

Seasonal dynamics and life histories of pelagic cladocerans (Crustacea; Cladocera) in an acid boreal lake

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ABSTRACT

In the surveyed anthropogenic acidified Lake Gjerstadvann with pH \approx 5.2 situated in southern Norway, spatial and temporal distribution of three characteristic planktonic cladocerans inhabiting acidified boreal biotopes, *Bosmina longispina*, *Holopedium gibberum*, and *Diaphanosoma brachyurum*, were studied over a period of one year. The major pelagic predator was Eurasian perch, *Perca fluviatilis*. The local perch probably balanced the cladoceran community and facilitated co-existence of all three species of cladocerans by removing significant portions of *B. longispina*, which could also be the case in similar types of boreal lakes. Invertebrate predators such as the dipteran larvae *Chaoborus flavicans* and carnivorous copepods did not seem to influence the cladoceran community. *B. longispina* was perennial, whereas both *H. gibberum* and *D. brachyurum* were recorded only during the ice-free period. The life cycle of these free-living pelagic species ranged from 2-3 in *D. brachyurum*, 3 in *H. gibberum* to approximately 6 annual generations in *B. longispina*. Wintering took place as resting eggs in *D. brachyurum* and *H. gibberum*, while *B. longispina* produced resting eggs in addition to an active planktonic stay. The warm water tolerant *D. brachyurum* was mainly distributed above the thermocline, whereas *H. gibberum* also inhabited deeper strata, and *B. longispina* most vertical strata of the lake. Maximum seasonal clutch volume of *B. longispina* coincided in time with peak in food abundance and may be a useful parameter to identify planktonic food availability in such lakes. Knowledge of the autecology and life history of species is fundamental for understanding ecosystem stress, such as anthropogenic acidification and recovery through liming or by natural causes. Seasonal depth isopleths combined with life history studies of commonly co-occurring cladoceran species from natural acid and anthropogenic acidified lakes on the Northern Hemisphere seem to be uncommon, and similar type of data is needed to fully understand the processes of acidification and recovery.

Key words: Cladocera, boreal, autecology, habitat, life history, clutch volume, predation

1. INTRODUCTION

The pelagic freshwater cladocerans range among the most intensively surveyed planktonic group, and the reason for their temporal and spatial changes has been the target of many studies during the last hundred years (Huitfeldt-Kaas 1906; Hutchinson 1967; Kerfoot 1980; Gliwicz 2004; Gliwicz *et al.* 2006; Lampert & Sommer 2007). Pelagic cladocerans are being affected to various degrees by the anthropogenic acidification processes, which include several abiotic and biotic ecosystem changes (Almer *et al.* 1974; Nilssen 1980; Yan & Strus 1980; Morling & Pejler 1990; Locke 1991; Stenson *et al.* 1993; Keller *et al.* 1999).

The dominant cladocerans in acidic and acidified lakes down to about pH = 5.0 include the planktonic *Bosmina* (*Bosmina*) *longirostris* (in the Nearctic in all likelihood not conspecific with the Palearctic species of the same name; De Melo & Hebert 1994), *B. (Eubosmina) longispina* (probably also different taxa in the Nearctic and Palearctic), *Diaphanosoma brachyurum*, *D. birgei*, *Holopedium gibberum*, *H. acidophilum*, *Daphnia catawba*, and further, benthic-pelagic species, such as *Chydorus sphaericus* and other taxa of littoral

origin form characteristic organisms in acidic waters (Skadovsky 1926; Sprules 1975; Fryer 1980; Nilssen 1980, 1984; Hobæk & Raddum 1980; Malley & Chang 1986; Tessier 1986; Morling & Pejler 1990).

Species substitutions within cladocerans during acidification are fairly well known (Roff & Kwiatkowski 1977; Nilssen 1980, 1984; Nilssen *et al.* 1984; Hobæk & Raddum 1980; Yan & Strus 1980; Uimonen-Simola & Tolonen 1987; Marmorek & Korman 1993), but their quantitative spatial and temporal distribution, ecology, and life histories during acidification are less well known. Such and similar types of information are available from non-acidic sites (Lynch 1980; Kankaala 1983; Hessen & Schartau 1988; Lampert 2001; Sarma *et al.* 2005; and references in all). Aquatic ecosystems have been studied in the present region since the early 1970s, including both anthropogenic acidification and their subsequent recovery during recent years. Pelagic cladocerans have also been investigated (Nilssen 1976, 1980, 1984; Hobæk & Raddum 1980; Hindar & Nilssen 1984; Raddum *et al.* 1986; Nilssen & Wærvågen 2002b), and their seasonal quantitative distribution has been described in several theses (Larsen 1982; Sandøy 1984; Demmo 1985; Næss 1985; Skov 1985; Wærvågen 1985). The majority of lakes were at the sampling time

of this study (1980-81) still strongly affected by acid out-fall (Drabløs & Tollan 1980; Nilssen 1980, 1982a).

During acidification, the important filter-feeding genus *Daphnia* (with the notable exception of *D. catwaba*; see e.g. Malley & Chang 1986) and the predatory species *Leptodora kindti* and *Bythotrephes longimanus* usually disappear from the plankton. However, they still survive as resting eggs in the sediment egg-bank, from where they may hatch and again inhabit the pelagial zone during chemical recovery of anthropogenic acidified lakes (cf. Nilssen & Wærvågen 2002b). Lake organisms, such as the pelagic cladocerans, are subject to large variations in abiotic and biotic factors, and it is therefore not surprising to find that they are not evenly distributed temporally and spatially. Many components of an organism's environment, such as its food supply, amount of predation, and the water's physical and chemical conditions vary through time and space, in amplitude, frequency, and the degree of predictability of all these factors.

As demonstrated in numerous field and enclosure studies, large-sized *Daphnia* species have the capacity to dominate most aquatic water bodies as key organisms if they are not subject to strongly acid or alkaline environments or intensive fish or invertebrate predation. The dominant *Daphnia* species in the present geographical area comprise *D. lacustris* and *D. longispina* (Nilssen 1980, 1984; Nilssen *et al.* 2007). It has been known for many decades that *D. longispina* is physiologically sensitive to low pH, like the rest of the species within the genus (Skadovsky 1926; Nilssen *et al.* 1984; Brett 1989). The two former species generally decrease strongly at pH below 5.0-5.5 (Nilssen 1980; Nilssen & Wærvågen 2002b; Bērziņš & Bertilsson 1990). Further, Wærvågen *et al.* (2002) presented evidence that low Ca-concentration of lake waters could be an important constraint on zooplankton species distribution, notably large *Daphnia* species. There is now an increased awareness of the consequences of the declining calcium concentrations in softwater lakes in many boreal regions (Skjelkvåle *et al.* 2005; Jeziorski *et al.* 2008; Cairns & Yan 2009).

Zoogeographical studies and palaeoecological core analysis demonstrate that the common pelagic cladoceran communities in this region, and in large parts of southern Norway before the anthropogenic acidification process, were composed of dominant species such as *D. lacustris*, *D. longispina*, *B. longispina*, *H. gibberum*, *D. brachyurum*, and scarce species such as *L. kindti*, *B. longimanus*, *Polyphemus pediculus*, *B. longirostris*, *Ceriodaphnia quadrangula*, and some few other daphniids (Nilssen 1976, 1980, 1984; Nilssen & Sandøy 1990; Nilssen & Wærvågen 2002b). Many of these species disappeared from the pelagial during peak anthropogenic acidification, in this region from approximately 1950 to 1990. During the last two decades a large number of lakes have been limed in Norway (Sandøy &

Romundstad 1995). Due to this liming and natural recovery since the mid 1990s, we now observe a large-scale re-establishment of the cladocerans *D. lacustris* and *D. longispina* strongly influencing the other pelagic biota (Nilssen & Wærvågen 2002a, 2002b; Wærvågen & Nilssen 2003).

Conspicuous changes are observed within the pelagic cladoceran communities during processes of ecosystem stress such as eutrophication and acidification, where physiological relationships to lake-water quality and life history patterns constitute important parameters for the outcome of the altered pelagic systems. The pelagic cladocerans have also different food threshold concentrations than filter-feeding copepods and rotifers, often improving their competitive ability at low food levels, such as in oligotrophic and acidic lakes (Muck & Lampert 1984; Lampert & Muck 1985). Embryonic development time can also vary within species of microcrustaceans (Herzig 1983). Such specificity in life history traits of cladocerans is probably important for the resulting community structure during anthropogenic acidification.

Biotic processes connected with invertebrate predators, which characterise acidic and fishless ecosystems, are of decisive importance in cladoceran ecology (Eriksson *et al.* 1980; Nyman *et al.* 1985; Yan *et al.* 1991). The susceptibility of cladocerans to invertebrate predators is fairly well documented in circumneutral lakes, whereas such knowledge is scanty for acidic lakes, except for their regular consumption by chaoborids (Nyberg 1984; Yan *et al.* 1991). Few studies have been devoted to the physiological tolerance of cladocerans against changes in water chemistry (e.g. Potts & Fryer 1979; Nilssen *et al.* 1984; Havens & Heath 1989; Keller *et al.* 1992).

During the process of acidification, all lakes go through different phases with respect to fish population, zooplankton structure, pH and water chemistry, with several characteristic categories. During the normal succession of anthropogenic acidification, lakes usually start with healthy fish populations, including planktivorous species with all ontogenetic stages. Acid-stressed lakes develop through a transition phase where, due to reproductive failure and local species extinction, the dominant predator classes progressively change to mainly adult benthivorous non-reproductive fish. Acidified lakes further develop to a chronically acidic, fish-barren phase when invertebrates take the role as dominant planktivorous predators. A healthy fish population exerts a completely different influence on the zooplankton than non-reproductive adult fish or invertebrate planktivorous predators (Eriksson *et al.* 1980; Nyman *et al.* 1985).

