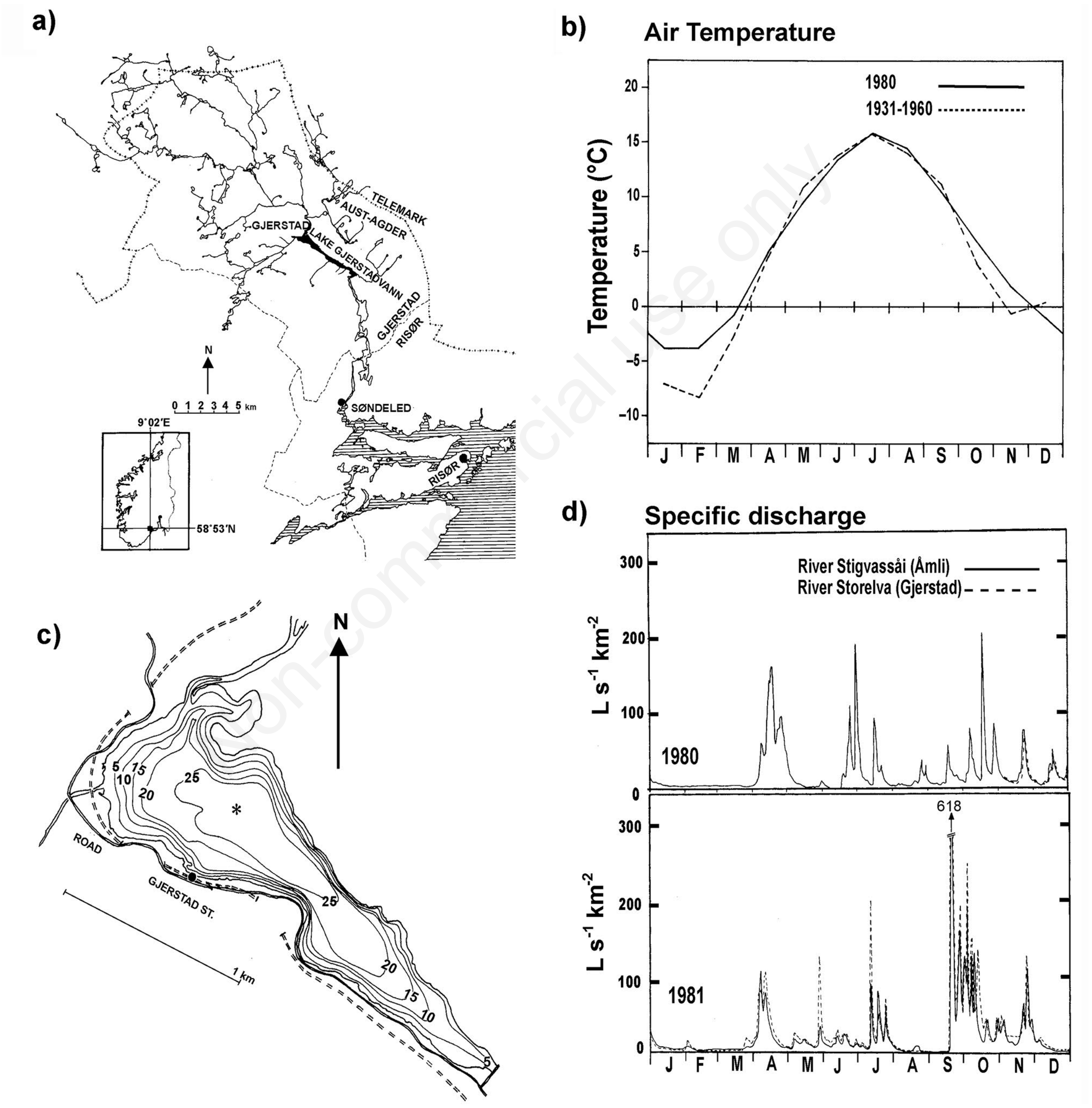

Fig. 1. Lake Gjerstadvann and its catchment area. a) Geographical position in southern Norway; b) catchment area climate (as mean monthly air temperature); c) depth map with sampling station (*); d) streamflow as specific discharge (L s^{-1} km^{-2}) of the dominating inlet River Storelva (---------, no available data before November 1980) and a neighbouring, continuously monitored River Stigvassåi (———, used as a proxy for River Storelva in 1980).

Duplicate quantitative zooplankton samples were collected in Lake Gjerstadvann using a 15 litre Patalas/Schindler device (Schindler, 1969), with an attached net with mesh size 45 µm. The volume proportions (Tab. 1) were calculated from a volumetric curve used to convert the total and mean population abundance at different depths of all species to individuals per m^3 (Bottrell *et al.*, 1976). Most metazoan zooplankton (Tab. 2) were identified to species level and counted (Rylov, 1963; Flößner, 1972; Ruttner-Kolisko, 1972; Einsle, 1975; Kiefer, 1978). Preserved with Lugol's solution, identification was primarily based on morphological characteristics included the lorica, foot, and anterior projections (Ruttner-Kolisko, 1972; Koste and Voigt, 1978; Pontin,

Tab. 1. Sampling depths of chemical and quantitative zooplankton samples in Lake Gjerstadvann 1980/81. The representative layers given in % and volume proportions.

Sample depths (m)	Representative layer (m)	Proportion (%)	Of total volume (m^3 x 10^6)
1	0-2	13	1.83
3	2-4	12	1.68
5	4-6	10	1.52
7	6-8	10	1.42
10	9-12	17	2.54
15	12-18	22	3.15
20	18-22	10	1.52
25	22-27	6	0.88
	Mean depth: 15.3 m	Max. depth: z_m = 27 m	Total volume: 14.54 x 10^6 m^3

