



## Diversity, abundance, and life histories of littoral chydorids (Cladocera: Chydoridae) in a subarctic European lake

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### ABSTRACT

Littoral chydorids were sampled with a bottom sledge in Takvatn, a 15 km<sup>2</sup> north Norwegian oligotrophic lake with poor vegetation. Three out of eight recorded species of chydorids were common, with abundance minima in late summer and maxima in autumn. *Eurycerus lamellatus* (O.F. Müller, 1776) and *Acroperus harpae* (Baird, 1835) were monocyclic, whereas *Chydorus sphaericus* (O.F. Müller, 1776) was seemingly acyclic. Females of *E. lamellatus* appeared in early June and grew to maximum sizes of 2–2.5 mm in early August. Parthenogenesis started in late July and two summer generations could be distinguished by size distributions. Gamogenesis took place in September. *Acroperus harpae* females appeared in early June and grew to maximum sizes of around 0.7 mm in early August. Parthenogenesis started in early July and gamogenesis took place in September and October. Parthenogenetic females of *C. sphaericus* appeared already at ice-break and had constant sizes of around 0.4 mm through the entire season. Males or ephippial females were not observed. The acyclic life history may be an adaptation to the challenging environment of this subarctic lake. Summer generations could not be distinguished in the two small-sized species, but both populations reached high abundances in autumn. The abundance of *E. lamellatus* increased from August, but then decreased, possibly as a result of fish predation. We argue that the present results are typical for large oligotrophic lakes in subarctic Europe.

**Key Words:** acyclic life history, bottom sledge, gamogenesis, growth, ice-free season, monocyclic life history, oligotrophic lakes, parthenogenesis

### INTRODUCTION

Planktonic microcrustaceans, predominantly daphniid and bosminid cladocerans and cyclopoid and calanoid copepods, dominate the open water communities in almost all lakes worldwide. Their taxonomy, genetics, diversity, behaviour, ecology, and life histories have been much studied, and the literature in the field is extensive (e.g., Flössner, 2000; Dumont & Negrea, 2002; Barnett & Beisner, 2007; Barnett *et al.*, 2007; Jensen *et al.*, 2013; Bledzki & Rybak, 2016). Benthic microcrustaceans in lakes and ponds, predominantly ostracods, chydorid cladocerans, and harpacticoid copepods, are in contrast remarkably less studied despite a much higher taxonomic diversity than in the zooplankton (Sandøy & Nilssen, 1986; Koksvik, 1995; Sacherova & Hebert, 2003;

Einarsson & Örnólfsson, 2004; Walseng *et al.*, 2006; Hessen *et al.*, 2007; Nevalainen, 2010; Jensen *et al.*, 2013).

Cladocera is a primarily freshwater, monophyletic group of Palaeozoic origin (Forro *et al.*, 2008). Chydoridae is by far the most diverse family of Cladocera, with 54 genera and about 300 species (Bledzki & Rybak, 2016). Using genetic analysis, Sacherova & Hebert (2003) concluded that chydorid lineages can be taken as far back as 400 mya. Their diversification clearly was coupled to the radiation of aquatic plants, and the littoral environment provided a high habitat and niche variation that gave high adaptation rates, morphological novelties, and prolific speciation (Sacherova & Hebert, 2003). From a detailed analysis of morphology, Fryer (1968) concluded that adaptive radiation in body form played a great part in their evolution and that chydorids exhibit

specializations associated with the exploitation of different substrates and different methods of locomotion and feeding. They can have clear niche segregations (Nevalainen, 2012), have a high functional diversity (Nevalainen & Luoto, 2017) and play an important role as benthos in lacustrine ecosystems by their role in the transformation of nutrients and energy (Nevalainen, 2010). The taxonomic diversity of European chydorids is well documented, with monographs of Smirnov (1996), Flössner (1972, 2000), and Bledzki & Rybak (2016). Walseng & Halvorsen (1996) and Walseng (2018) provide good surveys of the diversity and regional distribution of chydorid species in Norway. Based on surveys of nearly 2,500 lakes across the country, several authors also discuss various aspects on microcrustacean diversity and abundance, including the contribution of littoral crustaceans to zooplankton richness (Walseng *et al.*, 2006), energy input and richness (Hessen *et al.*, 2007), rarity and commonness (Hessen & Walseng, 2008), and diversity and dispersal by birds (Hessen *et al.*, 2019).

As pointed out by Adamczuk (2014) in a detailed study of niche separation, the role of environmental parameters for chydorids still remains unsolved, and only a few detailed ecological studies on Norwegian chydorids have been published (Eie, 1974; Sandøy & Nilssen, 1986; Koksvik, 1995; Jensen *et al.*, 2013, 2014), none of them from subarctic lakes. In subarctic Finland close to Norway, however, Korhola (1999) and Nevalainen *et al.* (2018) studied recent and fossil cladoceran assemblages, including chydorids, and their relation to environmental variables in two sets of lakes across the treeline, and Rautio (2001) correlated chydorid diversity, occurrences, and seasonal abundances to environmental factors in 17 fishless ponds. The studies by Adalsteinsson (1979), Einarsson & Örnólfssdóttir (2004), and Örnólfssdóttir & Einarsson (2004) on chydorid ecology in relation to habitat, predation, and phenology in Myvatn, Iceland, just south of the polar circle, are also relevant, but the general situation is that there are few detailed ecological studies on chydorids from subarctic Europe.

In light of this shortage of ecological studies, our study addresses the chydorid community of the subarctic Takvatn, a lake situated at 69°N in northern Norway. Four species of chydorids were identified from the shore region of the lake as part of a regional survey (Walseng & Halvorsen, 1993), and three additional species were found in fish stomachs (Jørgensen & Klemetsen, 1995), but no ecological studies had been undertaken. Our study therefore focuses on the diversity, seasonal abundance, life histories, and vertical movements of chydorids in Takvatn.