The investigated Lake Gjerstadvann is a typical acid transition lake, which at the time of study had pH fluctuating around 5.2 (see Fig. 2). Water chemistry, phytoplankton and zooplankton were surveyed

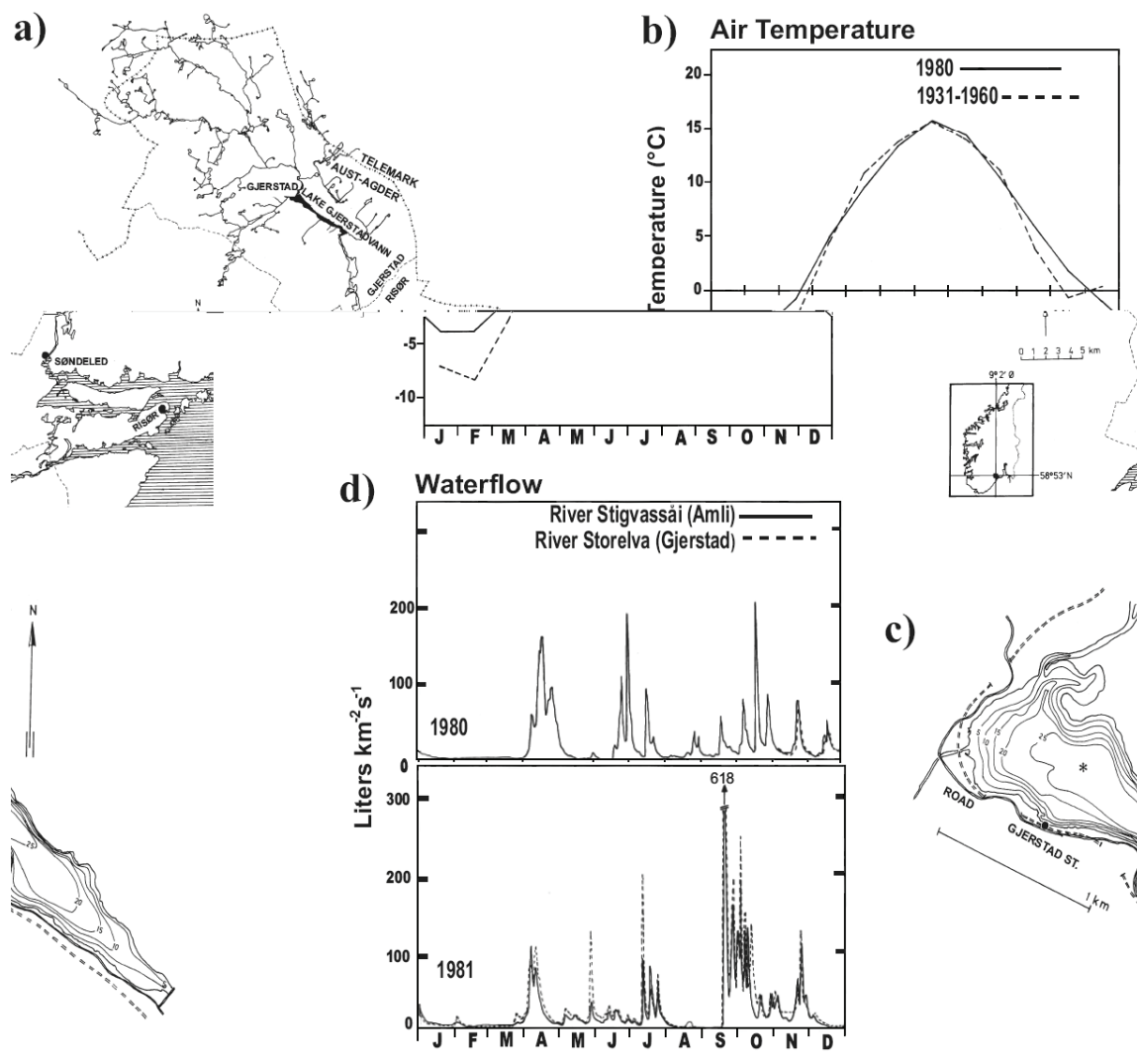


Fig. 1. Geographical position of Lake Gjerstadvann (upper and lower basin) in southern Norway (a), (b) catchment area climate of Lake Gjerstadvann (as mean monthly air temperature), (c) depth map of Lake Gjerstadvann upper basin with sampling station (*), and (d) waterflow of the most sizeable incoming River Storelva (-----; no available data before November 1980) and a neighbouring River Stigvassåi (—; used as a proxy for River Storelva in 1980).

(Wærvågen 1985). Fish sampling and analysis of fish food items were performed as described by Linløkken (1985) and Vethe (1988), respectively. Despite all fish species being negatively influenced by acidification to different degrees, perch still exerted a considerable pelagic predation pressure (Linløkken 1985; Vethe 1988). These studies formed part of a research program lasting for several decades on ecosystem stress and recovery in this region of southern Norway (Nilssen 1976, 1980, 1982a, 1982b, 1984; Nilssen & Sandøy 1990; Nilssen & Wærvågen 2002a, 2002b, 2003; Sandøy & Nilssen 1987; Wærvågen & Nilssen 2003, 2010).

The aim of the present paper is to describe the quantitative seasonal and vertical distribution of pelagic cladocerans in a boreal acid transition lake. The species' life histories are related to their tolerance of acidification processes, fish and invertebrate predation, and interspecific relationships.

2. METHODS

2.1. Study area

This region of southern Norway (Fig. 1) has a continental climate with a substantial oceanic influence and considerable seasonal changes in water chemistry; during spring due to snow melting and during autumn due to seasonal rainfalls (Fig. 1). The lake is situated 31 m a.s.l., below the previous post-glacial marine limit, about 100 m a.s.l. in this region. Usually lakes below the marine limit in this region show regularly higher pH, lower aluminium- and higher calcium concentrations, and less pronounced seasonal pH oscillations than Lake Gjerstadvann (Nilssen 1982a; Fjerdingsstad & Nilssen 1982). However, most of the catchment area of Lake Gjerstadvann is situated above the postglacial marine limit, and draining chronically acidified regions with

Tab. 1. Sampling depths where chemical and quantitative zooplankton samples were collected (**A**) and (**B**) mean values of water chemical parameters in Lake Gjerstadvann 1980/81. Total organic material as KMnO_4 -demand; water colour as Pt; RAl: reactive aluminium; ANC: acid neutralizing capacity; specific conductivity as K_{25} ; T = total.

(A)									
Sample depths (m)	Representative layer (m)		Proportion (%)		of total volume ($\text{m}^3 \times 10^6$)				
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: $14.54 \times 10^6 \text{ m}^3$				

(B)									
Parameter units	pH	KMnO_4 ($\text{mg O}_2 \text{ L}^{-1}$)	Pt (mg L^{-1})	Ca^{2+} (mg L^{-1})	Mg^{2+} (mg L^{-1})	Na^+ (mg L^{-1})	K^+ (mg L^{-1})	TFe (mg L^{-1})	TMn (mg L^{-1})
Annual means	5.2	5	20	1.9	0.38	1.2	0.46	0.32	0.06

Parameter units	SO_4^{2-} (mg L^{-1})	Cl^- (mg L^{-1})	SiO_2 (mg L^{-1})	RAl (mg L^{-1})	NO_3^- (mg L^{-1})	NH_4^+ (mg L^{-1})	TP ($\mu\text{g L}^{-1}$)	ANC ($\mu\text{ekv L}^{-1}$)	K_{25} (mS m^{-1})
Annual means	6.3	2.2	0.34	0.23	0.22	0.11	8	-6.7	2.7

mean pH 4.7 in 1980 (Hindar *et al.* 1984), including a chronically acidified and fishless site, Lake Heilandsvann (pH \approx 4.6; see Tab. 3) located 15 km northwest of Lake Gjerstadvann.

Lake Gjerstadvann had pH \approx 5.2, and was oligotrophic and oligo-mesohumic at the time of this investigation, based on the total phosphorous and KMnO_4 -demand/water colour, respectively (Tab. 1B). The colour of the epilimnetic lake water was 10-30 mg Pt L^{-1} , which increased considerably above the profundal sediments (Wærvågen & Nilssen 2010). Concentrations of reactive aluminium (RAl) were 200-250 $\mu\text{g L}^{-1}$ with a mean value of 230 $\mu\text{g L}^{-1}$ (Tab. 1B). The labile fraction (lAl) at these pH values is about 40-70 percent of the RAl values (Lydersen 1998), and combined with low ANC value suggests a negative water influence on all fish species present in the lake (Hesthagen *et al.* 2001).

2.2. Abiotic and biotic environment

Chemical and biological samples were taken simultaneously, approximately at mid-day, every fortnight during the ice-free period, and about monthly the rest of the year from primo February 1980 to medio March 1981. 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 table 1A. Chemical analyses were performed according to standard analytical methods, and parameters are shown in table 1B (further details see Wærvågen & Nilssen 2010).

