

Seasonal variations in the profundal Chironomidae (Diptera) assemblage of a subarctic lake

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Zoobenthos samples were collected over a 12-month period in the profundal zone of the subarctic Fjellfrøsvatn, a lake in northern Norway. Chironomid larvae numerically dominated the profundal zoobenthos and their mean density decreased with increasing depth. *Procladius* (*Holotanypus*) sp. A, *Mesocricotopus thienemanni*, *Psectrocladius* (*Mesopsectrocladius*) sp. and *Heterotrissocladius subpilosus* exhibited the highest densities at the depth of 20 m, whereas *H. subpilosus* dominated the chironomid assemblage at 30–40 m. At 20-m depth, the chironomid density was highest in June, decreased towards autumn, and was relatively stable during the ice-covered period. The peak density in June was mainly related to a strong seasonal pattern in the density of *Heterotrissocladius maeaeri* and *M. thienemanni*. At 30–40-m depth, no significant seasonal variations in total density of chironomid larvae were observed, although the density of *H. subpilosus* exhibited a significant seasonal peak in winter. Larval instar groups of *H. subpilosus* were identified from a classification based on head capsule width. The profundal dwelling *H. subpilosus* were hemivoltine, having predominantly a two-year life cycle.

Introduction

The profundal zone is the most homogenous benthic habitat of oligotrophic lakes with no vegetation present, usually a smooth bottom surface, and only minor seasonal variations in environmental factors such as temperature, light and water chemistry (Särkkä 1983, Wetzel 2001). In Arctic and subarctic lake systems, chironomids are particularly important in the macroinvertebrate community (Oliver 1968, Welch 1976, Moore 1978, 1980, Aagaard 1982, 1986, Hershey 1985, Nyman *et al.* 2005), and chironomid larvae, especially of the genus *Heterotrissocladius*, constitute the main profundal fauna in these

lakes (Brundin 1956, Sæther 1975a, Welch 1976, Aagaard 1982, 1986, Lindegaard and Mæhl 1992, Mousavi *et al.* 2002). Although profundal chironomids have frequently been used for lake classification and monitoring (e.g. Brundin 1949, Sæther 1975b, 1979, Wiederholm 1980, Gertsmeier 1989a, Johnson and Wiederholm 1989, Nyman and Korhola 2005, Bitusík and Svitok 2006), few studies have addressed seasonal variations in chironomid development, density and assemblage structure (but see e.g. Danks and Oliver 1972, Aagaard 1978a, 1982, Butler 1982, Gertsmeier 1989b, Johnson *et al.* 1990, Danks 2006). Studies during the ice-covered period are particularly few (but see Aagaard 1978b), even

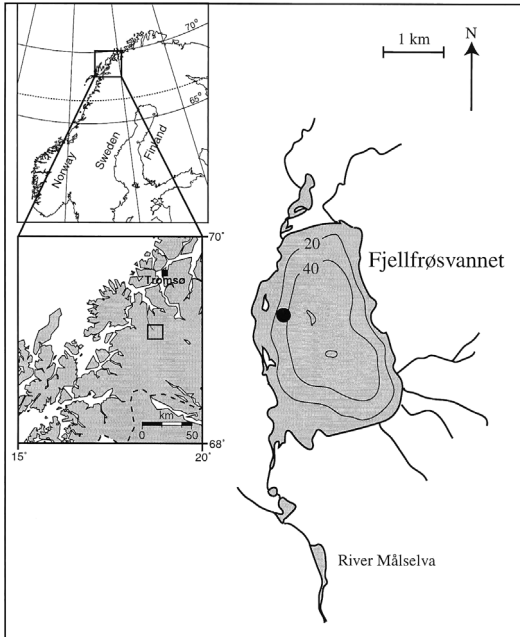


Fig. 1. Map of the study area, Fjellfrøsvatn, northern Norway.

though in subarctic and Arctic lakes the period of ice-cover often exceeds the length of the ice-free period. Furthermore, the life history of most zoobenthos, including the Chironomidae, in oligotrophic, cold (i.e. Arctic, subarctic and high mountain) lakes is not well known (Tokeshi 1995, Danks 2007).

In the present study, the species composition and seasonal variations in density of the profundal chironomid assemblage were investigated over a 12-month period in the subarctic oligotrophic Fjellfrøsvatn, northern Norway. In lakes of northern Scandinavia, larvae of the Orthoclaadiinae chironomid *Heterotrissocladius subpilosus* often dominate the profundal zoobenthos community (Brundin 1949, Sæther 1975a, Aagaard 1982). This was also the case in Fjellfrøsvatn, and due to the importance of *H. subpilosus*, the life history of this species was also investigated with respect to the presence of different larval instars.

Study area

Fjellfrøsvatn (69°05'N, 19°20'E) is an oligo-

trophic and dimictic lake situated 125 m above sea level in Troms county, northern Norway (Fig. 1). The lake is of a regular shape and has a single basin with a maximum depth of 88 m, a total surface area of 6.6 km² and a catchment's area of 90 km². The surrounding area consists of woodland, predominately birch (*Betula pubescens*), and treeless mountains. There are a few small farms and some cabins on the western side and a pine (*Pinus sylvestris*) planted area on the eastern side. The shore region is mostly sandy or stony with little emergent vegetation. The ice-free season usually lasts from early June to late November. Secchi disc transparency varied from 13–16 m, and the temperature in the profundal zone (measured at 30 m) ranged between 4–8 °C from June to November, and was 2.3 °C during the ice-covered period of 1998–1999.

Arctic charr (*Salvelinus alpinus*) and brown trout (*Salmo trutta*) are the only fish species present in the lake. Chironomid larvae and pupae are important food for fish in Fjellfrøsvatn and the nearby Takvatn (Amundsen and Klemetsen 1988, Amundsen 1989, Klemetsen *et al.* 1992, Jørgensen and Klemetsen 1995, Knudsen *et al.* 1997). In the profundal zone of both lakes, charr have been found to feed quite heavily on chironomids, mainly *H. subpilosus* (Knudsen *et al.* 1997, Amundsen and Knudsen 2009), and particularly on the pupae during the emergence period in summer (Klemetsen *et al.* 1992, Amundsen *et al.* 2008).