Chydorids have an exceptionally high genetic diversity (Sacherova & Hebert, 2003), a high morphological variation (Fryer, 1968; Flössner, 2000; Bledzki & Rybak, 2016), as well as high ecological variation (Duigan, 1992; Nevalainen, 2010; Adamczyk, 2014; Nevalainen & Luoto, 2017). We therefore proposed the hypothesis that chydorid species have different life histories related to different population developments and ecological niches in Takvatn. The heterogonous cladoceran life histories imply cyclic shifts between parthenogenetic and sexual reproduction. The cycles can be mono-, di-, or polycyclic (Flössner, 2000). Only one cycle per year is likely this far north, but we expected differences among species in 1) the seasonal timing of parthenogenesis and sexual reproduction (gamogenesis), 2) the number of parthenogenetic generations, and 3) the seasonal development of population abundances. As some chydorids can shift to the pelagic environment (Örnólfssdóttir & Einarsson, 2004; Walseng *et al.*, 2006), we also tested if there were any movements from the bottom and, if so, if there were differences in these movements between day and night or with season.

## METHODS

Takvatn is a 15 km<sup>2</sup> and 80 m deep oligotrophic (phosphorus concentration < 5 ppm) and dimictic lake at 214 m a.s.l. in the

Målselv river system, North Norway. The watershed has a mixed forest dominated by birch (*Betula*). There are two months of mid-night sun and two months of polar night, and the lake is icebound for five to six months. Maximum epilimnic temperatures are 14–15 °C in August. The lake has a fish community of arctic charr *Salvelinus alpinus* (Linnaeus, 1758), brown trout *Salmo trutta* Linnaeus, 1758 and three-spine stickleback *Gasterosteus aculeatus* (Linnaeus, 1758), and has been widely studied since 1980, see Amundsen *et al.* (2009, 2013) (food webs); Klemetsen & Knudsen (2013) (birds); Amundsen *et al.* (2007), Eloranta *et al.* (2013), Persson *et al.* (2013), and Knudsen *et al.* (2014) (fish ecology); Knudsen *et al.* (2008) and Soldanova *et al.* (2017) (parasites); Dahl-Hansen *et al.* (1994) and Primicerio (2000) (zooplankton); Klemetsen & Elliott (2010) and Frairer *et al.* (2016) (macrobenthos). An experimental mass removal of 35 mt of charr that influenced the fish community heavily was undertaken during 1984–89 (Klemetsen *et al.*, 2002; Persson *et al.*, 2007, 2013; Amundsen *et al.*, 2019).

The littoral zone covers about 30 % of the lake area and has exposed, hard bottom substrates without macro-vegetation to about 3 m depth. A vegetation belt dominated by *Nitella* (Chlorophyta) but also some angiosperms like *Myriophyllum* and *Potamogeton* are found in the 3–12 m zone. Samples were taken between 5 and 10 m depths in this belt. Temperatures at 5 m depth were 2–5 °C during sampling in June, 9–12 °C in July, 13–12 °C in August, 10–7 °C in September, and 6 °C in October.

A bottom sledge similar to, but smaller than, Beyer's sledge used for marine epi-benthos (Hesthagen, 1970), was constructed for the sampling. It had a frame of aluminium pipes with a 63 cm long net made from 300 µm mesh nylon cloth mounted inside. A 26 cm slip, which led substrate and vegetation into the net during towing, was mounted in front of the net. The sledge was towed slowly for ~30 s by an outboard powered boat. The length of the rope was standardised as three times the depth.

Sampling was done at daytime (14–16 hrs) with about two-week intervals between early June and October 1994 in Hauglibukta Bay on the SE side of the lake (69°05'N, 19°08'E). The first date (12 June) was 2 d after ice-break and the last sample was taken in October, giving a set of nine samples. The lake froze in November, and the time frame covered as much of the ice-free season as practically workable. The bay has a wide and gently sloping area with patches of vegetation in the 5–10 m depth zone. Six samples with substrate and vegetation were taken separately each time and the material was sifted in a nearby stream by placing the sample back in the net and washing from the outside with stream water. The sifted samples were then preserved in ethanol.

In order to explore if any species of benthic microcrustaceans performed movements into the pelagial, 1 m tall transparent funnel-shaped traps with a collection bottle on top were placed in the *Nitella* belt, six at the bottom and six at 0.5 m above the bottom. The traps were taken up, emptied, and replaced two times, day and night, at all sampling dates.

Sorting and identification were done using a stereomicroscope at 20–80× magnification. As this turned out to be very time-consuming due to much sediments and a high number of specimens, the material was reduced to one sample from each date. The selected samples had similar amounts of sediments and plants. Small amounts of substrate were examined successively in plankton-counting chambers until the whole sample was done. All microcrustaceans in each sample were counted and the cladocerans were identified after Flössner (1972), Enckell (1980), and Smirnov (1996). The nomenclature follows Bledzki & Rybak (2016). Macrobenthos (i.e. gastropods, bivalves, amphipods, insects, and mites) and planktonic crustaceans assumed to have been caught when the sledge was hauled to the surface (i.e. copepods and the cladocerans *Polyphemus pediculus* (Linnaeus, 1761), *Holopedium gibberum* Zaddach, 1855, *Daphnia* sp., and *Bosmina* sp.) were taken out at this stage.

Body lengths (from the front of the head to the end of the carapace) of the studied chydorids were measured with measure oculars in randomised subsamples of up to 50 specimens. Numbers of parthenogenetic and ephippial eggs were counted, and males were treated separately. We use the terms ‘spring generation’ for animals that hatch from overwintering ephippial eggs and ‘summer generation’ for animals that hatch from parthenogenetic eggs.