Duplicate quantitative zooplankton samples were collected using a 15 litre Patalas/Schindler device (Schindler 1969), with an attached net with mesh size 45 μm . Since the volume of water present at different

depths is not the same in lakes, conversion to ind. m^{-3} in Lake Gjerstadvann was weighted by the different depth factors shown in table 1A. Total and mean population densities of the different species were calculated according to occurrences in the representative layers (Tab. 1A). Qualitative zooplankton samples were collected with vertical tows from the bottom to the surface with plankton nets (diameter 25 cm, mesh size 90 and 224 μm). Most metazoan zooplankton (Tab. 2) were identified to species (Rylov 1963; Flössner 1972; Ruttner-Kolisko 1972; Einsle 1975; Kiefer 1978).

Calculation of the different generations of *B. longispina* was based on measurements of female total body lengths without mucro, and *H. gibberum* and *D. brachyurum* on total body length, as illustrated in Šrámek-Hušek (1962). Hatching of resting eggs was probably asynchronous, and probably took place during extended periods of the year (cf. Cáceres 1998). This, combined with the outstretched vertical distribution and fish predation, impeded the analyses of generations, and therefore only the main patterns of development of this species were identified (see Fig. 5). For *D. brachyurum*, and especially *H. gibberum* (see Fig. 8), the generations were more easily identified. To compare seasonal population densities and development of *B. longispina* with and without fish predation, the chronically acidic fishless Lake Heilandsvann was sampled quantitatively throughout the season (Tab. 3).

Life history attributes (see Fig. 4) were based on 5-225 (usually 10-20) specimens each date, depending upon population density of the species. The share of males was calculated as percentage males of total population, the share of females with eggs as percentage

Tab. 2. List of all metazoan species collected in the pelagial of Lake Gjerstadvann in 1980/81. Relative abundance within each group of animals is indicated as: XXX = dominating, XX = frequent, X = few specimens and R = rare.

Rotifera		Cladocera	
<i>Kellicottia longispina</i> (Kellicott, 1879)	XXX	<i>Bosmina longispina</i> Leydig, 1860	XXX
<i>Conochilus unicornis</i> /hippocrepis	XXX	<i>Holopedium gibberum</i> Zaddach, 1855	XX
Rousselet, 1892/(Schränk, 1803)		<i>Diaphanosoma brachyurum</i> (Liénen, 1848)	XX
<i>Polyarthra</i> spp. Ehrb. 1834	XXX	<i>Polyphemus pediculus</i> (Linnaeus, 1761)	X
<i>Keratella hiemalis</i> Carlin, 1943	XX	<i>Bythotrephes longimanus</i> Leydig, 1860	X
<i>Keratella cochlearis</i> (Gosse, 1851)	XX	<i>Ceriodaphnia quadrangula</i> (O.F. Müller, 1776)	X
<i>Keratella serrulata</i> (Ehrb., 1838)	X	<i>Leptodora kindti</i> (Focke, 1844)	X
<i>Keratella ticinensis</i> (Callerrio, 1921)	X	Chydoridae spp. Stebbing, 1902	X
<i>Keratella testudo</i> (Ehrb., 1832)	R	<i>Scapholeberis mucronata</i> (O.F. Müller, 1776)	R
<i>Collotheca</i> cf. <i>libera</i> (Zacharias, 1894)	X	<i>Sida crystallina</i> (O.F. Müller, 1776)	R
<i>Collotheca lie-petterseni</i> Bērziņš, 1951	X	<i>Daphnia lacustris</i> G.O. Sars, 1862	R
<i>Ascomorpha ecaudis</i> Perty, 1850	X		
<i>Lecane</i> sp. Nitzsch, 1827	X	Copepoda	
<i>Synchaeta</i> sp. Ehrb., 1832	X	<i>Eudiaptomus gracilis</i> (G.O. Sars, 1863)	XXX
<i>Euchlanis dilatata</i> Ehrb., 1832	R	<i>Heterocope saliens</i> (Lilljeborg, 1863)	R
<i>Trichocerca</i> sp. Lamarck, 1801	R	<i>Cyclops scutifer</i> G.O. Sars, 1863	XXX
<i>Asplanchna priodonta</i> Gosse, 1850	R	<i>Mesocyclops leuckarti</i> (Claus, 1857)	XX
<i>Gastropus styliifer</i> Imhof, 1891	R	<i>Thermocyclops oithonoides</i> (G.O. Sars, 1863)	X
<i>Gastropus minor</i> (Rousselet, 1892)	R	<i>Cyclops abyssorum</i> G.O. Sars, 1863	R
		<i>Diacyclops nanus</i> (G.O. Sars, 1863)	R
Fish		<i>Diacyclops bicuspidatus</i> (Claus, 1857)	R
<i>Perca fluviatilis</i> Linnaeus, 1758	XXX	<i>Megacyclops gigas</i> (Claus, 1857)	R
<i>Salmo trutta</i> Linnaeus, 1758	XX		
<i>Coregonus lavaretus</i> (Linnaeus, 1758)	X	Insecta	
<i>Salvelinus alpinus</i> (Linnaeus, 1758)	R	<i>Chaoborus flavicans</i> (Meigen, 1830)	X

Tab. 3. Mean monthly abundances of *Bosmina longispina* in Lake Gjerstadvann (1980) compared with the neighbouring fishless Lake Heilandsvann (1977, 1978). Clutch volume during 1980 of *B. longispina* (21. June¹, 07. July², 02. August³, 03. September⁴). Percentage of *B. longispina* (% wet weight) of the total Eurasian perch food items in Lake Gjerstadvann. Abundances of the advanced carnivorous ontogenetic stages (copepodid V and adults) of the cyclopoid copepod species in Lake Gjerstadvann.

Species	Location	Year	Unit	May	June	July	August	September
<i>Bosmina longispina</i>	Lake Heilandsvann	1977	(ind m ⁻³)	700	2280	9100	8515	8230
<i>Bosmina longispina</i>	Lake Heilandsvann	1978	(ind m ⁻³)	1175	6700	9645	11700	12700
<i>Bosmina longispina</i>	Lake Gjerstadvann	1980	(ind m ⁻³)	337	9061	3591	2241	165
<i>B. longispina</i> clutch volume	Lake Gjerstadvann	1980	(mm ³ × 10 ⁻⁴)	34.5	17.41	27.82	22.73	33.94
Perch food items	Lake Gjerstadvann	1981	(% ww)	2	10	6	3	0
<i>Cyclops scutifer</i>	Lake Gjerstadvann	1980	(ind m ⁻³)	950	347	103	31	7
<i>Mesocyclops leuckarti</i>	Lake Gjerstadvann	1980	(ind m ⁻³)	56	60	98	197	253
<i>Thermocyclops oithonoides</i>	Lake Gjerstadvann	1980	(ind m ⁻³)	309	162	60	62	95
Total cyclopoids	Lake Gjerstadvann	1980	(ind m ⁻³)	1315	569	261	290	355

of total females, and clutch size as mean number of eggs per egg-carrying females. Eggs per total females and eggs per litre were calculated from total egg numbers in the sample divided by total females and sample volume (in litres), respectively. Total body lengths were measured on adult females with eggs (if present). Clutch volume of *B. longispina* (Tab. 3) is the product of clutch size multiplied with egg-volume.

3. RESULTS

The annual mean pH in Lake Gjerstadvann was 5.2 (Tab. 1B), but slightly below this value during ice-break up, autumn and summer rain periods (Figs 1d and 2). Lake Gjerstadvann is dimictic, with bottom temperatures slightly above 4 °C in the ice-free period, and with a relatively deep circulating layer because of its consid-

erable flow-through (Figs 1d and 2). The epilimnetic oxygen content was slightly below 100 percent during most of the year, with an oxygen deficit close to the bottom during periods of stagnation (Fig. 2), most probably due to the inlets' transport of organic material (Figs 1 and 2). In 1980-81 the Ca²⁺ content was close to 2.0 mg L⁻¹, sulphate 6 mg L⁻¹, mean ANC value was -6.7 µekv L⁻¹, and other chemical parameters shown in table 1B.

By far the most abundant cladoceran species in Lake Gjerstadvann was *B. longispina* (Fig. 3), recorded throughout the water column, especially in the deeper strata. Maximum occurrence was during the early summer with a characteristically and pronounced mid-summer decrease. Population densities during winter were much lower, especially in 1980/81.

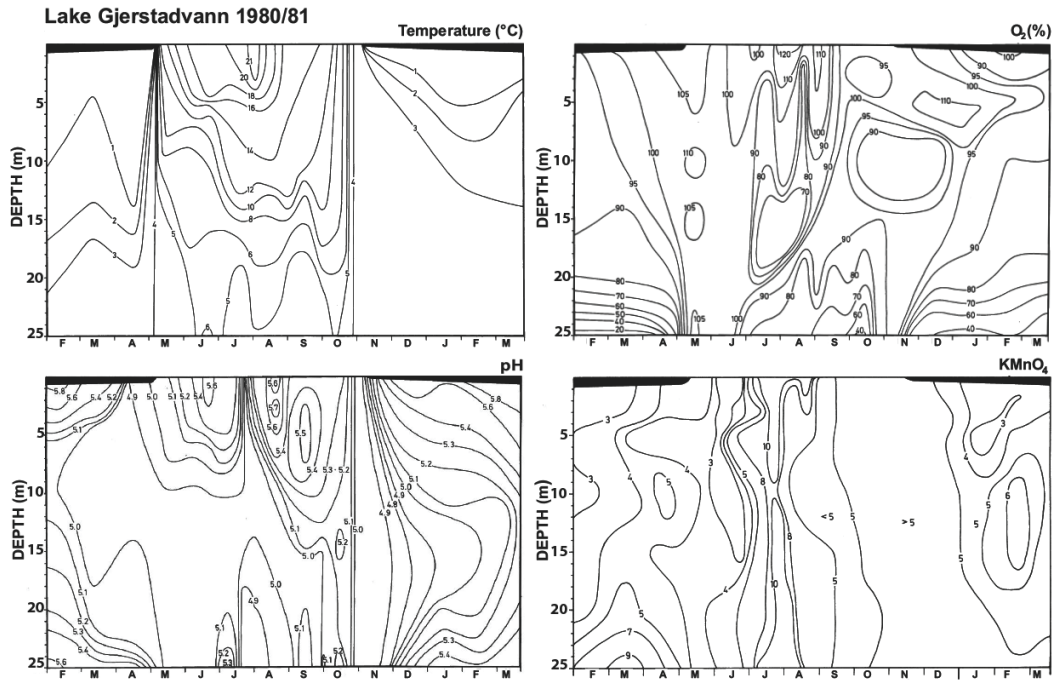


Fig. 2. Isoplots for temperature, oxygen (percentage), pH and organic contents as KMnO_4 -demand in Lake Gjerstadvann 1980-1981. Ice cover is shown in real dimensions as black bars here and in similar figures.