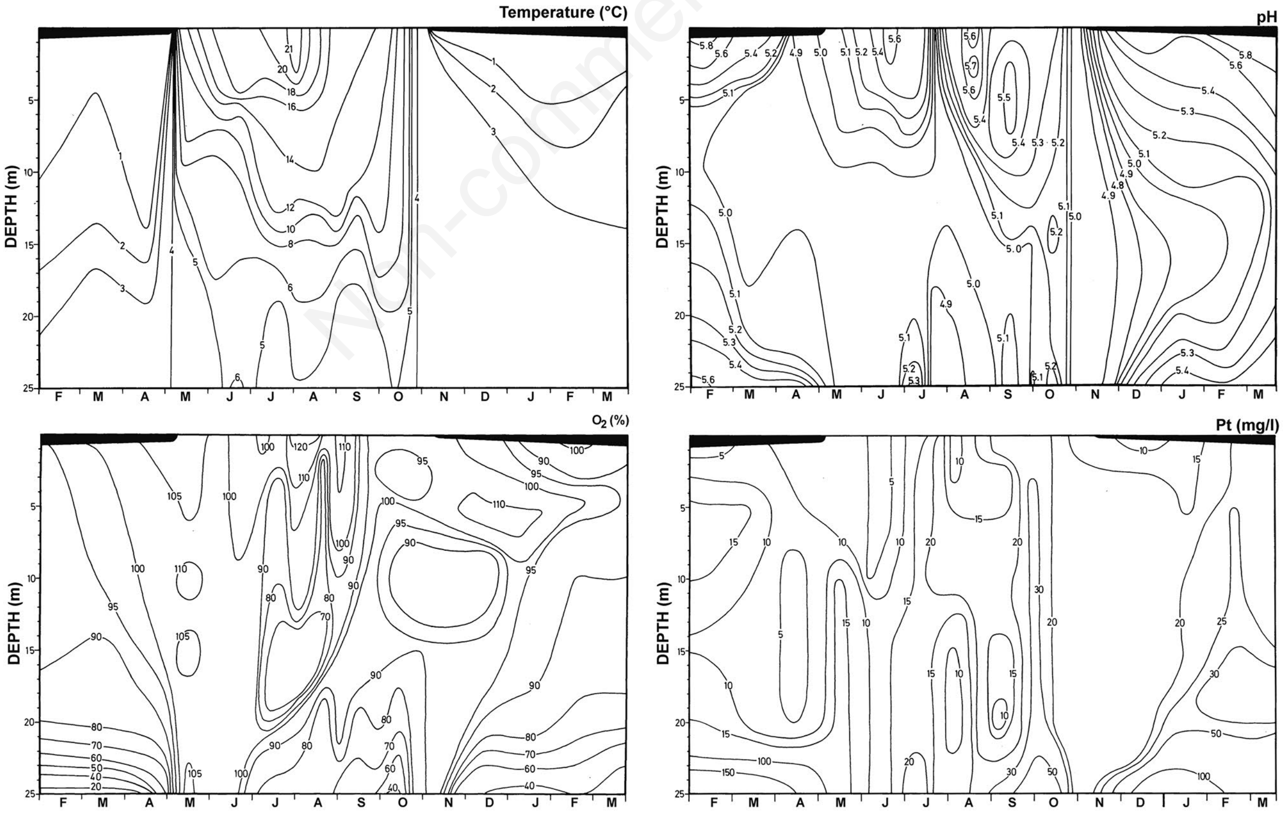

Fig. 2. Isoplots for temperature (°C), pH, oxygen (%) and water colour Pt (mg L^{-1}) in Lake Gjerstadvann 1980-1981. Ice covers are shown in real dimensions as black bars here and in similar figures.

1978; Nogrady *et al.*, 1993). Due to Lugol's-induced retraction, especially within the genera *Conochilus*, *Synchaeta*, *Polyarthra* and *Ascomorpha*, body size measurements were, in addition, performed under the microscope. Rotifers can be categorized as suspension feeders (*Keratella* spp., *K. longispina*, *Conochilus* spp.), raptorial graspers or specialised feeders (*Polyarthra* spp., *Synchata* spp., *Ascomorpha* spp., *Collotheca* spp.), and carnivorous/omnivorous species (*Asplanchna* spp., *Ploesoma* spp.) (Nogrady *et al.*, 1993; Walz, 1995, 1997; Obertegger *et al.*, 2011). Cladocerans, copepods, and fish species present in Lake Gjerstadvann are presented in Tab. 2.

Statistical analyses

Rotifer community structure was investigated by nonmetric multidimensional scaling ordination (NMDS; Minchin, 1987) using a Bray-Curtis dissimilarity measure calculated from fourth root-transformed rotifer abundances and the metaMDS function in the vegan package (Oksanen *et al.*, 2013). We excluded one sample, where no rotifers were detected, from the analysis. We also excluded two rotifer species (*Asplanchna priodonta* and *Keratella ticinensis*) with low occurrence (less than 20% of the samples). Relationships between rotifer community ordination axes and explanatory variables were investigated by permutation tests using the envfit function of the vegan package. The first two axes of a principal component analysis (PCA) of scaled and centered environmental variables explained 58% of the total variance. Based on the PCA biplot (Fig. 3) we chose temperature, oxygen, pH, and reactive aluminum (RAl) to represent the major environmental gradients. The first two represented the major seasonal and vertical gradients in the lake, while the latter two served as acidification indicators. We rep-

Tab. 2. List of all metazoan species collected in the pelagial of Lake Gjerstadvann in 1980/81.

Rotifera		**Cladocera**	
Conochilus unicornis Rousselet, 1892	XXX	*Bosmina longispina* Leydig, 1860	XXX
Conochilus hippocrepis (Schrank, 1803)	R	*Holopedium gibberum* Zaddach, 1855	XX
Polyarthra minor Voigt, 1904	XXX	*Diaphanosoma brachyurum* (Liéven, 1848)	XXXX
Polyarthra vulgaris Carlin, 1943	XX	*Polyphemus pediculus* (Linnaeus, 1761)	X
Polyarthra dolichoptera Idelson, 1925	R	*Bythotrepes longimanus* Leydig, 1860	X
Kellicottia longispina (Kellicott, 1879)	XXX	*Ceriodaphnia quadrangula* (O.F. Müller, 1776)	X
Keratella hiemalis Carlin, 1943	XX	*Leptodora kindti* (Focke, 1844)	X
Keratella cochlearis (Gosse, 1851)	XX	Chydoridae spp. Stebbing, 1902	X
Keratella serrulata (Ehrenberg, 1838)	X	*Scapholeberis mucronata* (O.F. Müller, 1776)	R
Keratella ticinensis (Callerrio, 1920)	X	*Sida crystallina* (O.F. Müller, 1776)	R
Keratella testudo (Ehrenberg, 1832)	R	*Daphnia lacustris* G.O. Sars, 1862	R
Collotheca libera (Zacharias, 1894)	X		
Collotheca liepetterseni Bērziņš, 1951	X		
Ascomorpha ecaudis Perty, 1850	X	**Insecta**	
Lecane spp. Nitzsch, 1827	X	*Chaoborus flavicans* (Meigen, 1830)	X
Asplanchna priodonta Gosse, 1850	X		
Synchaeta gr. *tremula-oblonga*	X		
Euchlanis dilatata Ehrenberg, 1830	R	**Copepoda**	
Trichocerca spp. Lamarck, 1801	R	*Eudiaptomus gracilis* (G.O. Sars, 1863)	XXX
Gastropus stylifer Imhof, 1891	R	*Heterocope saliens* (Lilljeborg, 1863)	R
Gastropus minor (Rousselet, 1892)	R		
		Cyclops scutifer G.O. Sars, 1863	XXX
		Mesocyclops leuckarti (Claus, 1857)	XX
Fish		*Thermocyclops oithonoides* (G.O. Sars, 1863)	X
Perca fluviatilis Linnaeus, 1758	XXX	*Cyclops abyssorum* G.O. Sars, 1863	R
Salmo trutta Linnaeus, 1758	XX	*Diacyclops nanus* (G.O. Sars, 1863)	R
Coregonus lavaretus (Linnaeus, 1758)	X	*Diacyclops bicuspidatus* (Claus, 1857)	R
Salvelinus alpinus (Linnaeus, 1758)	R	*Megacyclops gigas* (Claus, 1857)	R

Relative abundance within each group of animals: XXX, dominating; XX, frequent; X, few specimens; R, rare.

resented a second group of biotic explanatory variables as the fourth root-transformed abundances of two potential predators, *Chaoborus flavicans* (see *C. flavicans* in Fig. 4) and "Cyclopoids" (the sum of Cop IV-adult stages of all cyclopoid copepods) (Fig. 4 and Tab. 2). Furthermore, we included two potential competitors, *Bosmina longispina* and *Eudiaptomus gracilis* (as the sum of all its stages). Finally, we used the varpart function of vegan (Borcard *et al.*, 1992) to identify fractions of total redundancy analysis variance that could be explained uniquely by either environmental gradients or biotic interactions.