## RESULTS

A total of 37,280 specimens of benthic microcrustaceans were retrieved from the bottom-sledge sampling (Table 1). Ostracods (17,250) were particularly numerous, especially during summer, and benthic copepods (8,581) were also abundant. These were not treated further, but samples included three to four species of ostracods and two to three species of harpacticoid copepods. Among the 11,495 cladocerans sampled, we identified one daphniid (*Simocephalus vetulus* O.F. Müller, 1776), one ilyocryptid (*Ilyocryptus sordidus* (Lievin, 1848)), one macrothricid (*Lathonura rectirostris* (O.F. Müller, 1785)), one ophryoxid (*Ophryoxus gracilis* Sars, 1862), and five chydorids (*Euryercus lamellatus* (O.F. Müller, 1776), *Chydorus sphaericus* (O.F. Müller, 1776), *Alona affinis* (Leydig, 1860), *Alonopsis elongata* Sars, 1861, and *Acroperus harpae* (Baird, 1835)). The former chydorid subfamily Euryercinae has recently been raised to family level (Dumont & Silva-Briano, 1998; Kotov, 2000; Bledzki & Rybak, 2016), but herein we treat *E. lamellatus* as a chydorid for simplicity. *Chydorus sphaericus* has been recently revealed to be a complex of several species that cannot be distinguished by the morphology of parthenogenetic females (Belyaeva & Taylor, 2009; Kotov et al. 2016). We therefore treat it as a species *sensu lato*.

No chydorids were caught in the funnel traps during summer, and only very low numbers of *E. lamellatus* were taken during autumn, which suggests that the chydorids performed no upward migrations through or above the vegetation, neither during the midnight sun period (June–July) nor when the nights got dark (August–October). Our traps were, however, too tall to show migrations on a smaller scale, as found by Örnólfsson & Einarsson (2004) and Nevalainen (2008).

Chydorids (9,511) were by far the most abundant benthic cladocerans (there were also 1,286 specimens of *S. vetulus*, 146 *I. sordidus*, 18 *L. rectirostris*, and 488 *O. gracilis*), and their numbers increased markedly during the season (Fig. 1). Only four specimens of *A. elongata* were found, in July and August, all females without eggs. Along with *S. vetulus* and the macrothricids, it was not treated further. The relative abundances of the other four species varied during the ice-free season. *Alona affinis* occurred in low numbers (279) from late June to October but were most abundant in summer. Parthenogenetic eggs were found in late June, males in September, and ephippiae in October.

The numbers of *A. harpae* were low in early spring but increased rapidly to a peak in early July before decreasing to a minimum in early August (Fig. 1). Abundance rose to a very high level from late August and through September, before decreasing somewhat again in October. *Chydorus sphaericus* was the most

abundant species immediately after ice-break and the abundance was slightly higher in late June before decreasing markedly during summer and reaching a minimum number in early August. Abundance then increased sharply for the rest of the season, peaking in October. *Euryercus lamellatus* had the lowest abundance of the three common species. It appeared immediately after ice-break in June like the other species, and abundance increased in July before reaching a minimum in early August. Abundance increased somewhat after that but then again decreased to a very low level in October. The general tendency therefore was an increase in early summer followed by a minimum in late summer, and then a second increase in autumn that was very rapid in the two small-size species but much slower in *E. lamellatus*. This species and *A. harpae* decreased in October, whereas *C. sphaericus* had its highest abundance at that time.

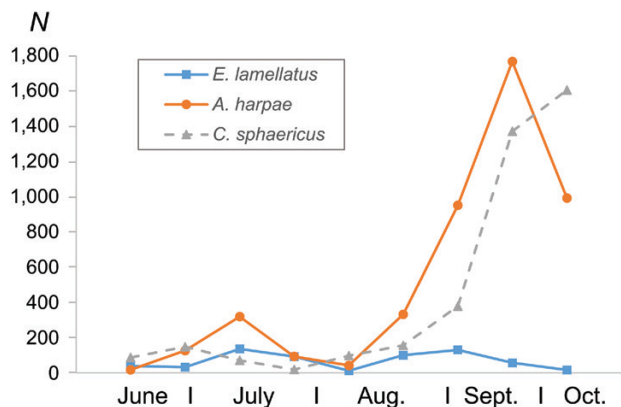
The first sample of *E. lamellatus* in June exclusively consisted of small females without eggs (Fig. 2), constituting the winter generation hatched from overwintering ephippial eggs. The first few females with parthenogenetic eggs were found in the early-July samples and juveniles of a first summer generation appeared in late July. The two generations were clearly seen co-occurring in early August (Fig. 2). The discrete size distributions in late August indicated that a second summer generation had appeared, i.e. there were now three (one spring and two summer) generations in the population (Figs. 2, 3). A possible fourth generation was indicated in early September. The ratio of ovigerous females varied from 2–37% among samples and the number of eggs in the brooding chambers varied from 2–8%. All ovigerous females from middle September and October were ephippial and the number of ephippial eggs were 1–4. Males occurred in both samples from September (14 and 16%) but not in October. Their sizes varied little (1.00–1.25 mm) and they were always smaller than ovigerous females. All October females were large-sized and there was a high incidence of ephippiae.

Body lengths of *E. lamellatus* grew steady and significantly from early June to early August in the first (spring) generation (Mann-Whitney U-test,  $P < 0.05$ ), and then levelled out (Fig. 3). A similar significant ( $P < 0.05$ ) growth in size was seen in the first summer generation from late July to October. The two samples of possible second and third summer generations also showed significant ( $P < 0.05$ ) growths.