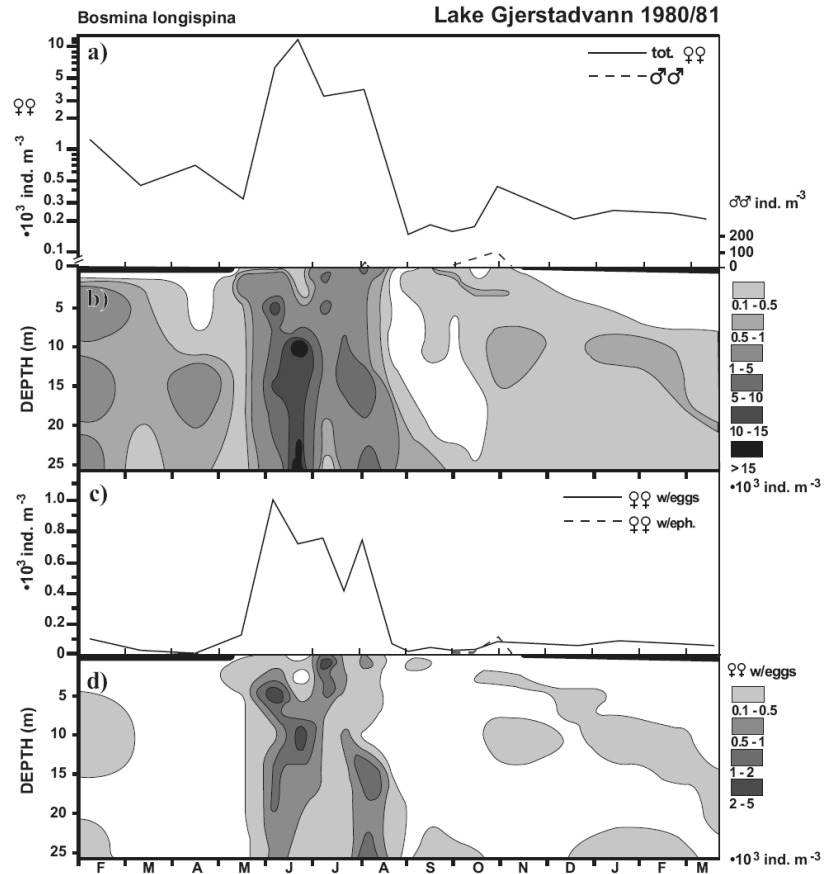


Fig. 3. Mean total population density of females (logarithmic scale, starting at $0.1 \times 10^3 \text{ ind. m}^{-3}$) and males (linear scale) (a), (b) vertical population density of females and males, (c) mean total fecund population density (linear scale) and (d) vertical population density of females with eggs and with ephippians of *Bosmina longispina* in Lake Gjerstadvann during 1980/1981.

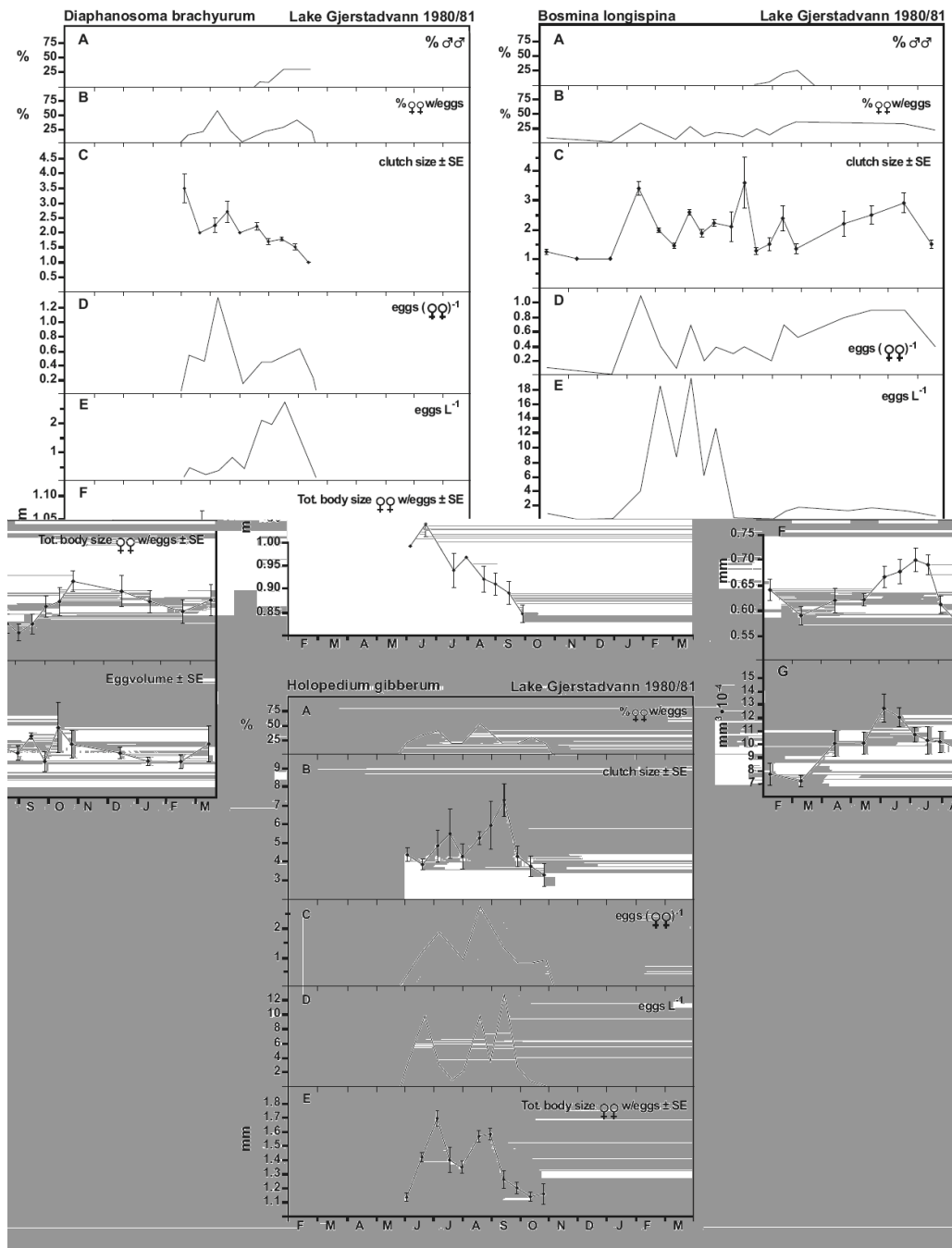


Fig. 4. Selected parameters of life histories of *Diaphanosoma brachyurum*, *Holopedium gibberum*, and *Bosmina longispina*; % males (not found in *H. gibberum*); % females with eggs; clutch size (eggs per egg-carrying female); eggs per total females; eggs per litre; total body size of adult females; and egg-volume (only *B. longispina*) in Lake Gjerstadvann during 1980/1981.

During June and part of August, mean population density exceeded 5 ind L^{-1} , with maximum density surpassing 30 ind L^{-1} ($>15 \times 10^3$ ind m^{-3} in figure 3) below the thermocline during late June. Parthenogenetic reproduction took place most of the year, and females with eggs peaked to 35 percent of the total population in all lake strata in mid May and the last part of October (Figs 3 and 4). The minimum fraction appeared in medio April with less than 2 percent egg-carrying females. The largest clutch sizes were observed during mid May and

early September, at the same time as the population showed lowest densities (Figs 3 and 4). The egg-volume of *B. longispina* was highest during summer and in early June with almost 13×10^{-4} mm^3 and with smallest sizes through the winter (Fig. 4). The body-size of *B. longispina* decreased from July to early September (Fig. 4), at the same time as the above mentioned mid-summer decrease.

B. longispina produced approximately 6 generations during one year, as illustrated in figure 5. The first gen-

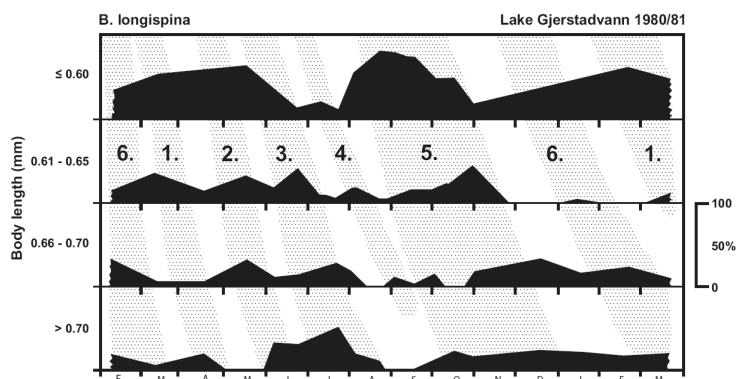


Fig. 5. Generation development of *Bosmina longispina* in Lake Gjerstadvann during 1980/1981, based on female total body-length distributions (the 6 generations are labelled, see text for further details).