Methods

The study was carried out from June 1998 to May 1999. Sampling was performed 4 times during the ice-free season (June, August, October, and November: before ice freezing) and 3 times during the ice-covered period (December, February and May). Zoobenthos samples were taken from the depths of 20, 30 and 40 m in the profundal zone. Five or three replicate samples were taken at each depth using a 225 cm² Ekman grab during the ice-free and ice-covered season, respectively (fewer replicates were used during winter sampling due to practical difficulties with the frozen lake surface). The samples were washed and sieved through a 250 μm mesh

net and were stored in 70% ethanol. The preserved materials were examined microscopically to sort out, prepare and identify the chironomid larvae to the genus or, whenever possible, to the species level. The process of identification and mounting mainly followed Wiederholm (1983), but other references were also used for identification of particular species (Pankratova 1970, 1983, Sæther 1975a, Coffman 1978, Schnell and Aagaard 1996, Vallenduuk 2009; see also Fauna Europaea database). All the preserved chironomid larvae were identified and counted, and other major benthic taxa were also examined and counted. Larval growth development of the dominant species, *H. subpilosus*, was investigated through the season by examining the size-class frequency. The larvae were classified in different instars by measuring the width of the head capsule and the body length (McCauley 1974, Hershey 1985, Lindegaard and Mæhl 1992).

A Kolmogorov-Smirnov one-sample test revealed that the density distributions of the chironomid samples significantly deviated from a normal distribution both for the total chironomid density ($p < 0.001$) and each individual taxa ($p < 0.05$). Hence, the Kruskal-Wallis test was used to test the significance of seasonal and depth variations in chironomid density. The correlation between body length and head capsule width of *H. subpilosus* larvae was tested with Pearson's product moment correlation.

Results

Composition of the profundal fauna

Chironomid larvae was the most abundant macroinvertebrate group in the profundal of Fjellfrøsvatn during all seasons, amounting on average to 73% of the total zoobenthos density, followed by Oligochaeta (14%), bivalves (6%), Nematoda (6%), and chironomid pupae (1%). Among the chironomid larvae, a total of 28 taxa were recorded in the samples (Table 1). Three species were related to Tanypodinae, one to Diamesinae, 13 to Orthoclaadiinae and 11 to Chironominae. The number of chironomid taxa decreased with increasing depth, and the observed species richness was 24, 19 and 14 at

20, 30 and 40 m depths, respectively. The average total density of chironomid larvae in the profundal was 1328 ± 136 SE indiv. m^{-2} . The species *Heterotrissocladus subpilosus* and *Procladius (Holotanypus)* sp. A dominated numerically, having average densities of 384 ± 24 and 273 ± 31 indiv. m^{-2} , respectively. *Heterotrissocladus subpilosus* was particularly dominant at the depth of 40 m. Other common species were (in order of their decreasing numerical importance) *Mesocricotopus thienemanni*, *Psectrocladius (Mesopsectrocladius)* sp., *P. (Monopsectrocladius) calcaratus*, *Heterotrissocladus maeaeri*, *Micropsectra* sp., *Procladius (Holotanypus)* sp. B, and *Paracladopelma* sp. (Table 1). The largest abundance of chironomid pupae was observed in the benthos samples in spring, decreasing towards August, but a minor abundance of chironomid pupae was also observed in late autumn (November). *Heterotrissocladus subpilosus* was recorded among the pupae in June and August, but not in November.

Bathymetric variations

In the profundal, the chironomid density decreased with increasing depth, being 2687 indiv. m^{-2} at 20 m, and 825 and 474 indiv. m^{-2} at 30 and 40 m, respectively (Kruskal-Wallis test: $K_2 = 59.93$, $p < 0.001$). Whereas most taxa exhibited significantly higher densities at 20 m than at 30 and 40 m, there were usually no significant differences in the densities of different taxa between 30 and 40 m. The species composition was also similar between the depths of 30 and 40 m (Table 1), and the data from 30–40-m depth were therefore pooled in the further analyses. While the abundance of most species decreased with increasing depth, the density of *H. subpilosus* was constant and its relative abundance greatly increased with increasing depth, constituting 14%, 51% and 74% of the total chironomid abundance at 20, 30 and 40 m depths, respectively. At 20 m, *P. (Holotanypus)* sp. A (613 indiv. m^{-2}), *M. thienemanni* (448 indiv. m^{-2}), *P. (Mesopsectrocladius)* sp. (426 indiv. m^{-2}) and *H. subpilosus* (369 indiv. m^{-2}) exhibited the highest mean densities, whereas *H. subpilosus* (392 indiv. m^{-2}) numerically dominated at 30–40 m. The most common chironomid species of the

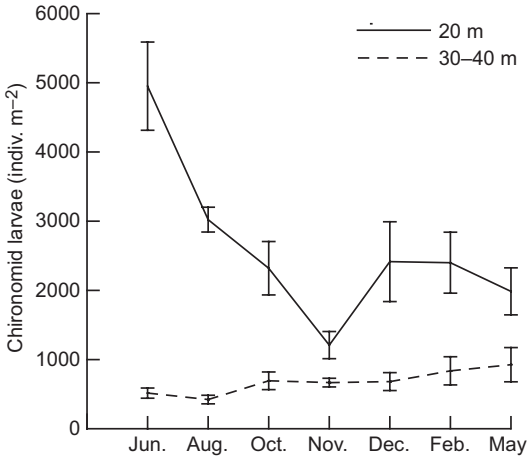


Fig. 2. Seasonal variations in total abundance (mean density \pm SE) of profundal chironomid larvae at 20 and 30–40 m depths.

profundal generally had the highest densities at 20 m, while the density of *H. subpilosus* and *Paracladopelma* sp. did not differ significantly with increasing depth (Kruskal-Wallis test: $K_2 = 1.96$, $p = 0.375$, and $K_2 = 0.795$, $p = 0.795$, respectively).