*Acroperus harpae* was also present throughout the season. Small females, and a single female of adult size but without eggs, were found in the sample from early June (Fig. 4). The first few parthenogenetic females appeared in late June, and a high proportion (78%) of the females had eggs in early July (Fig. 4). The average proportion of ovigerous females was high (56%) during the rest of the season as body lengths significantly increased ( $P < 0.05$ ) until early August, and then levelled out (Fig. 5). The number of parthenogenetic eggs was always two. A low number of juveniles (< 0.50 mm) were observed for the first time in the sample from late August, and again in September and October. Males occurred from early September to October (2–14%). Their sizes (0.50–0.70 mm) overlapped with the smaller ovigerous females. Only one of the ovigerous females from the 17 September sample

**Table 1.** Seasonal abundance of benthic microcrustaceans (Cladocera: Daphniidae, other Cladocera (Ilyocryptidae, Macrothricidae, Ophryoxidae), Chydoridae; Ostracoda; and Copepoda: Harpacticoida) in bottom sledge samples from the littoral zone in Takvatn, Norway, 1994; nc, not counted.

Date	12 June	30 June	10 July	24 July	08 Aug.	23 Aug.	04 Sept.	17 Sept.	11 Oct.	Total
Daphniidae			162	356	nc	183	74	104	407	1,286
Other Cladocera		2	98	289	8	125	70	55	5	652
Chydoridae	149	310	533	223	194	656	1,582	3,239	2,625	9,511
Ostracoda	2,220	783	5,355	2,606	873	1,041	1,644	1,438	1,290	17,250
Harpacticoida	860	334	1,108	835	140	697	1,233	1,098	2,276	8,581
Total	3,229	1,429	7,256	4,309	1,215	2,702	4,603	5,934	6,603	37,280



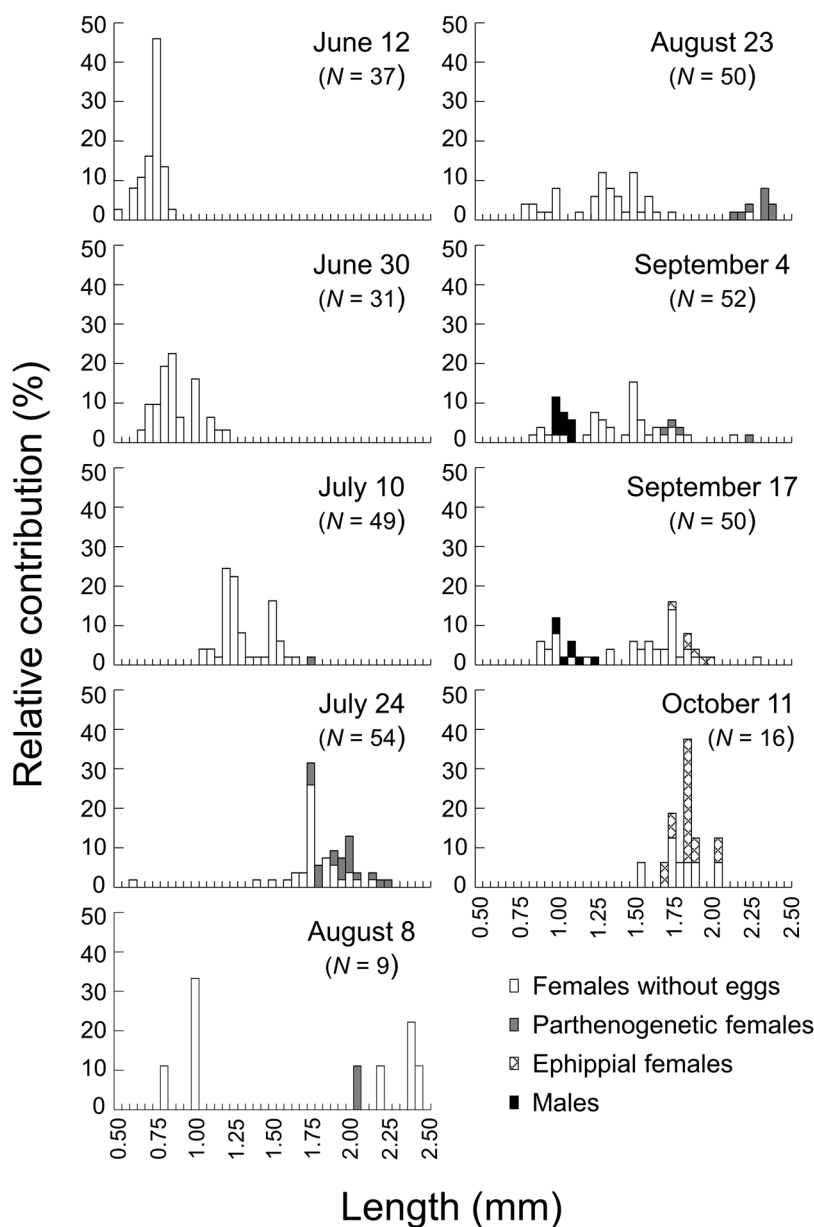
**Figure 1.** Abundance of *Eurycerus lamellatus*, *Acroperus harpae*, and *Chydorus sphaericus* in littoral bottom sledge samples during the 1994 ice-free season in Takvatn, Norway. This figure is available in colour at *Journal of Crustacean Biology* online.

had an ephippium, the rest were still parthenogenetic. All were ephippial in October and all ephippiae had one egg.