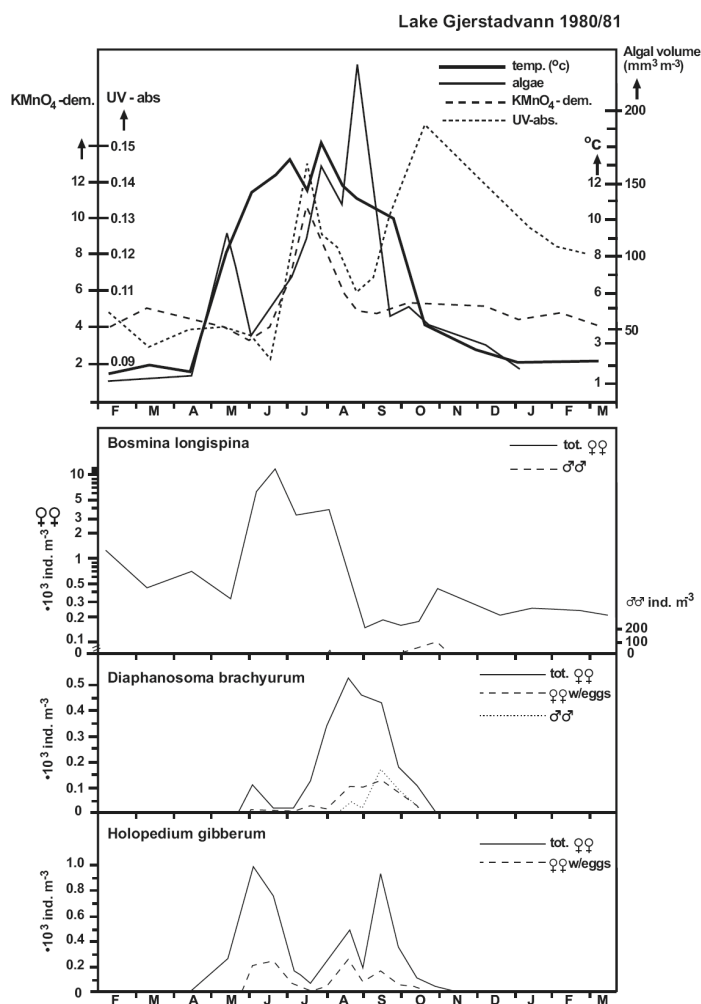


Fig. 6. Cladoceran mean total population densities (three lower panels) and their relationship to important life history parameters (mean values from all lake water strata): temperature (thick line) and food [algal biomass (thin line; mean values for 0-10 m strata); organic matter as KMnO_4 -demand (dashed line), UV-absorption (dotted line)] in Lake Gjerstadvann 1980/1981.

eration was the offspring of the pelagial winter (or the 6th) generation 1979/80, and produced medium clutch sizes just prior to ice break (Figs 4 and 5). This first generation experienced low algal levels and organic material as food (Fig. 6). The second generation (May-June) probably derived mainly from resting eggs in May

immediately following ice break, supported by offspring from the first generation. This generation, at spring phytoplankton outburst (Figs 5 and 6), produced maximum clutch volume (Tab. 3). The substantial third generation (June-July), comprising offspring both of the first and second generation, produced maximum abun-

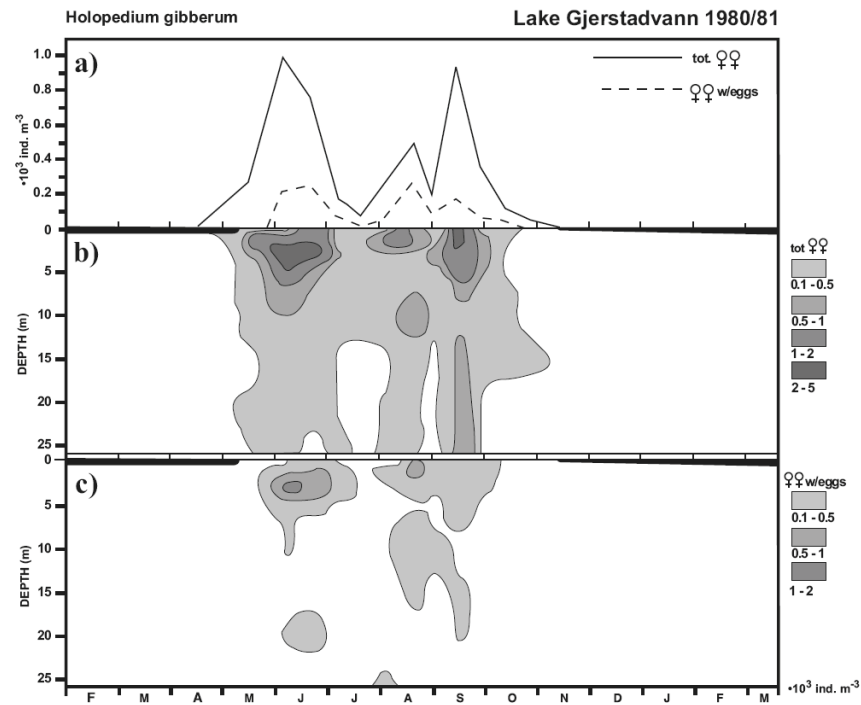


Fig. 7. Mean total population density of females and females with eggs (a), (b) vertical population density of total females, (c) vertical population density of females with eggs of *Holopedium gibberum* during 1980/1981. (No males were recorded).

dance of the species in the last part of June (Fig. 3). This generation developed into adults during the first part of July (Fig. 3), and the clutch volume (Tab. 3) thereafter decreased as the population declined at low food levels (Fig. 6).

The tiny fourth generation (July-August) derived from eggs hatching during the first part of July. The initial population density was high, but decreased substantially throughout August (Fig. 3) and thereafter disappeared gradually (Fig. 5) with small body sizes (Fig. 4). The numerically small and outstretched fifth generation (September-December) started with high food concentrations (Figs 5 and 6) and comparable clutch volumes to the spring (or the 2th) generation (Tab. 3). This generation was strongly decimated during autumn, and in October and early November ephippia appeared at the same time as males made up about 25 percent of the total population (Figs 3 and 4). Early November, immediately after females with ephippia were present, the sixth generation hatched. This generation could have been composed of late individuals of the fourth and fifth generations, and the females that were not fertilised during October (Figs 3 and 5). This winter generation appeared earlier the second investigated year, possibly due to higher autumn and winter temperatures in the lake water (Fig. 2).

The first juveniles of the macrofiltrator *H. gibberum* were recorded from mid April, and the synchronous hatching of resting eggs produced a rapid population increase to a June maximum of 3.2 ind L⁻¹. The population displayed three characteristic population peaks

(Fig. 7), due to the existence of three distinct annual generations (Fig. 8). The three reproduction maxima occurred from mid June until mid September, with 30-50 percent of the population carrying eggs (Fig. 4), the last generation predominantly spherical resting eggs. The mean total population density was usually well below 1 ind L⁻¹, and was distributed mainly in the upper water masses (Fig. 7).

The first generation originating from winter resting eggs was the least fecund (Figs 4, 7 and 8). Most egg-carrying females were recorded from the first part of June until mid July, coinciding in time with population maxima of *H. gibberum* (Fig. 7). The body size in July/August decreased considerably between the first and second generation (Fig. 4), coinciding with the lowest recorded pH (Fig. 2) and summer maximum of water through-flow (Fig. 1d). This first generation disappeared during June, which gave a generation time of approximately 35 days (Fig. 8), with a mean temperature of about 13 °C. The first generation exhibited high population densities with low phytoplankton abundances (Fig. 6), which probably caused the rapid population decrease (Fig. 7).

The second generation hatched during mid-July at a temperature of about 18 °C (Figs 2 and 8). Despite high detrital food abundance during July (Fig. 6), low population densities occurred, coinciding with the heavy acidic rainfall and flushing effect in the lake (Figs 1 and 2). The third generation exhibited a similar size to the first one (Fig. 7), and developed at a temperature of about 16.5 °C, with planktonic algae maximum. Strong

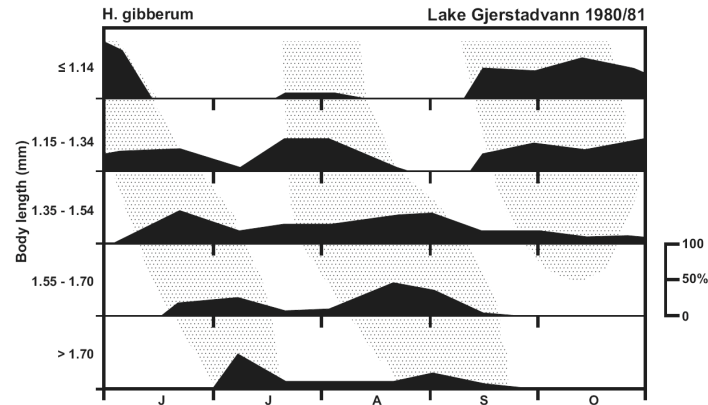


Fig. 8. Generation development of *Holopedium gibberum* in Lake Gjerstadvann during 1980/1981, based on total body-length distributions of females exceeding ≈ 1.1 mm in size at first reproduction.