RESULTS

The annual mean pH in Lake Gjerstadvann was 5.2, but dropped slightly below this value during the spring ice breakup and autumn and summer rain periods (Figs. 1d and 2). The epilimnetic oxygen content fluctuated around 100 percent during most of the year, with an oxygen deficit close to the lake bottom during periods of stagnation (Fig. 2), most probably due to accumulation of allochthonous organic material. The epilimnetic colour of the lake water was 10-30 mg Pt L^{-1} (≈1-3 mg TOC L^{-1}), and increased considerably (≈10-15 mg TOC L^{-1}) above the bottom sediments (Fig. 2). The close correlation between Pt and iron (Fe) in Fig. 3 indicates Fe-colour contribution to TOC under oxygen deficit close to the bottom. In 1980-81, the following mean concentrations were recorded: ca. 2.0 mg L^{-1} Ca^{2+}, 8 µg L^{-1} total phosphorus (TP), 6 mg L^{-1} sulphate, 2.2 mg L^{-1} chloride, and 230 µg L^{-1} reactive aluminium (RAl); specific conductivity, expressed as K_{25}, was 2.7 mS m^{-1} and the ANC value was -6.7 µekv L^{-1}.

The converged NMDS ordination had relatively high

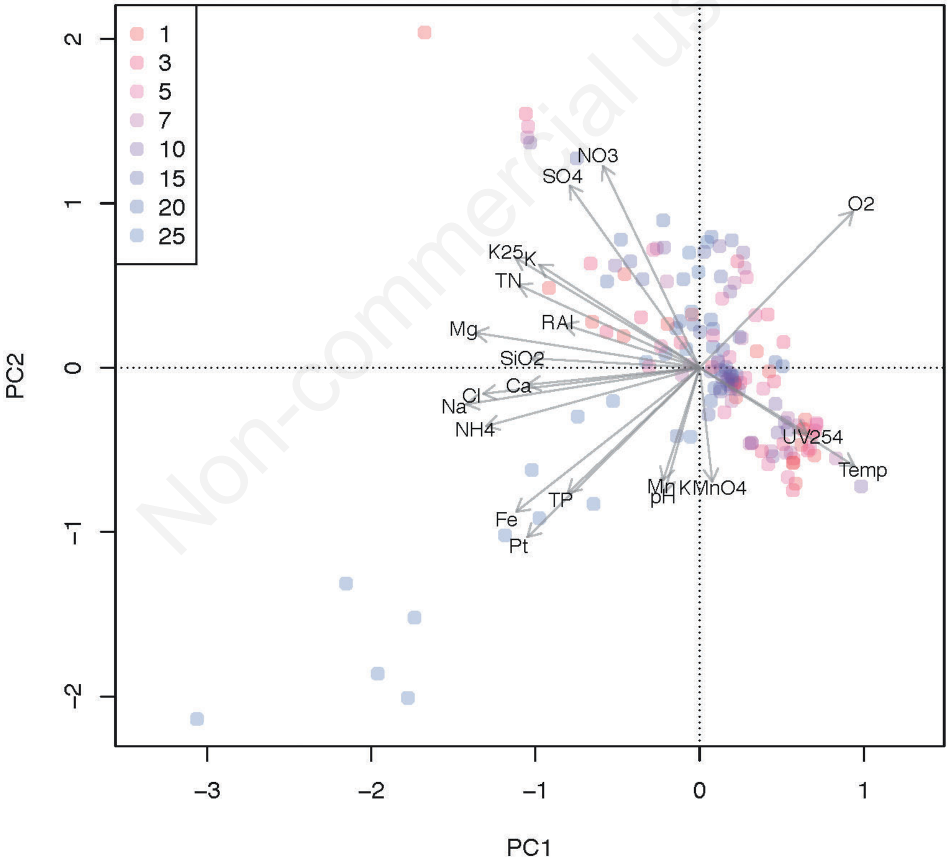

Fig. 3. Principal Components biplot of physical and chemical water quality parameters, based on variables that have been centred and scaled to zero means and unit standard deviations. Arrows represent loadings of the different parameters while dots represent scores of individual samples, colour coded according to sample depth (see top left in this Fig. and Tab. 1). PC1 and PC2 represented 39% and 19% of the total variance, respectively. Key to environmental parameters: Temp (temperature), O2 (% oxygen), pH, K25 (conductivity as K_{25}), RAl (reactive aluminium), TN and TP (total N and P), Fe and Mn (total Fe and Mn), SiO2 (SiO_2), UV254 (organic matter as UV-absorption at 254 nm), KMnO4 (organic matter determined by oxidation with $KMnO_4$), Pt (water colour expressed as mg Pt L^{-1}, closely related to TOC) and finally the ions Ca (Ca^{2+}), Mg (Mg^{2+}), Na (Na^+), K (K^+), SO4 (SO_4^{2-}), Cl (Cl^-), NO3 (NO_3^-), NH4 (NH_4^+).

stress (0.22) for 2 axes. Including 3 or 4 axes reduced the stress to 0.15 and 0.10, respectively, but Procrustes tests showed that all solutions were very similar in the first 2 axes (vegan protest function, all with P=0.001 on 999 permutations). The NMDS ordination diagram (Fig. 4) appears to capture the seasonal cycle with *Collotheca liepetterseni* and *Keratella hiemalis* as winter species, being replaced by *K. longispina*, *Polyarthra* spp., *Conochilus unicornis* and *Lecane* spp. in summer (June-August). *Ascomorpha ecaudis* and *Synchaeta* gr. *tremula-oblonga* have higher abundances in spring and late summer/autumn, while *K. cochlearis* is characteristic of the autumn/winter transition. The least common species included in the analysis, *K. serrulata* seemed to have no distinct environmental or seasonal preferences. The explanatory variables fitted to the ordination are represented by grey arrows in Fig. 4. Among the environmental gradient indicators there were significant effects of temperature and oxygen (P=0.001 and P=0.022), but not of the acidification indicators (pH and RAl: P=0.214 and P=0.156, respectively). Among the biotic variables, none of the predation indicators were significant (P=0.410 and P=0.493 for *C. flavicans* and "Cyclopoids", respectively), while both the competition indicators *B. longispina* and *E. gracilis* were highly significant (both with P=0.001). Temperature, which had the highest correlation to the ordination axes among the environmental variables, was mainly associated with the first NMDS axis, while oxygen had stronger associations with the second NMDS axis. The highly significant competition indicators (*B. longispina* and *E. gracilis*) were also mainly associated with first NMDS axis. A variance partitioning sensu Borcard *et al.* (1992) indicated that biotic interactions could explain 14% of the total community variance uniquely, while 19% of the variance could be attributed to environ-