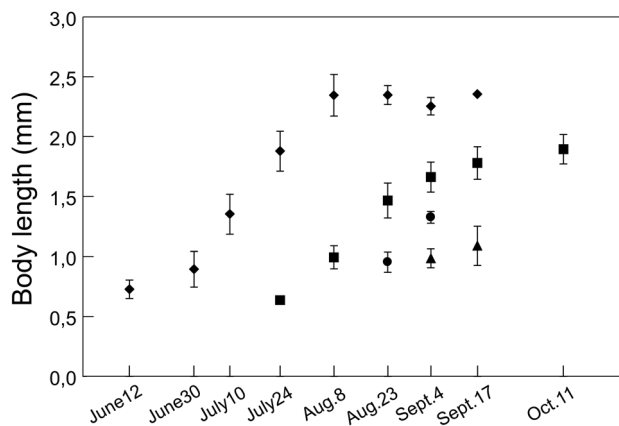
*Chydorus sphaericus* with parthenogenetic eggs were found in all samples, from early June to October (Fig. 6). The incidence of ovigerous females was always high, with a seasonal average of 68% and a peak at 95% in late July. The number of eggs was always two. A few juveniles were found in June but not later. Males, and females with ephippiae, were not recorded at any time. The mean carapace length of females was 0.43 mm without significant differences between any samples (Fig. 7;  $P < 0.05$ ).

DISCUSSION

Walseng & Halvorsen (1993) recorded *Chydorus sphaericus*, *Alonella excisa* (Fischer, 1854), *Alona guttata* Sars, 1862, and *Rhynchotalona falcata* (Sars, 1862) from the upper shore habitat in Takvatn, and Jørgensen & Klemetsen (1995) found *Eurycerus lamellatus*, *Alonopsis elongata*, and *Acroperus harpae* in fish stomachs.



**Figure 2.** Distributions of body (carapace) lengths of females without eggs, females with parthenogenetic eggs, females with ephippial eggs, and males of *Eurycerus lamellatus* during the 1994 ice-free season in Takvatn, Norway.



**Figure 3.** Mean carapace lengths with standard deviations of female *Eurycerus lamellatus* during the 1994 ice-free season in Takvatn, Norway. Diamonds, first (spring) generation; squares, second generation; circles and triangles, possible third and fourth generations.

Our collections added *Alona affinis*, thereby raising chydorid richness to eight species. In comparison, the Dokka river delta in south Norway had 28 chydorid species (Halvorsen *et al.*, 1996), and Målsjøen, a lake in central Norway, had 26 (Koksvik, 1995). Nevalainen (2010, 2011) found 10–26 species in lakes in southern Finland, and in Poland, Adamczuk (2014) reported 22 species in one lake. Fryer & Foreshaw (1979) found 17 species on the island of Rhum, UK (Inner Hebrides) and Fryer (1985) 21 species in a number of water bodies in Yorkshire. Surveys in southern Norway (Jenssen *et al.*, 2013) and across Finland (Luoto *et al.*, 2013) concluded that the availability of phosphorus was the most important variable in explaining the composition of assemblages of Cladocera. Apart from polluted and very productive lakes (Nevalainen, 2010), the diversity of littoral microcrustaceans tends to increase with trophic degree (Lemly & Dimmick, 1982; Nevalainen *et al.*, 2018). Chydorid diversity decreases with latitude in Norway (Walseng, 2018), and Hessen *et al.* (2007) found that low temperatures constrain the number of microcrustaceans in lakes. The low diversity in Takvatn is therefore as could be expected for a cool oligotrophic lake this far north. Similar numbers are reported from lakes and ponds in subarctic Finland (Korhola, 1999; Rautio, 2001; Nevalainen *et al.*, 2018). Chydorids are strongly adapted to the variation in space, substrate, and structure in the littoral environment, above all plant diversity (Sacherova & Hebert, 2003; Nevalainen, 2010, 2012; Adamczuk, 2014). The upper littoral of Takvatn is stony or sandy from strong wave action. There is no emergent or floating-leaf vegetation and the submerged vegetation is patchy and of low diversity. In addition to high latitude, a long ice period (5–6 mo), low summer temperatures, and low production, the poor vegetation is probably the main reason for the low diversity of chydorids in the lake.

The sampling regime with a bottom sledge of a novel design provided the possibility to explore the life cycles, somatic growth, and seasonal abundance variations of the common chydorids in the deeper littoral of the lake, with some minor restrictions of the size selection of the sampling net. The 0.3 mm mesh size should catch all individuals of *E. lamellatus*, and all instar I juveniles of *A. harpae* are  $\geq 0.37$  mm (Sinev, 2009). Instar I juveniles of *C. sphaericus* are  $\leq 0.29$  mm (Frey, 1980), but all other individuals of *C. sphaericus* should be caught as instar II juveniles are  $\geq 0.31$  mm.

As expected, the three common species of cladocerans had different life histories. *Eurycerus lamellatus* and *Acroporus harpae* both had a spring generation of juveniles that must have hatched from