Seasonal variations

Significant seasonal variations were found in total abundance of chironomid larvae at 20-m depth (Kruskal-Wallis test: $K_6 = 21.320$, $p = 0.002$; Fig. 2). The average density of chironomid larvae was at its highest in June (4951 indiv. m⁻²), decreasing rapidly during the ice-free season and being lowest in November (1209 indiv. m⁻²). The abundance then slightly

Table 1. Chironomid larvae and their relative abundance (%) in the profundal zone of Fjellfrøsvatn.

No.	Chironomid taxa	20 m	30 m	40 m
Tanypodinae				
1	<i>Conchapelopia melanops</i>	0.5	0.2	0.6
2	<i>Procladius (Holotanypus) sp. A</i>	22.8	20.7	8.7
3	<i>Procladius (Holotanypus) sp. B</i>	3.2	2.7	1.0
DIAMESINAE				
4	<i>Protanypus caudatus</i>	0.3	0.9	0.6
Orthoclaadiinae				
5	<i>Heterotanytarsus apicalis</i>	0.1	0.4	0.3
6	<i>Heterotrissocladius maeaei</i>	11.2	1.1	–
7	<i>H. marcidus</i>	0.7	0.4	–
8	<i>H. subpilosus</i>	13.7	51.4	74.1
9	<i>Psectrocladius (Alopsectrocladius) sp.</i>	–	0.4	–
10	<i>P. (Mesopsectrocladius) sp.</i>	15.6	4.2	0.6
11	<i>P. (Monopsectrocladius) calcaratus</i>	5.5	1.3	1.3
12	<i>P. (Psectrocladius) semicirculatus</i>	0.3	0.2	0.6
13	<i>P. (Psectrocladius) sordidellus</i>	0.1	–	–
14	<i>P. (Psectrocladius) sp. A</i>	1.7	–	–
15	<i>P. (Psectrocladius) sp. B</i>	–	0.2	–
16	<i>Mesocricotopus thienemanni</i>	16.6	10.2	5.5
17	<i>Tvetenia sp.</i>	0.2	–	–
Chironominae				
18	<i>Corynocera ambigua</i>	–	0.2	–
19	<i>Dicrotendipes sp.</i>	0.2	–	–
20	<i>Micropsectra sp./radialis</i>	4.2	0.9	2.3
21	<i>Microtendipes pedellus</i>	0.1	–	–
22	<i>Paracladopelma sp.</i>	0.7	4.2	3.6
23	<i>Paratanytarsus sp.</i>	0.6	0.2	0.3
24	<i>Polypedilum sp.</i>	0.1	–	–
25	<i>Sergentia coracina</i>	0.1	0.2	0.3
26	<i>Stictochironomus rosenschoeldi</i>	0.1	–	–
27	<i>Tanytarsus spp.</i>	1.2	–	–
28	<i>Tribelos intextum</i>	0.2	–	–