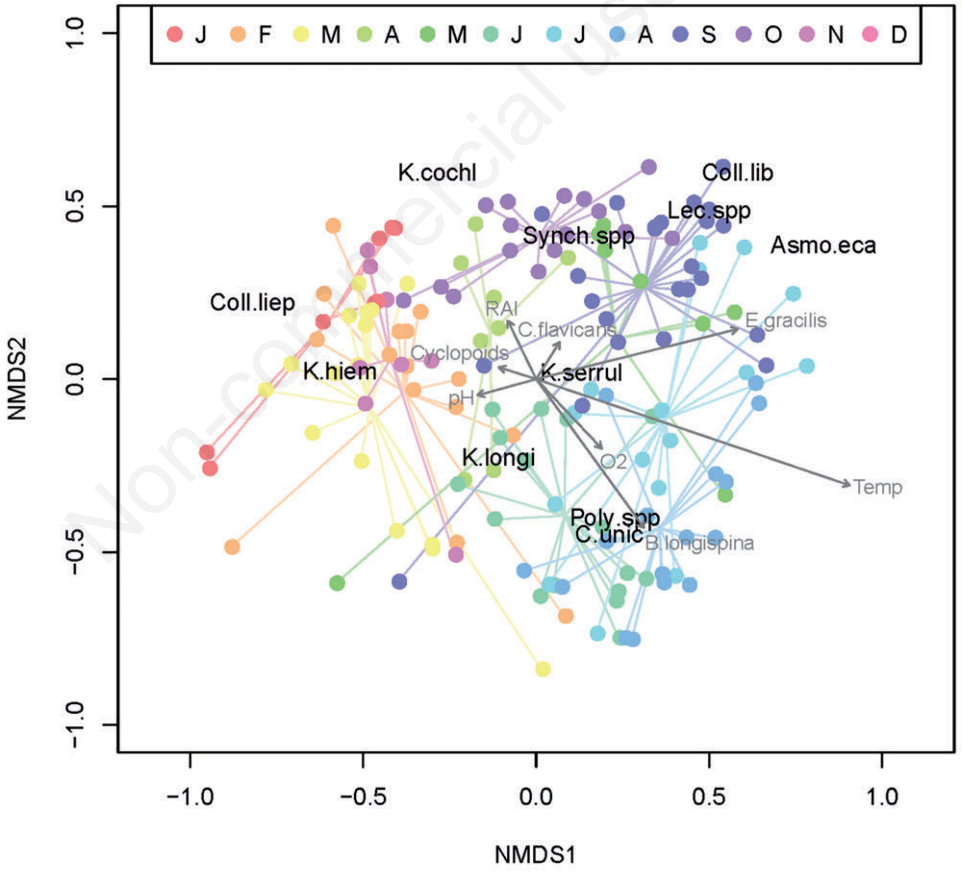

Fig. 4. NMDS ordination diagram based on Bray-Curtis dissimilarity of fourth root-transformed rotifer abundances, showing species loadings using the abbreviations below and with fitted environmental gradients and biotic interactions indicated by grey arrows. Sample scores are colour coded by month and indicated by thin lines from individual score points to the monthly centroid. The potential predators shown as *C. flavicans* (larvae) and Cyclopoids (see Methods), and finally the two potential competitors *E. gracilis* and *B. longispina*. Key to rotifer species: C.unic (*Conochilus unicornis*), Poly.spp (*Polyarthra* spp.), K.longi (*Kellicottia longispina*), K.hiem (*Keratella hiemalis*), K.cochl (*Keratella cochlearis*), K.serrul (*Keratella serrulata*), Coll.liep (*Collotheca liepetterseni*), Coll.lib (*Collotheca libera*), Asmo.eca (*Ascomorpha ecaudis*), Lec.spp (*Lecane* spp.), Synch.spp (*Synchaeta* gr. *tremula-oblonga*).

mental gradients. Twenty-three percent of the variance could not be resolved between biotic interactions and environmental gradients, while a residual of 44% could not be explained by any of the variables.

The majority of the *Conochilus* population in Lake Gjerstadvann was identified as *C. unicornis*, with some very few *Conochilus hippocrepis* specimens in addition. The colonial *C. unicornis* was most abundant in the upper water masses during summer (slightly above 100 ind. L^{-1}), but was also present under ice cover (Fig. 5a). The other species, *C. hippocrepis* was recorded in small numbers at all depths in the autumn overturn, but was not found during the spring overturn (Fig. 5a). *Polyarthra* spp. also displayed the largest population abundance during the ice-free period (close to 50 ind. L^{-1}), and much lower during winter (Fig. 5b). The most abundant species were *Polyarthra minor* and *Polyarthra vulgaris*, whereas *Polyarthra dolichoptera* was recorded in small numbers in the upper water masses during late autumn/early winter. The individual *Polyarthra* species relative to seasonal and vertical abundance are indicated in Fig. 5b, where *P. minor* was the predominant summer species and *P. vulgaris* was prevalent during the rest of the year.

The only typical perennial species recorded was *K. longispina*, showing distribution at all depths (Fig. 6a). Mean abundance of this species was lowest during winter with about 2-4 ind. L^{-1}, and it displayed two population peaks during early summer and early autumn at 8 and 10 ind. L^{-1}, respectively (Fig. 6a). The highest abundance approached 50 ind. L^{-1} in summer epilimnion and close to metalimnion during early autumn. Egg production took place at most water depths during the ice-free period, and at deeper water layers during the period with ice cover (Fig. 6a).

The typical cold-water species, *Keratella hiemalis*, displayed autumn and winter population peaks (Fig. 6b). Its abundance peaked close to the sediment with maximum mean abundance of about 1 ind. L^{-1} and with an absolute maximum of 20 ind. L^{-1} during February 1980. *Keratella hiemalis* carried eggs at depths close to the sediment surface during most of the year. *Keratella cochlearis* had relatively low abundance in Lake Gjerstadvann, with a maximum mean slightly above 1 ind. L^{-1} (Fig. 6c). It displayed population peaks in the deeper parts of the lake later than the periods of maximum abundance for most other rotifer species. It also produced eggs in that period of the year, whereas winter reproduction was almost absent.