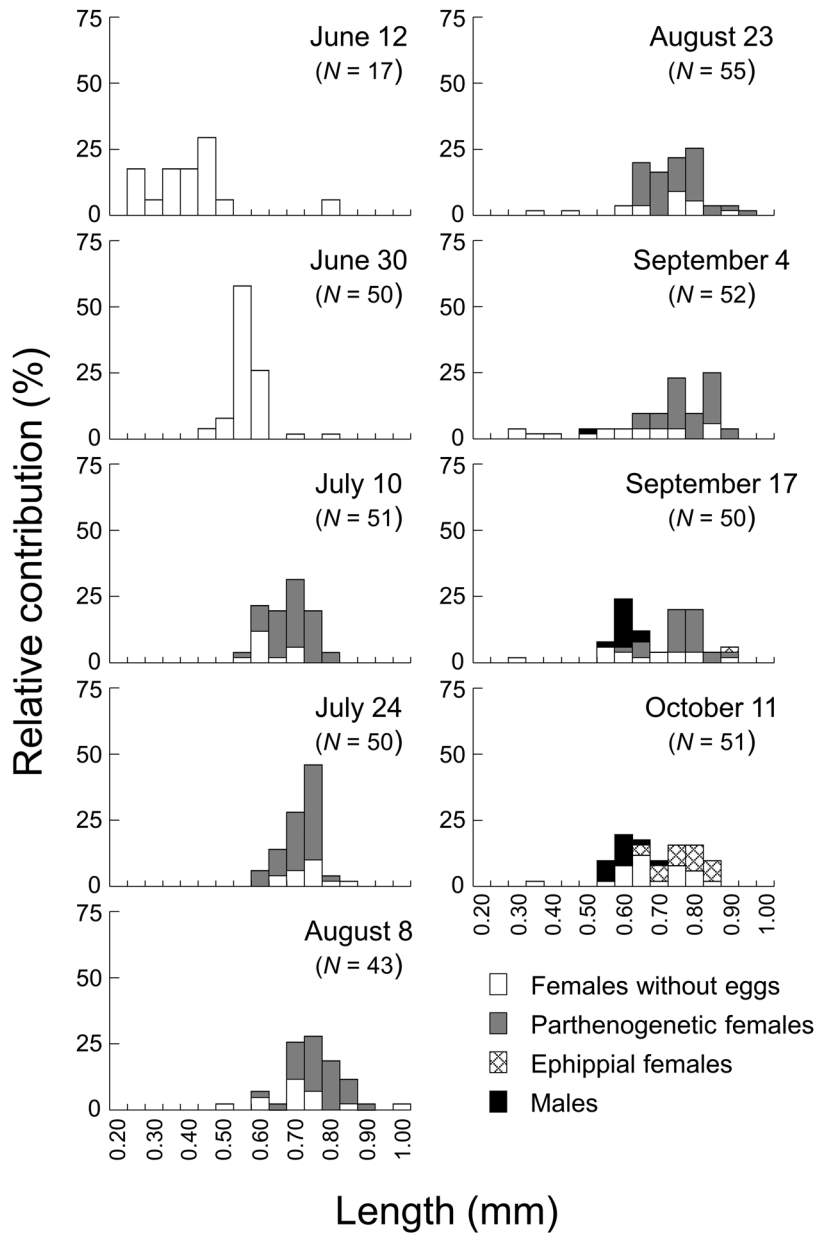
ephippial eggs, parthenogenesis in summer, and gamogenesis with new ephippiae in autumn. These species were monocyclic in Takvatn. In marked contrast, *Chydorus sphaericus* had ovigerous females already at ice-break, parthenogenesis in females with constant body sizes throughout the entire ice-free season, but never males or ephippial females and therefore no gamogenesis. We conclude that this species was acyclic in the lake.

The two monocyclic species did, however, develop differently with season. *Eurycerus lamellatus* had a period of parthenogenesis of about six weeks from late July to early September, whereas *A. harpae* reproduced asexually much longer, for at least ten weeks from late June/early July to late September. There was also a difference in the timing of gamogenesis. Both populations were dominated by ephippial females in October but as *E. lamellatus* had a high incidence of males in early September and *A. harpae* in late September, sexual reproduction probably started later in *A. harpae*. As the temperatures in Takvatn were low in late June/early July and late September/October, the early start of parthenogenesis and the later gamogenesis in *A. harpae* can be related to differences in temperature tolerance. This species is cold-adapted, even described as arctic because of its high frequency in the Arctic (Harmsworth, 1968). Its highest abundance in barren ponds at high altitudes in Finnish Lapland (Rautio, 2001) confirms this. Likewise, gamogenesis in *A. harpae* occurred close to freeze-over in Målsjøen, Norway (Koksvik, 1995) and in several lakes in Finland (Nevalainen & Sarmaja-Koronen, 2008).

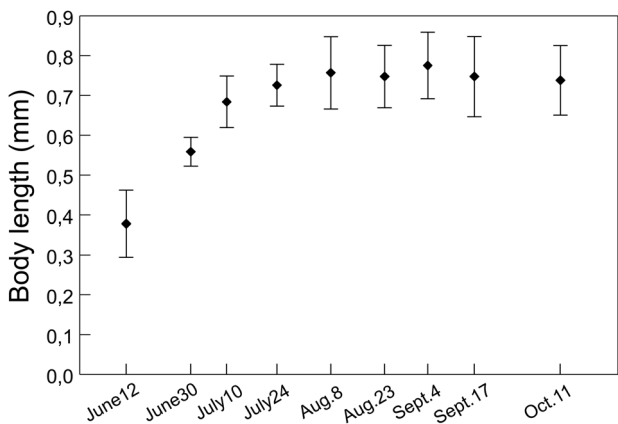
The expectation of different numbers of parthenogenetic generations among species could not be verified directly because small size differences and rapid growth obscured the size distributions in the two small species. As *E. lamellatus* clearly had three, possibly four, generations with the shortest period of asexual reproduction (Fig. 3), and the remaining two species produced large populations in autumn (Fig. 1), they probably also had at least three generations.

In *A. harpae*, the body sizes grew steadily with unimodal size distributions and with high proportions of parthenogenetic females (Fig. 4) until mid-September (Fig. 5). Despite the high abundance of ovigerous females already present from early July, no juveniles appeared until August and their numbers were always low. The abundance minimum in late summer (Fig. 1) suggests that the recruitment was insignificant during early summer when temperatures were low, although the spring generation had parthenogenetic eggs at this time. The juveniles that appeared from late August (Fig. 4), and particularly the very rapid population growth during September (Fig. 1), show that a strong recruitment from parthenogenesis took place in the population in autumn. The conditions for somatic growth are good at this time and the juveniles probably grew fast up to adult size. Such a condition is supported by the short duration times of 4–5 d that Bottrell (1975) found for *A. harpae* instars at temperatures that prevailed in Takvatn at this time.