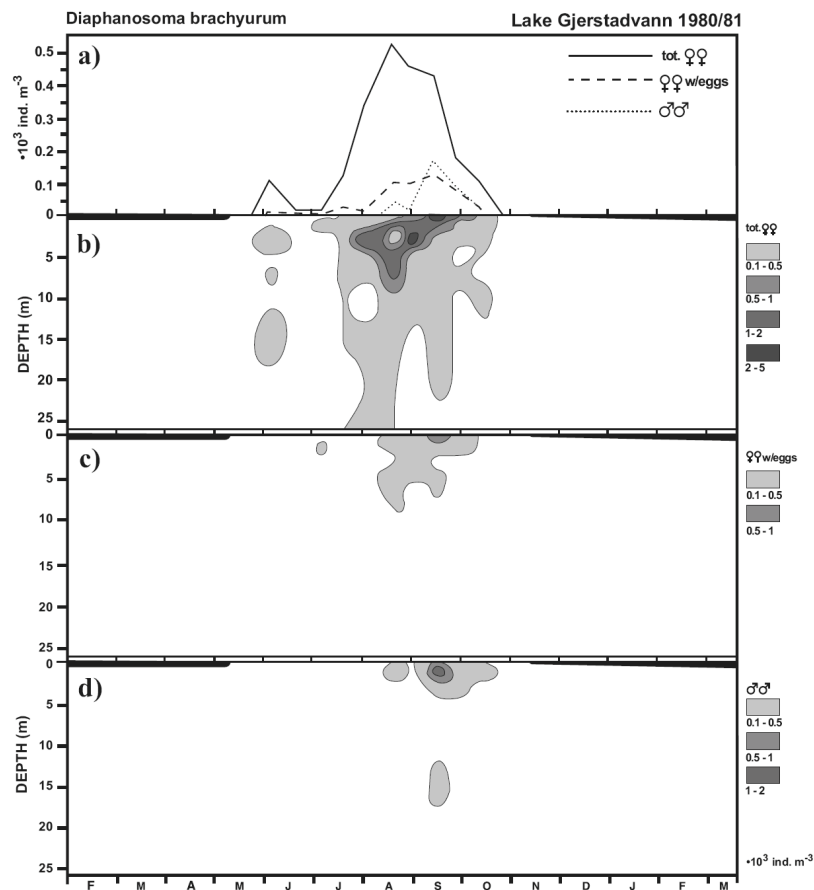


Fig. 9. Mean total population density of females, females with eggs and males (a), (b) vertical population density of females, (c) vertical population density of females with eggs and (d) vertical population density of males of *Diaphanosoma brachyurum* in Lake Gjerstadvann during 1980/1981.

rainfall during that period, combined with low temperatures during mid-September, may explain the rapid decrease in algal biomass and the subsequent decline in population densities of *H. gibberum*. The population in Lake Gjerstadvann was comparatively fecund during all population peaks, with more than 10 eggs L^{-1} (Fig. 4). The number of eggs per clutch was relatively high, and

often surpassed 5 eggs per female (Fig. 4). Except for the third generation with small body-sizes and small clutches (of predominantly resting eggs), clutch sizes were relatively high in this population, reaching 7 eggs per egg-carrying female (Fig. 4).

The microfiltrator *D. brachyurum* appeared in the plankton during early June (Fig. 9). The first generation

showing low population densities had large body-size and was very fecund (Fig. 4). This first generation originated mainly from resting eggs deposited in the littoral zone, which had terminated diapause earlier than in the main water body, due to earlier ice-melt and warming in this zone. Few animals were recorded during June/July following the initial small population peak (Fig. 9). *D. brachyurum* showed population maximum from early August until October, after which it declined rapidly and disappeared during late October (Fig. 9). The distribution throughout the whole water column during the main population peak of *D. brachyurum* may be explained by simultaneous epilimnetic reproducing females and hatching of resting eggs in the profundal sediment (Fig. 9). Moreover, the rapid population increase took place without a concurrent high density of females with eggs. Males appeared during late August-October (Figs 4 and 9). Based on the findings in figures 4 and 9, we hypothesise the existence of at least two annual generations of the warm-water species *D. brachyurum* in Lake Gjerstadvann.

The most numerous pelagic rotifers and copepods in Lake Gjerstadvann are presented in tables 2 and 3. Few specimens of the phantom midge *Chaoborus flavicans* were collected in the pelagial during regular quantitative and plankton net sampling (Tab. 2). However, the species was an important fish food item throughout most of the year in Lake Gjerstadvann (Vethe 1988).

4. DISCUSSION

The pelagic cladoceran species usually observed in anthropogenic acidified lakes in northern Europe are: *B. longispina* (mainly the *obtusirostris* and *lacustris* morphotypes; see Sars 1861/1993; Nilssen *et al.* 1980), *H. gibberum*, *D. brachyurum*, and *C. quadrangula* (Eie 1974; Almer *et al.* 1974; Nilssen 1976, 1980; Hobæk & Raddum 1980). The autecology, including life history traits, of all these commonly recorded species is insufficiently known due to few experimental and comprehensive field studies. Additionally, these taxa are very complicated to culture under controlled conditions. Furthermore, a lot of studies on anthropogenic acidification and recovery are based on vertical integrated plankton hauls, preventing information on the degree of interspecific spatial and temporal overlap, in addition to the whole plankton community organisation.

4.1. Controlling factors of the cladocerans in Lake Gjerstadvann

4.1.1. Water chemistry and physics

Lake Gjerstadvann comprises an oligotrophic lake with relatively high through-flow. Due to the two sizeable incoming rivers, the circulating layer of Lake Gjerstadvann was situated at depths which probably exceeded the trophogenic layer (Fee *et al.* 1996; Urabe *et al.* 2002). The inlets transport large amounts of

organic matter (both particulate and dissolved) into the lake, associated with heavy rainfalls. This produces strong, mainly surface, currents which transport biotic matters from the circulating layer through the outlet. However, turbulence is also increased by these heavy through-flows, supported by the observations that littoral species such as the rotifer genus *Lecane* and chydorids are flushed into the pelagial (Tab. 2; Wærvågen & Nilssen unpubl. data).

It is crucial for the understanding of recovery of anthropogenic acidification to distinguish between different categories of acidified lakes (Nilssen & Wærvågen 2002a; Wærvågen & Nilssen 2003), especially chronically acidic lakes and so-called transition lakes (Henriksen 1979, Henriksen 1980), to which Lake Gjerstadvann belongs. In the chronically acidic lakes such as Lake Heilandsvann, the bicarbonate buffering capacity is inoperative and pH has stabilised at a low level (usually pH: 4.4-4.8), e.g. Nilssen (1982a). All fish species are eliminated and the new top predators are different species of invertebrates, especially pelagic corixids (Hemiptera), chaoborids (Diptera), and water beetles (Coleoptera). The transition lakes (in nature encompassing a continuum between unaffected and chronically acidified lakes) are localities where the bicarbonate buffering capacity is insignificant and the pH level is strongly fluctuating and low (usually pH: 4.8-5.5). Many organisms, including most fish species, are negatively affected or have disappeared altogether. A typical lake within this category contains mostly old fish (often perch; see Nyberg *et al.* 1995), while young planktivorous or brook-living stages are missing. Many controversies concerning species succession and substitutions in anthropogenic acidic ecosystems and their recovery could have been avoided if the existence of the largely different acidic lake categories with partly contrasting pelagic systems had been carefully considered.

Lake Gjerstadvann as a so-called acid transition lake, displays strongly fluctuating pH throughout the year, with low pH during spring and rainfalls during the ice-free periods. The major stress from the water chemistry is probably low pH, frequently below pH 5.3, and the increased level of RAI (150-250 $\mu\text{g L}^{-1}$). These concentrations are noticeable and indicate that many species of phytoplankton, zooplankton, and fish are sublethally, negatively affected by the lake water (Hörnström & Ekström 1983; Hörnström *et al.* 1984; Marmorek & Korman 1993; Hesthagen *et al.* 2001; Frost *et al.* 2006). Nevertheless, perch still produced a considerable biomass in Lake Gjerstadvann.

Intensive regional biotest surveys from the Swedish west coast documented that total Al concentrations as low as 100 $\mu\text{g L}^{-1}$ caused reduced growth for many phytoplankton species. Al concentration of 200 $\mu\text{g L}^{-1}$ inhibited growth of about 70 percent of the phytoplankton tested, among which were diatoms and desmids (Hörnström *et al.* 1984). At the latter Al concen-

tration, serious morphological damages were observed (Hörnström *et al.* 1984). Comparable Al concentration was observed in Lake Gjerstadvann, which indicates that the lake water composition negatively influenced potential food of filter-feeding cladocerans.

Another thorough investigation on zooplankton concluded that the following species of pelagic cladocerans, *L. kindti*, *B. longimanus*, all *Daphnia* spp., *D. brachyurum*, and *H. gibberum*, were negatively affected by Al concentrations exceeding 200 µg L⁻¹. In their study only *B. longispina* and *C. quadrangula* were able to tolerate such water chemistry, and even these tolerant species were negatively affected by a pH below 5.0 (Hörnström & Ekström 1983). The amount of humic material is also of decisive importance, because it may de-toxify large amounts of Al and heavy metals (Nilssen 1982a; Hörnström *et al.* 1984). Many other studies support these observations from northern Europe (Almer *et al.* 1974; Eie 1974; Nilssen 1980, 1984, Nilssen *et al.* 1984; Hobæk & Raddum 1980; Bērziņš & Bertilsson 1990; Hessen *et al.* 1990).