Collotheca libera occurred in all water masses in a very restricted period during autumn (Fig. 6d), with a mean abundance of about 3 ind. L^{-1}, whereas *C. liepetterseni* showed maximum abundance during late winter and spring (Fig. 6d). *Ascomorpha ecaudis* (Fig. 6e) and the genus *Lecane* spp. (Fig. 6f) both showed three separate peaks during the ice-free period, with maximum mean abundance of 0.2 and 0.6 ind. L^{-1}, respectively. The *Lecane* spp. were identified as *Lecane mira*, *L. bulla*, *L. lunaris*, *L. scutata* and *L. closterocerca.*

Some of the rotifer species with least abundance are summarised in Fig. 7. *Keratella serrulata* was nearly perennial while *K. ticinensis* showed autumn and winter population peaks, both were recorded close to the sediment surface. Population maxima for *Synchaeta* gr. *tremula-oblonga* occurred in summer and winter/spring, but also with minor perennial presence. Population numbers of the carnivorous/omnivorous species *A. priodonta* peaked in a restricted period during autumn with a mean abundance of about 0.3 ind. L^{-1}. The most abundant rotifer species in Lake Gjerstadvann are shown together with major ecological factors such as temperature and food; algae (usually well below 200 mm^3 m^{-3}) and organic matter were calculated as TOC in mg L^{-1} (Fig. 8).

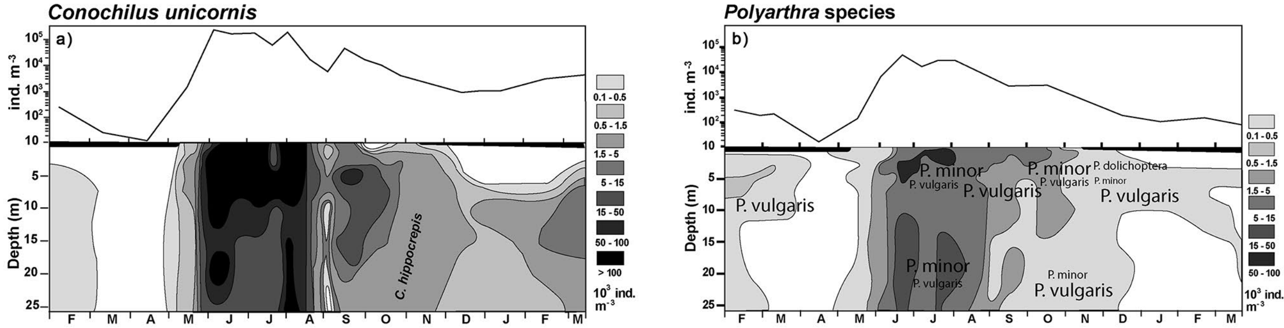

Fig. 5. Population abundance (logaritmic scale) and vertical distribution of the two most abundant rotifer species in Lake Gjerstadvann during 1980/1981. a) *Conochilus unicornis* and some few specimens of *Conochilus hippocrepis* recorded at all depths in the autumn overturn (marked in the graph); b) *Polyarthra* spp., where *Polyarthra vulgaris* was the most abundant species during late summer epilimnion, early autumn, and the whole winter, whereas *Polyarthra minor* dominates most of the summer season. *Polyarthra dolichoptera* was recorded in small numbers in the upper water masses during late autumn/early winter. The font sizes indicate the individual species abundance.

DISCUSSION

Lake Gjerstadvann forms part of an investigated region of small lakes with a variety of pelagic fish, invertebrate predation and acidification (Nilssen, 1980, 1984; Fjerdingstad and Nilssen, 1982). Many are oligotrophic perch-lakes (Demmo, 1985; Næss, 1985), such as Lake Gjerstadvann (Linløkken, 1985, 1988), but also meso- and eutrophic lakes with low fish predation dominated by large-sized *Daphnia* spp. (Larsen, 1982; Nilssen and Wærvågen, 2002a; Wærvågen and Nilssen, 2003). A small group of strongly acidified, fishless lakes have communities dominated by pelagic rotifers during the whole year (Sandøy, 1984), probably a consequence of intensive predation of *Chaoborus* spp. larvae on crustaceans (Nyberg, 1984). Rotifers are normally controlled by a combination of factors: the physiological relationship to