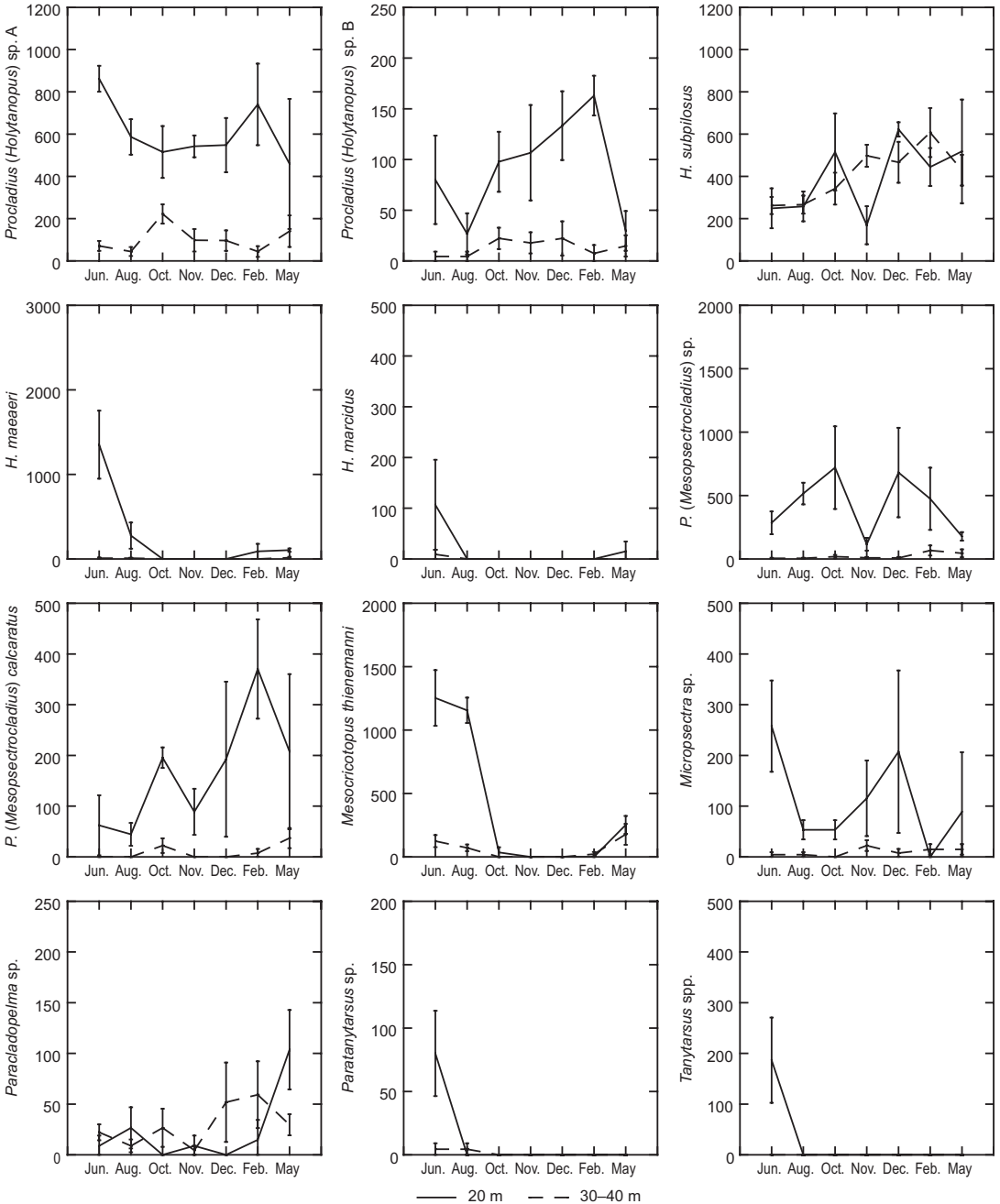


Fig. 3. Seasonal fluctuations in abundance (mean density ± SE, indivi. m⁻²) of the most common chironomids in the profundal at 20 and 30–40 m depths. (Note the different scales on the y-axis).

increased after ice covering, with no significant changes during winter. Significant seasonal changes were observed in abundance of *H. maeaeeri* (Kruskal-Wallis test: $K_6 = 25.146$, $p < 0.001$), *M. thienemanni* (Kruskal-Wallis test:

$K_6 = 25.748$, $p < 0.001$), *Paratanytarsus sp.* (Kruskal-Wallis test: $K_6 = 21.371$, $p = 0.002$), and *Tanytarsus spp.* (Kruskal-Wallis test: $K_6 = 21.357$, $p = 0.002$) (Fig. 3). All four taxa had their highest density in early summer, declin-

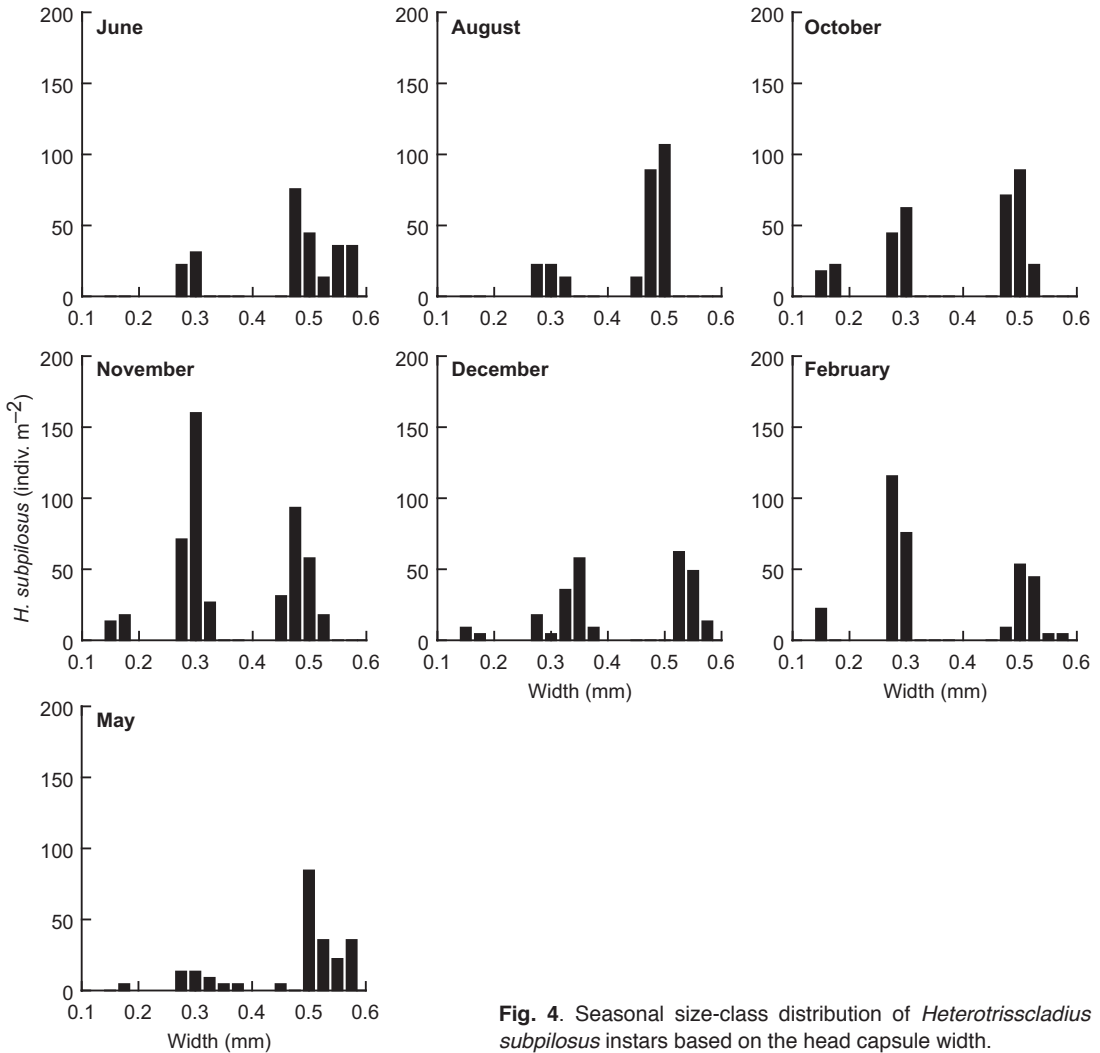


Fig. 4. Seasonal size-class distribution of *Heterotrisscladius subpilosus* instars based on the head capsule width.

ing rapidly and being low during the rest of the year. At 30–40-m depth, there was no significant seasonal variation in total chironomid abundance (Kruskal-Wallis test: $K_6 = 10.565$, $p = 0.103$; Fig. 2), although significant seasonal changes were observed in the population abundance of *M. thienemanni* (Kruskal-Wallis test: $K_6 = 29.907$, $p < 0.001$), and *H. subpilosus* (Kruskal-Wallis test: $K_6 = 20.835$, $p = 0.002$) (Fig. 3). *Mesocricotopus thienemanni* exhibited the highest densities in May and June, whereas *H. subpilosus* had the highest densities in late winter, and lowest in June and August. The remaining taxa did not show any significant seasonal changes.