It is not surprising that the tolerant *B. longispina* dominated the cladocerans in Lake Gjerstadvann, together with the calanoid copepod *Eudiaptomus gracilis* (Wærvågen & Nilssen 2010). Even in chronically acidified lakes in southern Norway, these two species were the dominant crustaceans (Nilssen 1976, 1980; Spikkeland 1977; Hobæk & Raddum 1980). *H. gibberum* and *D. brachyurum* are usually absent from chronically acidic lakes, but especially *H. gibberum* produced a substantial population in Lake Gjerstadvann. This indicates that acid transition lakes are not yet suffering like the chronically acidic lakes, where many species have become extinct (Nilssen & Wærvågen 2002b). However, the scarcity of *L. kindti*, *B. longimanus* and all *Daphnia* spp. indicated that water quality negatively affected the biota of the lake, combined with perch predation on all these species (Vethe 1988; Wærvågen & Nilssen 2002a). Furthermore, the decrease in population numbers of some planktonic rotifer species (Wærvågen & Nilssen, unpubl. data) and cladocerans during the short-term acidic period with summer rain, could also be due to the inferior water chemistry. The general low population density of *D. brachyurum* could be caused by lake chemistry conditions.

4.1.2. Food composition and availability

Zooplankton are regulated bottom-up by e.g. food and temperature. When these two factors increase within limits, development rates and reproduction increase considerably for all groups of planktonic animals (Węglenska 1971). Many studies have followed the premise that populations from most water bodies have not realised their potential growth and reproductive capacities, because of low food availability (Węglenska 1971; Wærvågen & Nilssen 2010).

Chrysophyceans formed the dominant phytoplankton group throughout most of the year, whereas cryptophyceans dominated during summer (Wærvågen 1985). Dinophyceans were not so important a group as in chronically acidified lakes (Hörnström & Ekström 1983), while µ-algae and chlorophyceans were important during spring. Most of these algae are attractive food items for cladoceran filter-feeders. However, the total standing crop of phytoplankton (after zooplankton grazing pressure) was very low, less than 200 mm³ m⁻³. It was at a minimum after spring bloom, which could be due to grazing from the considerable populations of both *B. longispina* and *H. gibberum* during that period. Particulate organic carbon also comprises an important food item for cladoceran species (Hessen 1998, Hessen *et al.* 1990). In Lake Gjerstadvann, this allochthonous organic matter is transported into the lake throughout the year, with a maximum in July of the investigated year. This indicates that competition between the different species of zooplankton during specific periods potentially could be substantial in Lake Gjerstadvann.

Species with slow-growing individuals, such as the majority of the investigated species in Lake Gjerstadvann, have been shown to possess the greatest competitive advantages in oligotrophic systems (Romanovsky 1984, 1985). The three pelagic cladocerans have slightly different feeding niches: *H. gibberum* filters large particles, *D. brachyurum* small particles, and *B. longispina* medium or a variety of particles (Geller & Müller 1981; Hessen 1985). Even if the three species had distinguishable feeding niches, they in addition displayed slightly different spatial distribution in Lake Gjerstadvann. Two of these species inhabited different vertical strata of the lake, *B. longispina* mainly below the thermocline and *H. gibberum* partly in the epilimnion. *D. brachyurum* overlapped spatially with *H. gibberum* during autumn, but the range of vertical distribution was much larger for the latter species. In addition, at the time of overlap, food availability showed an annual maximum in the epilimnion. The tolerance of overlap for the "species pair" *D. brachyurum* and *H. gibberum* was low in a humic non-acidic lake (Hessen & Schartau 1988). It is apparent that all three species displayed a prolonged occurrence in Lake Gjerstadvann during the ice-free period, in contrast to nutrient-rich lakes where species substitutions are more frequent (Pejler 1961). It was further found that *C. quadrangula* was an inferior competitor compared to both *D. brachyurum* and *H. gibberum* (Hessen & Schartau 1988), which could probably explain the low abundance of this species in Lake Gjerstadvann.

B. longispina in Lake Gjerstadvann was recorded at mean densities up to about 12 ind L⁻¹, which are considered high (Larsson 1978), since numbers are integrated over the whole water column. Comparable densities in Norwegian lakes were recorded by other authors (Huitfeldt-Kaas 1906; Larsson 1978; Synnes 1982). Since the

six different generations of *B. longispina* inhabited strata with diverse temperatures and food availability, development time differed strongly from 100-110 days in the cold part of the year (generations 1 and 6) to 30-36 days (generations 3-5) during summer and autumn (Wærvågen 1985). In Lake Gjerstadvann a close relation was observed between maximum growth of *B. longispina* and the abundance of phytoplankton and organic matter. Detritus with associated bacteria was probably the main food for *B. longispina* in other studies (Larsson 1978; Hessen 1998). *B. longispina* can also regularly show winter maxima (Skov 1985; Nilssen, unpubl. data), probably due to lessened competition from other species during winter, combined with available detrital/bacterial food.

H. gibberum is often described as a surface water species (Lampert & Krause 1976; Larsson 1978; Synnes 1982). As in the present study, it can also be recorded in or below the thermocline (Sandøy 1984; Demmo 1985; Nilssen, unpubl. data). The mean density of *H. gibberum* in Lake Gjerstadvann was close to 1 ind L⁻¹, comparable to lakes in the English Lake District (Smyly 1968), but relatively low compared to more than 60 ind L⁻¹ in other studies (Makarewicz & Likens 1979; Lampert & Krause 1976). Most densities in Norwegian, Swedish and Canadian lakes are about 1/10 of these values (Davis 1972, 1976; Eriksson *et al.* 1974; Larsson 1978; Nilssen, unpubl. ms). *H. gibberum* had low population numbers in Lake Gjerstadvann, which could be due to harsh water chemical conditions and interspecific competition, but its high reproductive effort indicated satisfactory food conditions.

The maximum density of 0.5 ind L⁻¹ for *D. brachyurum* is even lower than Sandøy (1984) reported from chronically acidic headwater lakes in the same catchment area, where it was the sole pelagic cladoceran, however. In other lakes in the region, 6-10 ind L⁻¹ has been recorded, even in lakes with intensive fish predation (Demmo 1985; Næss 1985). Such densities have also been recorded in other studies (Nauwerck 1963; Johnsen 1983). The species is considered one of the most typical warm-water species (Herzig 1984; Bertilsson *et al.* 1995). The fact that this species also originates from resting eggs in the littoral has been recorded by other authors (Herzig 1984). The males of *D. brachyurum* in Lake Gjerstadvann occurred for a prolonged period of time, as is likewise observed for *Daphnia* species in limed, acid-stressed lakes in this region (Nilssen & Wærvågen unpubl. data). This could indicate that the present population was negatively affected by the water chemical conditions.

4.1.3. Fish and invertebrate predation

The influence of juvenile and adult perch is generally quite considerable in freshwater ecosystems (Klements 1973; Mills & Schiavone 1982; Mills *et al.* 1987; Mills & Forney 1983; Henrikson *et al.* 1984).

Mills & Forney (1983) and Guma'a (1978) found the strongest predation impact from juvenile perch from June to October. In Lake Gjerstadvann, a strong decline in *B. longispina* abundance was observed from the last part of July until September, simultaneously with a distinct reduction in body length. At the same time the *B. longispina* population was recorded at successively greater depths. This large mid-summer *B. longispina* generation seems to disappear. The fact that all this course of events occurred at the same time is a strong indication for predation by juvenile or adult perch, also supported by the fish predation survey in Lake Gjerstadvann (Vethe 1988).

Fish predation in Lake Gjerstadvann influenced mostly *B. longispina*, whereas the two other species were only negligibly influenced. This could also be due to the fact that *B. longispina* was much stronger coloured (see also Johnsen & Raddum 1987) than the two hyaline taxa *H. gibberum* and *D. brachyurum*. The dominance of *B. longispina* in this lake would have been much stronger if perch did not consume a considerable proportion of this population. Perch in this manner probably balanced the cladoceran community by removing significant portions of *B. longispina*, facilitating all three species to co-occur.

In the earlier-mentioned, fishless Lake Heilandsvann, *B. longispina* during two consecutive investigated years showed a relatively constant or increasing population size during the same period as the species nearly disappeared in Lake Gjerstadvann (Tab. 3). Moreover, *B. longispina* displayed a relatively constant body size of between 0.60-0.65 mm throughout the year in this fishless lake (Nilssen, unpubl. data), demonstrating an effect of absence of fish predation on *B. longispina* body size.

Vethe (1988) investigated predation from perch and brown trout in Lake Gjerstadvann from May 1981 until October 1982. He observed that perch consumed *B. longispina* to a major degree in the pelagial, mainly in the 0-6 m strata in summer and to some extent in the 0-14 m strata in autumn, together with *B. longimanus*, which by far was the major pelagic food item, together with *Chaoborus flavicans*. This consumption of *B. longispina* was primarily restricted to the warm water period, the months May-August (Tab. 3).

Population sizes of the two other cladocerans, *H. gibberum* and *D. brachyurum*, on the other hand, increased during the period with intense perch predation on *B. longispina*, and in addition the two species inhabited the upper water masses where the perch was capturing its main food items (Linløkken 1985, 1988; Vethe 1988). These facts support the finding that the two species were relatively unaffected by perch predation in Lake Gjerstadvann.