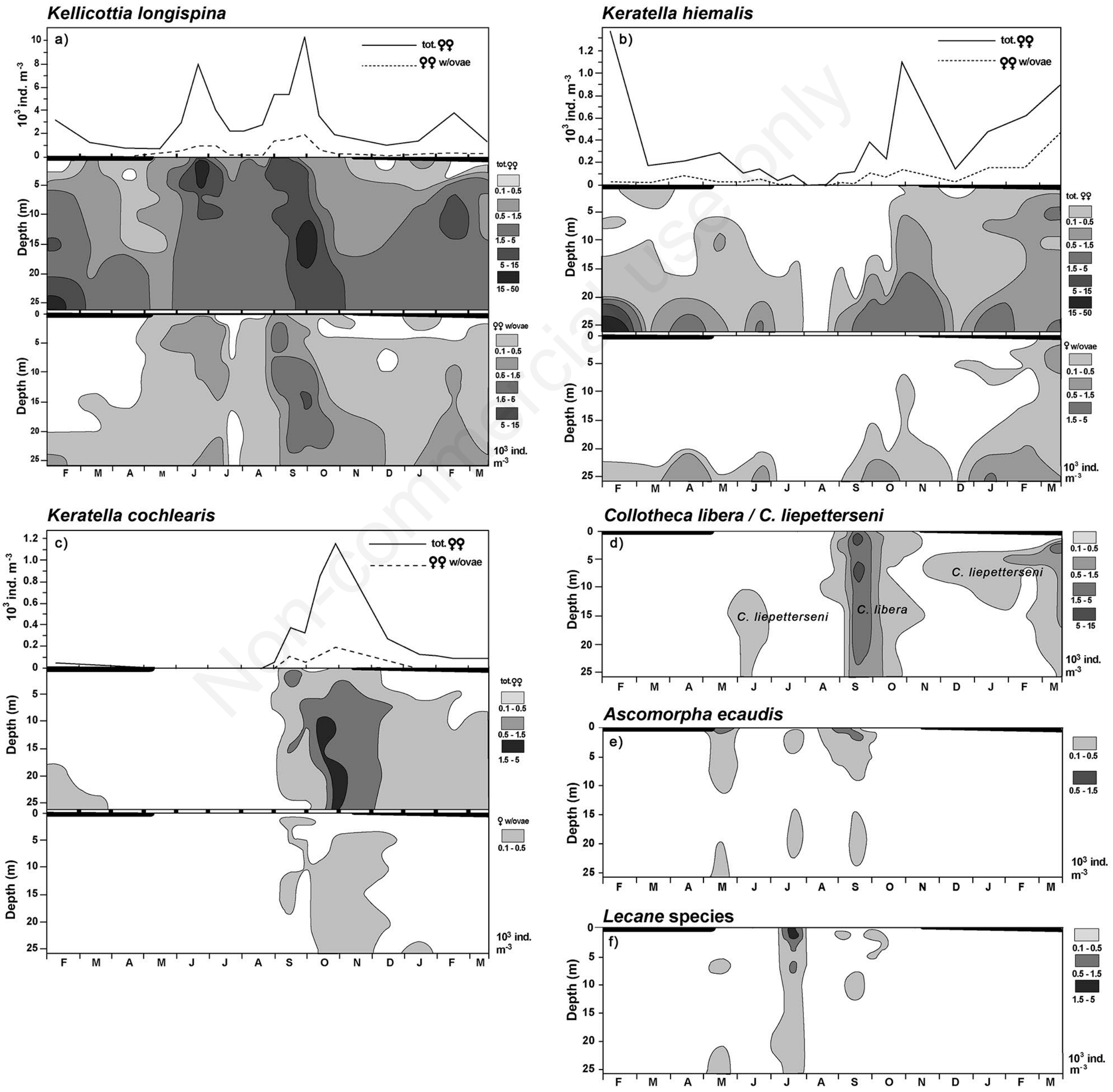

Fig. 6. Population abundance and vertical distribution of the medium abundant rotifer species in Lake Gjerstadvann during 1980/1981. a) *Kellicottia longispina*; b) *Keratella hiemalis*; c) *Keratella cochlearis*; d) *Collotheca libera* and *C. liepetterseni*; e) *Ascomorpha ecaudis*; f) *Lecane* species (see text for the different *Lecane* spp.).

their ambient environment, available food (bottom-up), invertebrate and vertebrate predation (top-down), and interspecific competition with cladocerans (especially large-sized *Daphnia* spp.), herbivorous stages of copepods (such as *E. gracilis*), as well as between rotifer species (Herzig, 1987; Gonzalez and Frost, 1992; Arndt, 1993; Kirk, 1997a, 1997b; Brandl, 2005; Sarma *et al.*, 2005).

Rotifers are commonly sub-divided into assemblages and species groups related to their quantitative and vertical distribution, where season, temperature and oxygen are important factors (Carlin, 1943; Larsson, 1971; Zimmermann, 1974; Elliott, 1977; Hofmann, 1987; Mikschi, 1989). Usually, perennial epilimnetic forms are considered eurytherms, while perennial hypolimnetic forms and summer-surface forms are mainly viewed as cold-stenotherms and warm-stenotherms, respectively (Larsson, 1971). The above classifications are often helpful, but seasonal and vertical distributions of rotifers may also be strongly influenced by hatching events in the benthic egg-bank (Nipkow, 1961; Sandøy, 1984; Herzig, 1987), as indicated by *e.g. Ascomorpha*, *Synchaeta*, *Collotheca* and *Asplanchna* in the present study. Thus, the same species can show contrasting seasonal and vertical distributions between neighbouring lakes, and even between years in the same lake (Elliott, 1977; Larsen, 1982; Synnes, 1982; Sandøy, 1984; Herzig, 1987). As in many other studies, we found the majority of *K. cochlearis* in the deeper lake regions (Demmo, 1985; Næss, 1985; Hofmann, 1987). Further, we found *K. hiemalis* and *P. dolichoptera* to be cold-water species, the latter also having been thusly characterised by Bērziņš (1976). Stenson (1983) found that *P. vulgaris* replaced *P. dolichoptera* following an interplay of available food when fish were eliminated from the system. In the oxygen-depleted zone close to the sediments of Lake Gjerstadvann, a zone which often contains high abundance of detritus-associated bacteria (Hessen, 1998), we found high abundances of *Conochilus*, *Polyarthra*, and most *Keratella* species.

Rotifer species response to physiological factors

Lake Gjerstadvann was a typical acid-transition lake with low pH and high concentration of toxic aluminium species especially during spring, but with pH increasing to above 5.5 in the upper water masses during summer periods with less acid rain. We found no significant effects of the acidification indicators pH and RAl on the total rotifer community, even though some individual species may be affected. Lake Gjerstadvann was oligo- to meso-humic, which may be a possible reason for the lack of such acidification response, since humus is known to de-

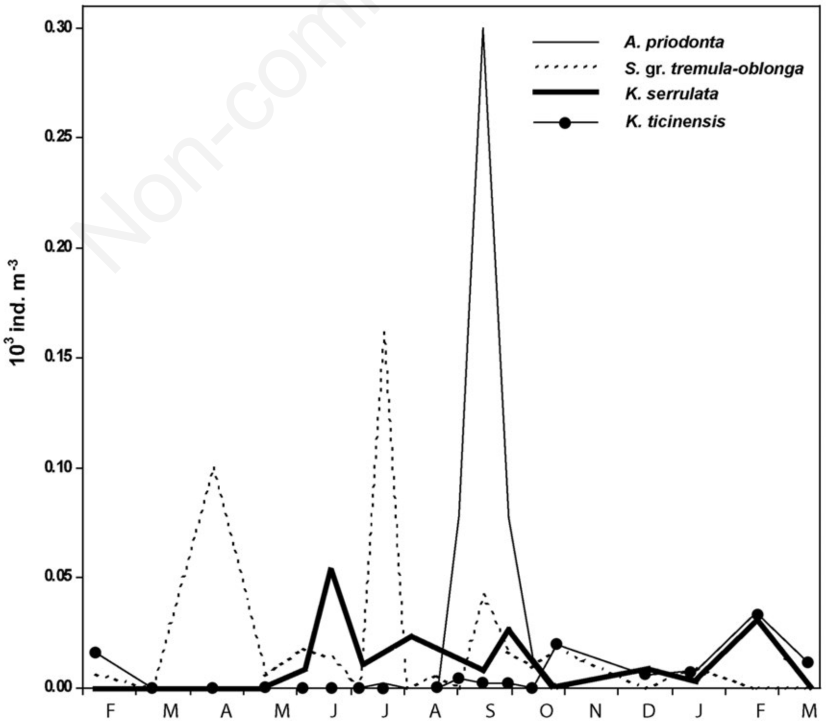

Fig. 7. Population abundance of the less abundant species: *Asplanchna priodonta, Synchaeta* gr. *tremula-oblonga*, *Keratella serrulata* and *Keratella ticinensis* in Lake Gjerstadvann during 1980/1981.

toxify poisonous heavy metals and Al in acidic lakes (Degerman, 1987; Lydersen, 1998). The strong relationship between rotifer community ordination axes and temperature and oxygen illustrates the important effects of seasons and vertical stratification. Rotifer assemblages in Lake Gjerstadvann were similar to communities of other acid-transition lakes in southern Norway (Hobæk and Raddum, 1980; Wærvågen and Nilssen, 2003), with no or few carnivorous/omnivorous species of rotifers such as *A. priodonta* and *Ploesoma hudsoni.* Correspondingly, no omnivorous species of rotifers were found in the strongly acidified Lake Gårdsjön in Sweden, but were observed in larger numbers following aquatic recovery (Svensson and Stenson, 2002). Few studies, mostly *in situ*, have been devoted to the physiological tolerance of rotifers against changes in water chemistry (Havens and De Costa, 1988; Havens and Heath, 1989; Keller *et al.*, 1992), so many questions are still to be answered.