In *Chydorus sphaericus*, parthenogenetic females of constant sizes were present at all times, from early spring to late autumn, whereas almost no juveniles were found (Fig. 6). As can be seen, the incidence of ovigerous females increased through summer, until it was very high (95%) in late July. Abundance first went slightly up but then decreased and reached a minimum (Fig. 1). The absence of juveniles indicates that recruitment was insignificant up to this time. The very high incidence of ovigerous females in late July (Fig. 6) followed by the sharp increase (49%) and higher abundance of females without eggs in early August (Fig. 1), suggests that the first parthenogenetic summer generation took place during this two-week interval. The very rapid population increase which followed indicates that the conditions for growth (food, temperature) became optimal. As duration times for *C. sphaericus* instars were found to be 4 d at 10 °C and 3 d at 15 °C (Bottrell, 1975), the instar II juveniles probably grew very fast up to the size of the smallest



**Figure 4.** Distributions of body (carapace) lengths of females without eggs, females with parthenogenetic eggs, females with ephippial eggs, and males of *Acroperus harpae* during the 1994 ice-free season in Takvatn, Norway.

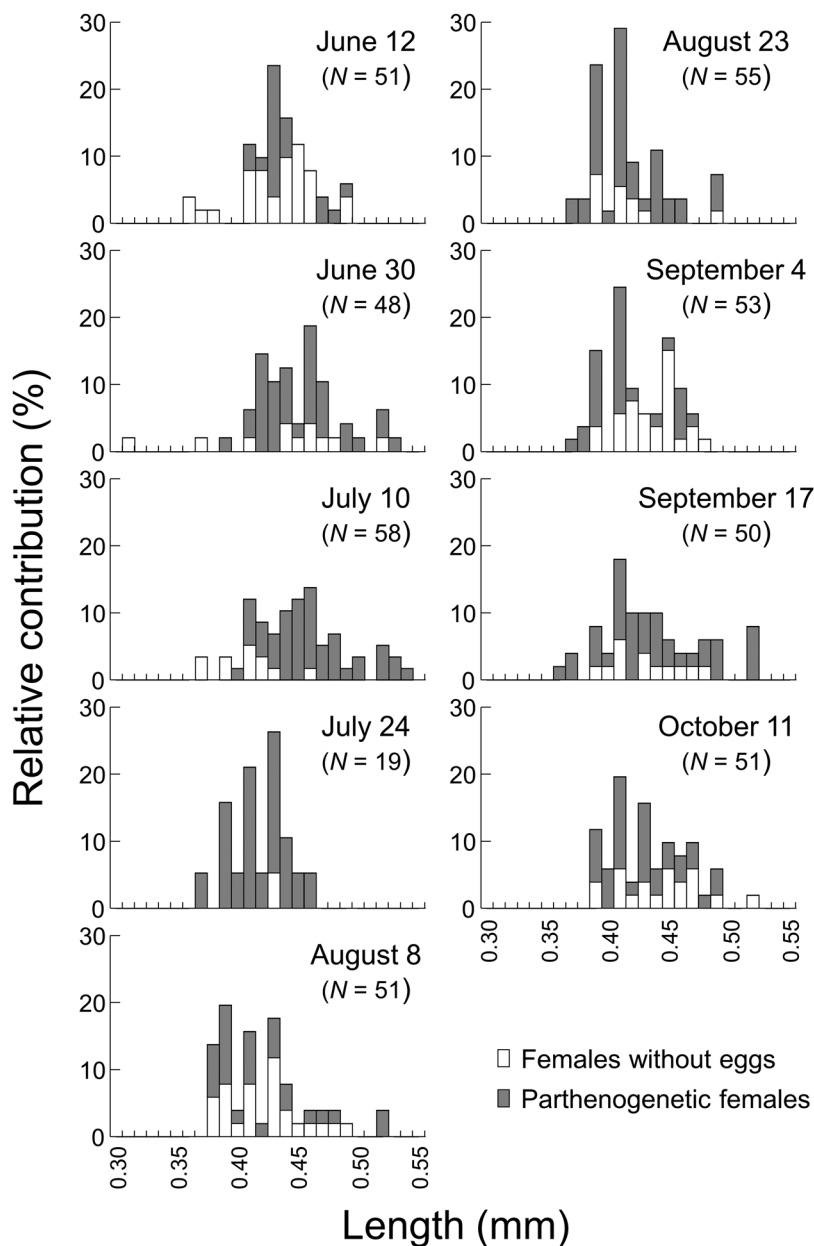


**Figure 5.** Mean carapace length with standard deviations of female *Acroperus harpae* during the 1994 ice-free season in Takvatn, Norway.

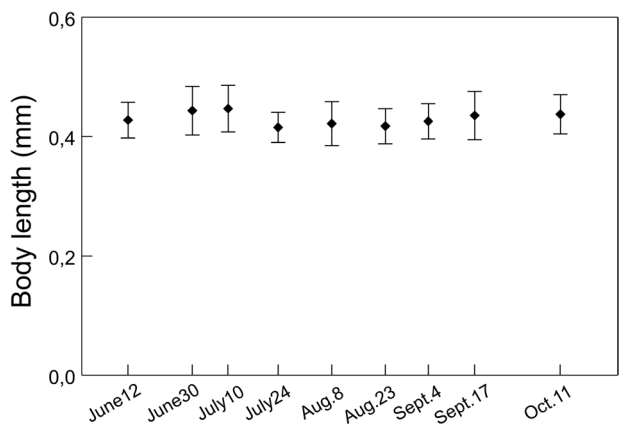
ovigerous females (0.36 mm; Fig. 7) under the favourable conditions in August and September, with temperatures of 11–13 °C.