The intense influence of *Chaoborus* spp. on the total zooplankton community and particularly the cladocerans is well documented (Nyberg 1984; Yan *et al.* 1991;

Keller *et al.* 1992; Gonzáles 1998). *C. flavicans* in Lake Gjerstadvann was seldom collected in the lake pelagial, even in coarse (224 µm) plankton nets drawn from the sediment to the surface, except for a restricted period during the late autumn stratification period with low hypolimnetic oxygen content. The species was therefore distributed mainly in the sediment during daytime (Wærvågen 1985), and in the deep hypolimnion during night (Wærvågen, unpubl. data), in accordance with the historical observations by Berg (1937). The species was strongly selected by both Eurasian perch and brown trout throughout the year (Vethe 1988), and we therefore conclude that it was unlikely that *C. flavicans* predation influenced cladoceran biomass significantly in Lake Gjerstadvann, apart from the deep water population of *B. longispina*.

Communities in chronically acidic lakes have low abundance of predatory cyclopoid copepods (Sandøy & Nilssen 1987; Nilssen & Wærvågen 2003), and this indicates that predation pressure from this omnivorous group is much reduced in such ecosystems. Acidic transition lakes, by contrast, show a high diversity of pelagic cyclopoid copepods (Nilssen & Wærvågen 2003), with a potential negative influence on pelagic cladocerans (Anderson 1970; Karabin 1978; Gilbert & Williamson 1978; Brandl & Fernando 1979; Stemberger 1985). Lake Gjerstadvann was in a process of continuous acidification in 1980/81, and some of the cyclopoids were probably suffering from this inferior water quality (Sandøy & Nilssen 1987; Wærvågen & Nilssen 2010).

The density and body size of both *T. oithonoides* and *M. leuckarti* were probably too low to exert any negative influence on the cladoceran populations (Tab. 3, Wærvågen & Nilssen 2010). These copepods were both summer-active species, mainly distributed in the epilimnion. The spatial overlap with the dominant cladoceran, *B. longispina*, was therefore restricted. Both *H. gibberum* and *D. brachyurum* overlapped with these copepods. Due to its jelly coat *H. gibberum* probably has a refuge from copepod predation, which increases its effective size relative to the copepods (Stenson 1987). The third cyclopoid copepod species in Lake Gjerstadvann, *C. scutifer*, was present perennially in the plankton (Wærvågen & Nilssen 2010). Its predatory instars were present in high numbers mainly during a restricted period of time (Tab. 3), immediately following ice break, when *H. gibberum* was showing large numbers. However, based on the spatial population data we conclude that the total predatory influence from cyclopoid copepods on these three cladocerans probably was negligible or very low in Lake Gjerstadvann. Because of fish predation, the calanoid predator *H. saliens* was very uncommon in the lake, resulting in low predator influence from this species on any pelagic cladoceran. The herbivorous and omnivorous species *E. gracilis* was abundant in Lake Gjerstadvann, and could potentially compete with cladocerans at specific times

of the year (Muck & Lampert 1984). This influence was probably not extremely strong in Lake Gjerstadvann since their spatial niches seldom overlapped considerably with *E. gracilis* in the lake (Wærvågen & Nilssen 2010).

4.2. Population densities and habitat structure of cladocerans in Lake Gjerstadvann

The dominant cladoceran species *B. longispina* was recorded throughout the lake water column. Population densities during winter were much lower than during the ice-free period, especially in 1980/81. This winter had very clear ice compared with the previous winter with abundant snow, and the deeper vertical distribution in 1980/81 could be due to UV avoidance. A pronounced decline in the *B. longispina* abundance was observed from the end of July until September, coinciding with a strong decrease in body length. The species was recorded over the entire pelagial, but with a tendency to accumulate deeper in the water masses, also including the predation-vulnerable females with eggs. The fact that the whole of this course of events occurred at the same time is a strong indication of perch predation (Linløkken 1985; Vethe 1988), and possible competition from *D. brachyurum* displaying peak abundance at that time. In lakes, pelagic fish are a major controlling factor for structuring the cladoceran community, both spatially, seasonally, and morphologically (Zaret 1980; Gliwicz 2004; Lampert & Sommer 2007).

The production of *B. longispina* generations is dependent upon water temperature and food (Larsson 1978; Vijverberg 1980). The wide temperature range and food niche of *B. longispina* in Lake Gjerstadvann would consequently lead to different generation times and a partly spatial overlap between different generations, and only the main patterns of development could be identified. *B. longispina* produced approximately 6 generations annually in Lake Gjerstadvann, comparable to other studies from Norway where 5 (Larsson 1978) and 6 (Synnes 1982) were observed. The first generation displayed medium clutches and clutch volumes just prior to ice break, due to low food levels. Food conditions for the second generation were much poorer, reflected by both low clutch sizes and clutch volumes. The third generation produced the maximum abundance of the species, experiencing peak algae production. The fourth generation gradually disappeared, most probably due to perch predation combined with low algal food, and increased competition from other cladocerans. During June, July and August, considerable amounts of *B. longispina* were recorded in the stomachs of perch (Tab. 3, Vethe 1988), at the same time as the smallest mean body-size of *B. longispina* was recorded. The species produced most offspring during the period from June to August, even though the total population density declined during that period due to perch predation.

The macrofiltrator *H. gibberum* was recorded exclusively during the ice-free period, and produced three distinct population peaks, due to the existence of three annual generations. The species inhabited primarily the upper, circulating water masses, which was especially conspicuous for females with eggs. The body-size of the adult female population decreased considerably in July/August, at low food abundance. Its main distribution in the upper water masses underscores its ability to avoid fish predation, which is probably due to its hyaline body with minor pigmented parts (Stenson 1973). The first generation of *H. gibberum* produced maximum annual population size, notwithstanding low algal standing crop. Despite high food concentration of organic detritus during July, the population exhibited summer minimum, which could be explained by the previous heavy acidic rainfall and the subsequent flushing effect. The third generation produced an almost similar population abundance size to the first one, coinciding with phytoplankton maximum. A strong rainfall in that period combined with low temperatures during mid-September caused the rapid decrease in algal biomass with a subsequent decline in population density of *H. gibberum*. The number of generations in Lake Gjerstadvann was similar to other findings where one generation (Freidenfeldt 1920; Stenson 1973), two (Schindler & Novén 1971; Sandøy 1984), and 4-6 generations (Larsson 1978; Synnes 1982) have been reported. The number of generations can also vary in the same population between years (Hutchinson 1967).

Population size of *H. gibberum* in this lake was relatively high compared with neighbouring sites, and this also supported the earlier view that fish predation in Lake Gjerstadvann was negligible on this species. The warm-water species *D. brachyurum* displayed a relatively low population density in Lake Gjerstadvann, and produced 2-3 annual generations. It appeared in the plankton in early June from resting eggs in the littoral, due to early warming in this zone. The hyaline *D. brachyurum* was not selected by fish (Vethe 1988), and did not display any pronounced seasonal changes in population size coinciding with maximum pelagic fish predation. Its modest occurrence in the lake could be caused by the hostile chemical conditions, or interspecific competition from *H. gibberum* (Raddum *et al.* 1986).

5. CONCLUSION

The three characteristic planktonic cladocerans inhabiting acidified boreal biotopes, *Bosmina longispina*, *Holopedium gibberum*, and *Diaphanosoma brachyurum* display considerable different life histories. *B. longispina* is usually perennial, whereas both *H. gibberum* and *D. brachyurum* are recorded only during the ice-free period. Therefore, *B. longispina* displays more generations (here approximately 6 annually) than *D. brachyurum* and *H. gibberum* (here 2-3 annually). Wintering strategy of *D. brachyurum* and *H. gibberum*

is solely resting eggs, while *B. longispina* produces resting eggs in addition to an active planktonic stay. Maximum seasonal clutch volume of *B. longispina* coincided in time with peak in food (phytoplankton and detritus) abundance and may be a useful parameter to identify planktonic food availability in such lakes. *B. longispina* is much stronger coloured than the two hyaline species *H. gibberum* and *D. brachyurum*, and therefore fish predation may influence life history and seasonal abundance mainly for *B. longispina*. The local perch probably balanced the cladoceran community and facilitated co-existence of all three species of cladocerans by removing significant portions of *B. longispina*, which could also be the case in similar types of boreal lakes.

Separation of the different categories of acid transitional lakes and chronically acidified lakes, seems essential for the understanding of the stress and recovery of such systems and its trajectories. Knowledge of the autecology and life history of species is fundamental for understanding ecosystem stress, such as anthropogenic acidification and recovery through liming or by natural causes. Especially, information on pelagic invertebrate predators and their effects on prey species in such and similar types of lake systems is needed. Lake Gjerstadvann constitutes a typical acid transition lake, a special category of lakes which has not been chronically acidified, and with most pelagic species present. Acid transition lakes in boreal regions frequently exhibit relatively similar community structures and seasonal cycles, with the same dominant cladoceran species as in Lake Gjerstadvann. With pH above 5.3 and RAI below 150 $\mu\text{g L}^{-1}$ small populations of *Daphnia* spp. may still persist in some ecosystems. Chronically acidified lakes, by contrast, are structurally impoverished and frequently inhabited only by the acid tolerant cladoceran species *B. longispina*, and the copepods *E. gracilis* and *H. saliens*, in addition to some rotifer species. Recovery periods are severely prolonged in strongly disturbed, chronically acidified ecosystems. Transition lake ecosystems, such as Lake Gjerstadvann, and sites which were limed before all fish species were lost, and before significant dominance shifts had taken place within the invertebrates, appear to recover more quickly and predictably.

Seasonal depth isoplots combined with life history studies of commonly co-occurring cladoceran species from natural acid and anthropogenic acidified lakes on the Northern Hemisphere seem to be uncommon, and similar type of data is needed to fully understand the processes of acidification and recovery.

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