Conochilus unicornis was the most abundant rotifer species in Lake Gjerstadvann. The species is usually absent in chronically acidified lakes (Almer *et al.*, 1974; Holopainen, 1992; Wærvågen and Nilssen, 2003), and rarely observed in high abundance below a pH of 5.0-5.2 in other acidic regions (Roff and Kwiatkowski, 1977; Havens and De Costa, 1988; Marmorek and Korman, 1993). *Conochilus hippocrepis* was a minor species in Lake Gjerstadvann, but was abundant in many other acid-transition lakes with pH below 5.0-5.2 in this region (Nilssen and Wærvågen, 2001). The two closely related species probably display slightly contrasting relationships to their ambient environment, and may serve as a good niche differentiation indicator genus (Wærvågen and

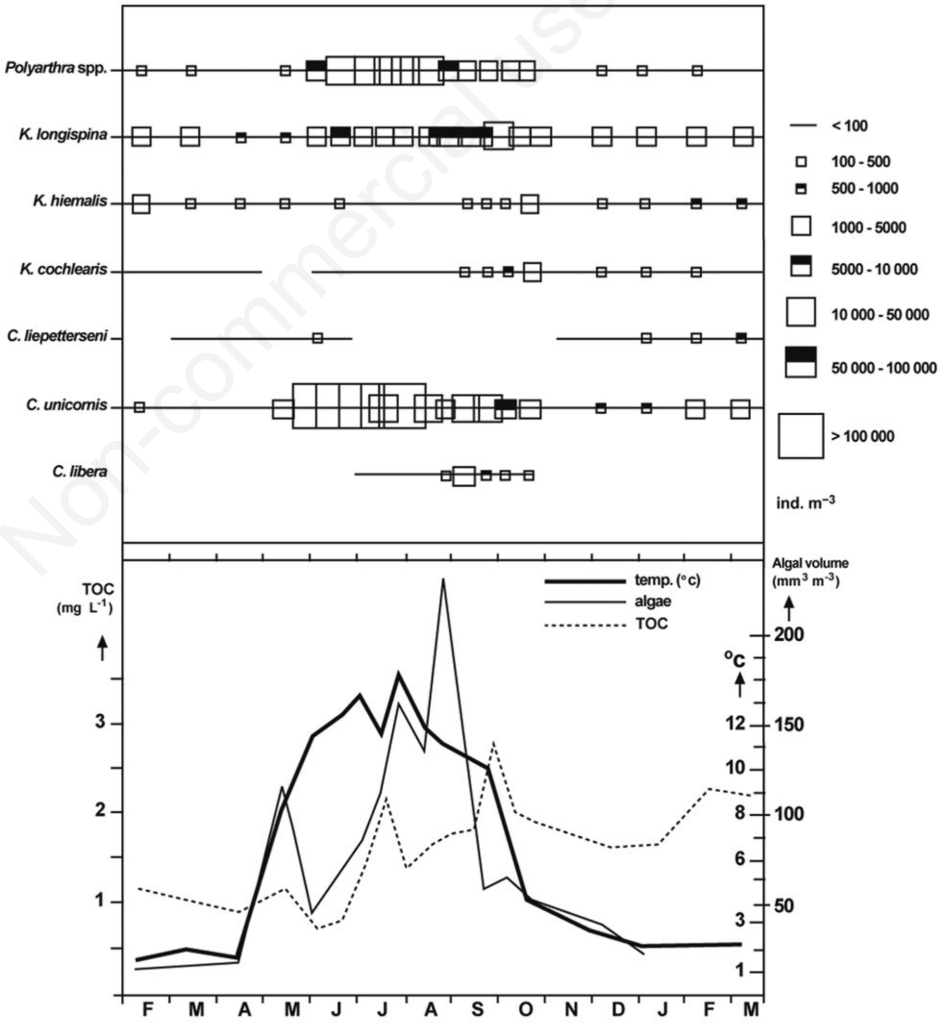

Fig. 8. Total rotifer abundance and their relationship to mean values (0-10 m depth) of temperature and potential food as algae (mm^3 m^{-3}) and organic matter calculated as TOC (mg L^{-1}) in Lake Gjerstadvann in 1980/1981. See text for further details.

Nilssen, 2003; see also Hampton, 2005). Other dominant rotifers in Lake Gjerstadvann were *Polyarthra* spp. and *K. longispina*, which are commonly found in both chronically acidic and acid-transition lakes in southern Norway (Hobæk and Raddum, 1980; Nilssen, 1980; Sandøy, 1984; Wærvågen and Nilssen, 2003).

The low abundance of *K. cochlearis* in Lake Gjerstadvann may demonstrate its physiological vulnerability to acidified waters, but food availability could also play a decisive role (Havens and De Costa, 1988; Gonzalez and Frost, 1994). It is recorded in very acidic environments in western Sweden and Finland (Arvola *et al.*, 1986; Hörnström and Ekström, 1986; Bērziņš and Pejler, 1987; Morling and Pejler, 1990), but never recorded in high abundance at low pH in Norway (Hobæk and Raddum, 1980; Wærvågen and Nilssen, 2003). Wærvågen and Nilssen (2003) found that *K. cochlearis* increased significantly with increasing pH in many lakes in southern Norway. In North America *K. cochlearis* was recorded at both low pH (Roff and Kwiatkowski, 1977) and at higher pH levels (Orcutt and Pace, 1984; Siegfried *et al.*, 1984; Carter *et al.*, 1986; Mac Isaac *et al.*, 1987). As observed in *K. cochlearis,* the apparently contrasting ability of tolerance and relationship towards acidic waters may be explained by the existence of populations with different ecological adaptations (Pejler, 1977; Hofmann, 1980; Dumont, 1983; Cieplinski *et al.*, 2017).