As expected, population abundance developed differently with season in the three common species in Takvatn. All had an initial population increase, which was followed by a decrease that ended at very low abundances in late July/early August (Fig. 1). Low densities in summer are often found in lacustrine microcrustaceans, as well documented for *C. sphaericus* and *E. lamellatus* in Myvatn, Iceland (Örnólfssdóttir & Einarsson, 2004). In Takvatn, this is likely to be related to low temperatures and slow development of the littoral vegetation in early summer. In August and September, however, when the vegetation reaches maximum biomass and stem height and the water is warmest, the populations of *A. harpae* and *C. sphaericus* grew very fast towards their autumn peaks in abundance.

The very low population abundance of *E. lamellatus* in autumn (Fig. 1) is probably related to fish predation, which can have substantial impact on large littoral cladocerans (Robertson, 1988).



**Figure 6.** Distributions of body (carapace) lengths of females without eggs and females with parthenogenic eggs of *Chydorus sphaericus* during the 1994 ice-free season in Takvatn, Norway.



**Figure 7.** Mean carapace length with standard deviations of female *Chydorus sphaericus* during the 1994 ice-free season in Takvatn, Norway.

Einarsson & Örnólfsson (2004) found a marked reduction in *E. lamellatus* abundance by predation from sticklebacks in Myvatn, Iceland. High densities of sticklebacks, arctic charr, and brown trout feed in the littoral zone in Takvatn (Klemetsen *et al.*, 2002; Eloranta *et al.*, 2013; Amundsen *et al.*, 2019). Sticklebacks are small fishes (< 7 cm) and Jørgensen & Klemetsen (1995) found that benthic microcrustaceans dominated their stomach contents from August and out the ice-free season. *Acroporus harpae* and *C. sphaericus* were eaten in low numbers, whereas there was a clear preference for *E. lamellatus* in volume and occurrence. Small charr (< 17 cm) had also preyed on *E. lamellatus* in autumn but not on the other species. Only a slight mortality was therefore caused by one fish predator on the small chydorids, whereas the large individuals of *E. lamellatus* had a double predation pressure from two fish species.

The literature (Flössner, 1972, 2000; Bledzki & Rybak, 2016; Walseng, 2018) describes *E. lamellatus*, *C. sphaericus*, and *A. harpae* as euryplastic species that are commonly found in the littoral of oligotrophic lakes and have wide distributions in

Europe, including the northern latitudes. There are nevertheless differences among them, as revealed by our study. Their life histories most certainly reflect other niche differences. Although beyond the scope of this study, we know from the literature that *E. lamellatus* and *A. harpae* are strongly associated with macrophytes (Fryer, 1968; Flössner, 1972; Duigan, 1992; Rautio, 2001; Nevalainen *et al.*, 2018) but can also be found on open substrates (Fryer, 1968; Flössner, 1972), whereas *C. sphaericus* tolerates a wide range of conditions, including effective clinging to plants and moving through mud and detritus (Fryer, 1968). *Euryercus lamellatus* can swim forcibly in small bursts, but the typical behaviour is to move along stems and leaves, feeding on diatoms and other periphyton (Flössner, 1972, 2000). It avoids finely disintegrated particles that smaller species frequently utilizes. *Acroperus harpae* feeds on detritus and periphytic algae on various kinds of plants (Fryer, 1968), whereas *C. sphaericus* is a microfilter-feeder (Duigan, 1992; Flössner, 2000) and also vigorously scrapes diatoms off surfaces (Fryer, 1968).

That *C. sphaericus* did not reproduce sexually in autumn was an unexpected result. It is also unlikely that sexual reproduction took place during winter because the lower limit for gamogenesis has been estimated to be 2 °C for cladocerans including *C. sphaericus* (Nevalainen & Luoto, 2010) and the temperatures under the ice in the upper 12 m in Takvatn were 0.1–0.4 °C (Klemetsen *et al.*, 2003). The occurrence of full-grown parthenogenetic females with eggs at ice-break supports the conclusion that *C. sphaericus* was acyclic in the lake. Acyclic life histories are not uncommon in planktonic cladocerans like e.g. *Daphnia*, and are also known in *C. sphaericus*. But as discussed by Flössner (1972), this kind of strategy is usually found in large, deep lakes with small seasonal variations. It was therefore surprising that *C. sphaericus* is acyclic in Takvatn, which is a typical dimictic lake with long ice-periods and challenging environmental variations. Similar results, with no males or ephippial females at any time of the year, have been reported from lake Målsjøen in central Norway (Koksvik 1995). This may suggest that acyclic life histories can be a poorly known strategy for *C. sphaericus* in northern lakes having many months of winter ice.

Takvatn is a large oligotrophic lake where long winters with ice cover and very low temperatures, cool summer temperatures, low production, barren shores, poor vegetation, and fish predation are demanding factors that result in a low chydorid diversity. Eight species are nevertheless present in the lake and three of them, all ecologically plastic and widespread, are abundant and co-exist by adapting to ecological niches that differ in several ways, but mainly in relation to vegetation usage, preferred substrates, predation exposure, and life histories. Similar large lakes (areas > 10 km<sup>2</sup>) are commonly found in subarctic Europe, i.e. northern Scandinavia and Finland and northwestern Russia. We assume that the present results on chydorid diversity and life histories are likely to be typical for large oligotrophic lakes in the region.

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