Larval growth development of *H. subpilosus*

Three larval instar groups could be identified from a classification based on the head capsule width of the species *H. subpilosus*. The three groups were represented by three distinct size-classes of head capsule width ranging from 150–175 (mean 161), 275–375 (298) and 450–575 (505) μm , which are indicative of instars II, III and IV, respectively (Fig. 4). First instars and a large proportion of the second instar larvae were apparently sieved through the washing net (mesh size 250 μm), and were thus not present in the samples. A strong correlation existed between

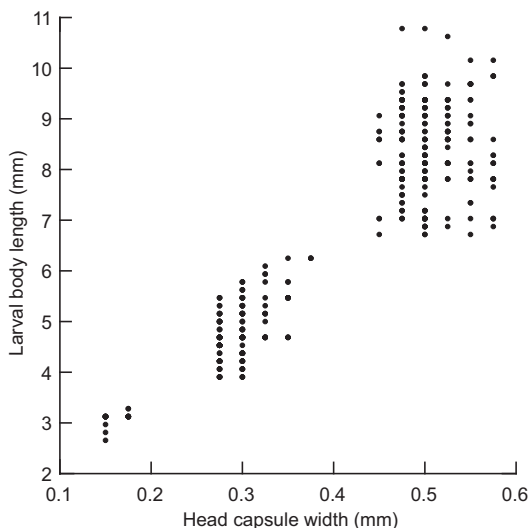


Fig. 5. The relation between head capsule width and body length in larvae of *H. subpilosus*.

body length and head capsule width of the larvae (Pearson's product moment correlation: $r = 0.92$, $p < 0.001$; Fig. 5). The body length range was 2.65–3.28 (mean = 3.10), 3.90–6.25 (4.83) and 6.71–10.78 (8.40) mm for instars II, III and IV, respectively.

Second instar larvae of *H. subpilosus* were not present in the samples taken during June–August, but appeared from October to February and were also present in low densities in May (Fig. 6). Third and fourth instars were present in all sampling periods. Third instar larvae increased in density from August towards February, but then decreased in May, possibly due to molting to the fourth instar. Fourth instar larvae were present in high densities all months. Large specimens of the fourth instar were particularly abundant during May and June (Fig. 4), and reduction in the number of these large specimens or fourth instar larvae from June to August suggests that the main pupation and emergence time of *H. subpilosus* occurred at the beginning of the ice-free season.

Discussion

Chironomid larvae dominated the profundal fauna of Fjellfrøsvatn, as is also commonly

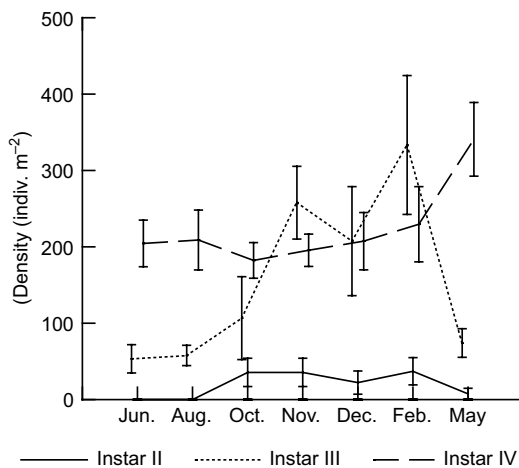


Fig. 6. Density (mean density \pm SE) of *H. subpilosus* instars through the season.

observed in other oligotrophic Scandinavian lakes (Brundin 1956, Sæther 1975a, Aagaard 1978a, Mousavi *et al.* 2002). The average total abundance of profundal chironomid larvae recorded in our study (1328 ± 136 SE indiv. m^{-2}) was almost similar to that reported by Brundin (1956) from a lake in northern Sweden, Lindgaard and Mæhl (1992) from an arctic lake in Greenland, and Tatosova and Stuchlik (2006) from a mountain lake in Slovakia. A total of 28 chironomid taxa were recorded, but the species richness decreased with increasing depth. Also the density of profundal chironomid larvae generally decreased with increasing depth. Some of the numerically important taxa like *H. maeaeeri* and *M. thienemanni*, but also *H. marcidus*, *Paratanytarsus* sp. and *Tanytarsus* spp., were present mainly at 20 m and almost absent at 30–40 m. According to Sæther (1975a), *H. maeaeeri* is a northern, cold-stenothermic species, which constitutes a qualitatively important part of the littoral and the upper profundal zone of subarctic Fennoscandian lakes (Brundin 1949, 1956). *Heterotrissocladius marcidus* also prefer the littoral zone of lakes, being rare at greater depths (Brundin 1949). Overall, *H. subpilosus* was the most important chironomid species in the profundal of Fjellfrøsvatn, as has also been found for other Scandinavian subarctic lakes (Brundin 1949, Sæther 1975a, 1979, Aagaard 1986, Mousavi *et*

al. 2002). This is also in agreement with the classification of this species as an indicator taxon for deep ultra-oligotrophic/oligotrophic lakes (Brundin 1956, Sæther 1975b).

Seasonal fluctuations in total chironomid density were quite profound at 20-m depth, but almost absent at 30–40-m depth. At 20 m, a distinct density maximum in early summer characterized the seasonal pattern, the abundance declining rapidly during summer and being low during the rest of the sampling period. In particular four taxa; *H. maeaeri*, *M. thienemanni*, *Paratanytarsus* sp. and *Tanytarsus* spp., showed significant seasonal variations in density, having a distinct peak in June followed by a sharp decrease and a low density throughout most of the year. A similar, although not statistically significant pattern was also observed for *H. marcidus*. The observed seasonal density variations of these species suggest a one-year life cycle, with pupation and emergence of adults in early summer. In Øvre Heimdalsvatn, Norway, *M. thienemanni* was observed to emerge during July and August (Aagaard 1978a). Similarly, a presence of pupae in the beginning of July and a univoltine life cycle was reported for *H. maeaeri* and *H. marcidus* from other Scandinavian subarctic lakes (Brundin 1949, Sæther 1975a). One emergence period was also reported for *H. marcidus* from two non-stratifying mountain lakes in Austria (Pechlaner *et al.* 1972, Pechlaner and Zaderer 1985).