Exploitative competition and/or bottom-up relations

Pelagic freshwater food webs are in general based upon phytoplankton production, especially in clear-water lakes. Consumers in humic lakes may also, by a similar degree, be subsidised by detritus-associated bacterial food (Hessen, 1998). Phytoplankton was a scarce food source in Lake Gjerstadvann, usually well below 200 $mm^3\ m^{-3}$, comparable to chronically acidified lakes (Hindar and Nilssen, 1984; Raddum *et al.*, 1986). Further, the amount of particulate and dissolved humic substances in Lake Gjerstadvann was also limited compared to other oligo- to mesohumic lakes (Salonen *et al.*, 1990; Sarvala *et al.*, 1999; see also Brett *et al.*, 2009, 2012, 2017). Resource limitation and food competition may therefore be important factors shaping rotifer populations in Lake Gjerstadvann. Efficient filter-feeder cladocerans can monopolise shared food resources and suppress rotifers (Gilbert, 1988; Mac Isaac and Gilbert, 1989; Sanni and Wærvågen, 1990). The only cladoceran with sufficient abundance to potentially suppress rotifer species in Lake Gjerstadvann was *B. longispina*, which is found in both fertilised and acidic lakes (Brettum *et al.*, 1984; May, 1995). The omnivorous copepod species *E. gracilis* was relatively common in Lake Gjerstadvann (Wærvågen and Nilssen, 2010), and could also be able to compete with rotifers during specific parts of the year. The highly significant associations between rotifer community ordination axes and abundances of both *B. longispina* and *E. gracilis* could be taken as indications of such competitive relationships. In Lake Gjerstadvann, we found mostly suspension feeders (*Conochilus* spp., *K. longispina* and *Keratella* spp.) following the phytoplankton level maxima in spring and autumn. Furthermore, in the mid-summer and early autumn, the levels of raptorial species (*Polyarthra* spp., *A. priodonta* and *Ascomorpha* spp.) peak in near coincidence with TOC-peaks (mostly allochtonous organic matter). Even with some succession overlap, the raptorial *Polyarthra* spp. peaked together with a cladoceran (*B. longispina*) in Lake Gjerstadvann, as was also found by Obertegger *et al.* (2011). Furthermore, algal and detrital food abundance was low in the water masses during June, which could be due to grazing by *B. longispina* at peak abundance.

Keratella cochlearis avoids most rotifers in time and space in Lake Gjerstadvann, probably due to a higher threshold food concentration than the other pure suspension feeders, such as *C. unicornis* and *K. longispina* (Gilbert and Bogdan, 1984). *Kellicottia longispina* has a lower threshold food concentration than *K. cochlearis* (Walz, 1997), which indicates that *K. longispina* is a superior competitor at lower food levels (Stemberger and Gilbert, 1985). These species can apparently coexist in lakes with sufficient food (Salonen *et al.*, 1990; Sarvala *et al.*, 1999), while under eutrophic conditions *K. cochlearis* was found to be a better competitor than *K. longispina* (Zimmermann, 1974; Sterzynski, 1979; Lair and Oulad Ali, 1990). In other non-acidic neighbouring lakes, *K. cochlearis* was among the dominant rotifer species (Larsen, 1982; Demmo, 1985; Næss, 1985), and outside South Norway it was the dominant rotifer in many non-acidic lakes (Pejler, 1961; Larsson, 1971; Zimmermann, 1974; Eloranta, 1982; Laxhuber, 1987; Andrew and Andrew, 2005; May and O' Hare, 2005). The abundance of rotifers in Lake Gjerstadvann was relatively low compared with a neighbouring lake with similar food availability and very low cladoceran abundance (Sandøy, 1984), in accordance with the highly significant relationship between rotifer community composition and abundance of both *B. longispina* and *E. gracilis*.

Predation influence or top-down relations

Cyclopoid copepods generally exert negative influence on rotifers (Anderson, 1970; Monakov *et al.*, 1972; Vardapetyan, 1972; Gilbert and Williamson, 1978; Karabin, 1978; Brandl and Fernando, 1979; Stemberger, 1985; Plassmann *et al.*, 1997). There is a certain controversy regarding which species of pelagic rotifers are vulnerable to predatory cyclopoid copepods, and whether this applies mainly to soft-bodied forms without lorica (*e.g. Synchaeta* spp.) (Monakov *et al.*, 1972; Vardapetyan, 1972;

Plassmann *et al.*, 1997; and references herein), or all sorts of smaller forms irrespective of body structure and the presence of lorica (Karabin, 1978; Walz, 1995; and references in all). The predation indicator from "Cyclopoids" was not significant (P=0.493) in Lake Gjerstadvann, probably due to the relatively small cyclopoid populations. The abundance of the summer-active, mainly epilimnetic species *Thermocyclops oithonoides* and *Mesocyclops leuckarti* (both winter diapausing) was relatively low in Lake Gjerstadvann (Wærvågen and Nilssen, 2010) and several other Norwegian lakes (Nilssen and Wærvågen, 2000). *Cyclops scutifer* was perennially present in the plankton in Lake Gjerstadvann (Wærvågen and Nilssen, 2010). Despite this, we found no significant predation effects of this species which is known to predate upon rotifers (Monakov *et al.*, 1972; Vardapetyan, 1972). Furthermore, its predatory instars were present in high numbers mainly following ice break when few rotifers normally are present in the plankton. The coloniality tendency in *Conochilus* probably protects individuals from predation by copepods and carnivorous/omnivorous rotifers (Anderson, 1977; Stemberger and Gilbert, 1987a; Matveeva, 1989; Diéguez and Balseiro, 1998), as for *C. unicornis* in this study. Finally, Lake Gjerstadvann was in a process of continuous acidification at the time of sampling, and some of the cyclopoid species were suffering (Wærvågen and Nilssen, 2010), as was also found in nearby upstream lakes (Sandøy and Nilssen, 1987).

In fishless ecosystems Stenson (1982) found that the abundance of suspension feeders within the rotifers decreased strongly. Under low fish predation, and a potentially high abundance of *Chaoborus* spp. as a consequence, the latter may exert a strong predation influence on the relative abundance and spatial distribution of their preferred prey rotifers in addition to the total zooplankton community (Nyberg, 1984; Yan *et al.*, 1991; Moore *et al.*, 1994). In Lake Gjerstadvann, such larvae represented the most important fish food item during most of the year (Linløkken, 1988; Vethe, 1988), although they were very seldom collected in the quantitative zooplankton samples (Wærvågen, 1985). We found no significant predation indicator from *C. flavicans* (P=0.410) in Lake Gjerstadvann. The species resided mainly in the sediment during daytime, and migrated into the hypolimnion during the night where it was highly selected by both Eurasian perch and brown trout (Vethe, 1988).

CONCLUSIONS

The major ecological factor influencing rotifer abundance and seasonal occurrence in Lake Gjerstadvann was the perennial low abundance of food, which indicates that resource limitation and food competition are important factors in structuring rotifer seasonal population dynamics. The lake has both relatively low allochtonous input of organic matter and low autochtonous pelagic algae production, and therefore the basis for high abundance levels of rotifers in Lake Gjerstadvann was therefore not fulfilled. But, Lake Gjerstadvann still had several common rotifer species present, and possible reasons may be the fact that we found no significant effects of the acidification indicators pH and RAl on the total rotifer community in this lake, even though some individual species may have been affected. Furthermore, we found no significant predation indicator from *C. flavicans* or predator stages of cyclopoid copepods (Cop IV-adult stages). The most significant competition indicator species were *B. longispina* and *E. gracilis*, in good accordance with their dominance as cladoceran and copepod species in Lake Gjerstadvann, respectively (Wærvågen and Nilssen, 2010, 2011). Among the highly significant environmental gradient indicators were temperature and oxygen, illustrating the important effects of the seasonal cycle and vertical density stratification in the rotifer community.

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