Interestingly in Fjellfrøsvatn, the species exhibiting distinct seasonal density variations and univoltine life cycles were identical to those species that mainly were present in the upper part of the profundal, and rare or absent at 30–40 m. This suggests that the occurrence of a one-year life cycle may be restricted to species with a predominant distribution in the littoral zone, where the summer temperatures after the establishment of a thermocline in early summer are much higher than in the profundal. For most of the recorded chironomid species, in contrast, and particularly those living at 30–40-m depth, seasonal density variations appeared to be almost absent, suggesting that their lifecycles are predominantly hemivoltine.

Size classification by measuring the head capsule width of chironomid larvae is well

established for the separation of instar groups (McCauley 1974, Welch 1976, Lindegaard and Mæhl 1992), and also worked well for the *H. subpilosus* larvae in Fjellfrøsvatn. There was also a strong correlation between body length and head capsule width of the larvae. However, a separation of instars only by measuring the body length may be difficult due to the curved shape of the larval body and a potential overlap in length between instar groups (Sæther 1975a, Welch 1976, Hershey 1985). The head capsule and body length of fourth instars larvae ranged in our study between 0.48–0.58 (mean = 0.50) mm and 6.80–10.80 (mean = 8.40) mm, respectively, which is highly similar to the respective measurements of 0.49–0.54 (mean = 0.50) mm and 6.11–9.07 (mean = 8.11) mm reported by Sæther (1975a). The size range of the head capsule of second instar larvae was 150–175 μm . If we assume an approximate percentage increase of 58% from first to second instar as indicated by Welch (1976), the head-capsule size range of the first instar larvae would be 95–110 μm or possibly even smaller. As the samples were sieved through a washing net of 250 μm , all of the first and probably a large proportion of the second instar larvae were not retrieved, and complete density estimates were likely achieved only for the third- and fourth-instar larvae. Furthermore, early-instar larvae of some species appear to have a planktonic phase or at least some free-swimming habits, and may thus avoid being sampled by the Ekman grab (Whiteside and Lindegaard 1980, Aagaard 1982).

During most of the year, larval instars II, III and IV of *H. subpilosus* occurred simultaneously in the samples, suggesting a hemivoltine life cycle of this species. The second instar was not recorded from June to August, but planktonic specimens of instar II may have been present in the lake during the last part of this period, as found by Aagaard (1982) in Langvatn, Norway. Furthermore, large specimens of instar IV were mainly observed in May and June, and pupae of *H. subpilosus* in June and August. Combined with the seasonal density fluctuations of instars III and IV (Fig. 6), these observations suggest a predominant two-year life cycle of profundal *H. subpilosus* in Fjellfrøsvatn. Pupation and emergence of adults appear mainly to take place

from June to July, when *H. subpilosus* pupae have been reported to be the main prey of the Arctic charr in this area (Klemetsen *et al.* 1992, Jørgensen and Klemetsen 1995). If the eggs hatch within a month, the first instar larvae are present from mid-summer, and probably molt to second instar sometime between August and October. In Langvatn, Aagaard (1982) found the second instar present in July and August, and the third instar in November. In Fjellfrøsvatn, the increase in density of third-instar larvae from August to February suggests that most instar II larvae molt to instar III during this period, but some remained at instar II even until May (Figs. 4 and 6). The main fraction of third-instar larvae molted to the fourth instar between February and May, whereas some third-instar larvae also appeared in the samples in May, June and August. The density of the fourth-instar larvae was stable during the whole year except for an increase from February to May after the decline in instar III larvae. This suggests a development time of one year for the fourth instar followed by the initiation of pupation around ice-break in May–June, giving a total life cycle of two years. The fraction of the second-instar larvae that apparently did not molt to third instar before the end of the winter may have a delay in their life cycle as compared with the majority of the cohort. Seemingly, they were still in their third instar during May, June and August and probably molted to fourth instar sometime later in the autumn or during the winter. Due to this delay they may have to use a third year to complete their life cycle, but if the duration of fourth instar is reduced, they will still be able to pupate and emerge the following spring together with the rest of the cohort, and thus within a two-year cycle. The accumulation of younger larvae in their third instars from November to December may even be related to a diapause, but additional studies including observations of adult emergence (Tokeshi 1995) would be needed to reveal such potential subtleties in the subarctic life-cycle of this species.

In Fjellfrøsvatn and the nearby Takvatn, the emergence of *H. subpilosus* appears to be restricted to the spring and early summer period (Klemetsen *et al.* 1992, this study). Both spring and autumn emergence have, however, been

reported for *H. subpilosus* from Scandinavia and its North-American sister species *H. oliveri* (Brundin 1949, Sæther 1975a), but the length of their life cycles was not estimated in these studies. In areas with cold climates and large year-to-year variations, chironomid may respond by different voltinism, cohort splitting, photoperiodic control of growth, and adjustments of dormancy or diapause (Danks 1991, 2006). The life-cycle length of chironomids is dependent on a number of factors including altitude, latitude, bathymetry, and other lake-specific and regional variations (Wülker 1961, Jónasson 1965, 1972, Aagaard 1982, Lindegaard and Mæhl 1992, Armitage 1995). In Arctic and subarctic lakes, the life cycle of chironomids frequently exceeds one year, and species such as *H. subpilosus* and *H. oliveri* have been shown to take at least two to three years to complete their life cycles (Oliver 1968, Welch 1976, Aagaard 1982). Prolonged development lasting more than one year per generation seems to be a general pattern in some cold-adapted chironomid species. Likewise, some proportion of individuals may spend an extra year or more in diapause or have a prolonged larval development (Welch 1976, Danks 2006, 2007).

In conclusion, this study is to our knowledge the first to explore seasonal variations including also the winter period of a profundal chironomid assemblage in a subarctic lake. Our findings reveal large temporal and depth variations in density and species composition of chironomid larvae. The seasonal variations were larger at 20-m than at 30–40-m depths. This was related to the fact that the dominant chironomid species at 20-m depth mainly were univoltine, whereas *H. subpilosus*, the dominant species at 30–40-m depth, was hemivoltine with predominantly a two-year life-cycle. The highest densities were observed at 20-m depth, and the chironomids numerically dominated the profundal fauna of the lake.

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References

- Aagaard K. 1978a. The Chironomidae of the exposed zone of Øvre Heimdalsvatn. *Holarct. Ecol.* 1: 261–265.
- Aagaard K. 1978b. The Chironomidae of Lake Målssjøen. A phenological diversity and production study. *Norw. J. Entomol.* 25: 21–37.
- Aagaard K. 1982. Profundal chironomid populations during a fertilization experiment in Langvatn, Norway. *Holarct. Ecol.* 5: 325–331.
- Aagaard K. 1986. The chironomid fauna of North Norwegian lakes, with a discussion on methods of community classification. *Holarct. Ecol.* 9: 1–12.
- Amundsen P.-A. 1989. Effects of intensive fishing on food consumption and growth of stunted Arctic charr (*Salvelinus alpinus* (L.)) in Takvatn, northern Norway. *Physiol. Ecol. Japan Spec. vol. 1*: 265–278.
- Amundsen P.-A. & Klemetsen A. 1988. Diet, gastric evacuation rates and food composition in a stunted population of Arctic charr (*Salvelinus alpinus* L.) in Takvatn, northern Norway. *J. Fish Biol.* 33: 697–709.
- Amundsen P.-A. & Knudsen R. 2009. Winter ecology of Arctic charr (*Salvelinus alpinus*) and brown trout (*Salmo trutta*) in a subarctic lake. *Aquat. Ecol.* 43: 765–775.
- Amundsen P.-A., Knudsen R. & Klemetsen A. 2008. Seasonal and ontogenetic variations in resource use by two sympatric Arctic charr morphs. *Env. Biol. Fish.* 83: 45–55.
- Armitage P.D. 1995. Behaviour and ecology of adults. In: Armitage P.D., Cranston P.S. & Pinder L.C.V. (eds.), *The Chironomidae: The biology and ecology of non-biting midges*. Chapman and Hall, pp. 194–224.
- Bitusík P. & Svitok M. 2006. Structure of chironomid assemblages along environmental and geographical gradients in the Bohemian Forest lakes (central Europe): An exploratory analysis. *Biologia, Bratislava* 61(Suppl. 20): 467–476.
- Brundin L. 1949. Chironomiden und andere Bodentiere der südschwedischen Urgebirgsseen. *Rep. Inst. Freshwater Res. Drottningholm* 30: 1–914.
- Brundin L. 1956. Die Boden faunistischen Seetypen und ihre Anwendbarkeit auf die Sudhalbugele. Zugleich eine Theorie der glazialen Erosion. *Rep. Inst. Freshwater Res. Drottningholm* 37: 186–235.
- Butler M.G. 1982. A 7-year life cycle for two Chironomus species in arctic Alaskan tundra ponds (Diptera: Chironomidae). *Can. J. Zool.* 60: 58–70.
- Coffmann W.P. 1978. Chironomidae. In: Merritt R.W. & Cummins K.W. (eds.), *An introduction to the aquatic insects of North America*, Kendall/Hunt, Dubuque, Iowa, USA, pp. 644–652.
- Danks H.V. 1991. Life-cycle pathways and the analysis of complex life cycles in insects. *Can. Entomol.* 123: 23–40.
- Danks H.V. 2006. Key themes in the study of seasonal adaptations in insects II. Life cycle patterns. *Appl. Entomol. Zool.* 41: 1–13.
- Danks H.V. 2007. How aquatic insects live in cold climates. *Can. Entomol.* 139: 443–471.
- Danks H.V. & Oliver D.R. 1972. Seasonal emergence of some high arctic Chironomidae (Diptera). *Can. Entomol.* 110: 667–669.
- Gerstmeier R. 1989a. Lake typology and indicator organisms in application to the profundal chironomid fauna of Starnberger See (Diptera: Chironomidae). *Arch. Hydrobiol.* 116: 227–234.
- Gerstmeier R. 1989b. Seasonal patterns in the abundance, size, and production of profundal Chironomidae in Starnberger See (Bavaria, FRG). *Spixiana* 12: 261–273.
- Hershey A.E. 1985. Littoral chironomid communities in an Arctic Alaskan lake. *Holarct. Ecol.* 8: 39–48.
- Johnson R.K. & Wiederholm T. 1989. Classification and ordination of profundal macroinvertebrate communities in nutrient-poor, oligo-mesohumic lakes in relation to environmental data. *Freshw. Biol.* 21: 375–386.
- Johnson R.K., Wiederholm T. & Erikson L. 1990. The influence of season on the classification and ordination of profundal communities of nutrient-poor, oligo-mesohumic Swedish lakes using environmental data. *Verh. Internat. Verein. Limnol.* 24: 646–652.
- Jónasson P.M. 1965. Factors determining population size of *Chironomus anthracinus* in Lake Esrom. *Mitt. Int. Ver. Theor. Angew. Limnol.* 13: 139–162.
- Jónasson P.M. 1972. Ecology and production of profundal benthos in relation to phytoplankton in Lake Esrom. *Oikos Suppl.* 14: 1–148.
- Jørgensen L. & Klemetsen A. 1995. Food resource partitioning of Arctic charr, *Salvelinus alpinus* (L.) and three-spined stickleback, *Gasterosteus aculeatus* L., in the littoral zone of Lake Takvatn in northern Norway. *Ecol. Freshw. Fish* 4: 77–84.
- Klemetsen A., Muladal H. & Amundsen P.-A. 1992. Diet and food consumption of young, profundal Arctic charr (*Salvelinus alpinus*) in Lake Takvatn. *J. Freshw. Res.* 67: 35–44.
- Knudsen R., Kristoffersen R. & Amundsen P.-A. 1997. Parasite communities in two sympatric morphs of Arctic charr, *Salvelinus alpinus* (L.), in northern Norway. *Can. J. Zool.* 75: 2003–2009.
- Lindegaard C. & Mæhl P. 1992. Abundance, population dynamics and production of Chironomidae (Diptera) in an ultraoligotrophic lake in south Greenland. *Neth. J. Aquat. Ecol.* 26: 297–308.
- McCaughey V.J.E. 1974. Instar differentiation in larval Chironomidae (Diptera). *Can. Entomol.* 106: 179–200.
- Moore J.W. 1978. Some factors influencing the diversity and species composition of benthic invertebrate communities in twenty Arctic and subarctic lakes. *Int. Rev. Gesamt. Hydrobiol.* 63: 757–771.
- Moore J.W. 1980. Factors influencing the composition, structure and density of a population of benthic invertebrates. *Arch. Hydrobiol.* 88: 202–218.
- Mousavi S.K., Sandring S. & Amundsen P.-A. 2002. Diversity of chironomid assemblages in contrasting subarctic lakes, impact of fish predation and lake size. *Arch. Hydrobiol.* 154: 461–484.
- Nyman M.T. & Korhola A.A. 2005. Chironomid-based classification of lakes in western Finnish Lapland. *Boreal Env. Res.* 10: 239–254.

- Nyman M., Korhola A. & Brooks S.J. 2005. The distribution and diversity of Chironomidae (Insecta: Diptera) in western Finnish Lapland, with special emphasis on shallow lakes. *Global Ecol. Biogeogr.* 14: 137–153.
- Oliver D.R. 1968. Adaptation of arctic Chironomidae. *Ann. Zool. Fennici* 5: 111–118.
- Pankratova V.Ya. [Панкратова В.Я.] 1970. [Larvae and pupae of midges of subfamily Orthoclaadiinae (Diptera: Chironomidae = Tendipedinae) of USSR fauna]. *Opre-deliteli Fauny SSSR* 102: 1–343. [In Russian].
- Pankratova V.Ya. [Панкратова В.Я.] 1983. [Larvae and pupae of non-biting midges of the subfamily Chironominae (Diptera, Chironomidae, Tendipedidae) of the USSR fauna]. *Opre-deliteli Fauny SSSR* 134: 1–296. [In Russian].
- Pechlaner R., Bretschko G., Gollmann P., Pefeifer H., Tilzer M. & Weissenbach H.P. 1972. The production processes in two high-mountain lakes (Vorderer and Hinterer Finstertaler See, Kuhtai, Austria). In: Kajak Z. & Hillbricht-Ilkowska A. (eds.), *Productivity problems of freshwaters*, PWN Polish Scientific Publication, Warsaw, pp. 239–269.
- Pechlaner R. & Zaderer P. 1985. Interrelations between brown trout and chironomids in the alpine lake Gosseköllesee (Tyrol). *Verh. Internat. Verein. Limnol.* 22: 2620–2627.
- Sæther O.A. 1975a. Nearctic and Palaearctic *Heterotrissocladius* (Diptera: Chironomidae). *Bull. Fish. Res. Bd. Can.* 193: 1–67.
- Sæther O.A. 1975b. Nearctic chironomid as indicators of lake typology. *Verh. Internat. Verein. Limnol.* 19: 3127–3133.
- Sæther O.A. 1979. Chironomid communities as water Quality indicators. *Holarct. Ecol.* 2: 65–74.
- Särkkä J. 1983. A quantitative ecological investigation of the littoral zoobenthos of an oligotrophic Finnish lake. *Ann. Zool. Fen.* 20: 157–178.
- Schnell Ø.A. & Aagaard K. 1996. Chironomidae. In: Aagaard K. & Dolmen D. (eds.), *Limnofauna Norvegica*, Tapir Forlag, Trondheim, pp. 112–248.
- Tatosova J. & Stuchlik E. 2006. Seasonal dynamics of chironomids in the profundal zone of a mountain lake (Ladove pleso, the Tatra Mountains, Slovakia). *Biologia, Bratislava* 61(Suppl. 18): 203–212.
- Tokeshi M. 1995. Life cycles and population dynamics. In: Armitage P.D., Cranston P.S. & Pinder C.V.L. (eds.), *The Chironomidae: Biology and ecology of non-biting midges*, Chapman and Hall, London, pp. 225–269.
- Vallenduuk H. 2009. Larvae of the Tanypodinae (Diptera: Chironomidae): New (neglected) characters and the making of a new key. *Proc. Neth. Entomol. Soc. Meet.* 20: 55–66.
- Welch H.E. 1976. Ecology of Chironomidae (Diptera) in a polar Lake. *J. Fish. Res. Bd. Can.* 33: 227–247.
- Wetzel R.G. 2001. *Limnology*, 3rd ed. Academic Press, San Diego, CA.
- Whiteside M.C. & Lindegaard C. 1980. Complementary procedures for sampling small benthic invertebrates. *Oikos* 35: 317–320.
- Wiederholm T. 1980. Use of benthos in lake monitoring. *J. Water Poll. Cont. Fed.* 52: 537–547.
- Wiederholm T. 1983. Chironomidae of the Holarctic region. Key and diagnoses. Part 1. Larvae. *Entomol. Scand. Suppl.* 19: 1–457.
- Wülker W. 1961. Studien zur Morphologie und Verbreitung der Gattung *Sergentia* Kieff. (Dipt. Chironomidae). *Arch. Hydrobiol. Suppl.* 25: 307–331.