

New records of *Metretopus alter* Bengtsson, 1930 and *Metretopus borealis* (Eaton, 1871) (Ephemeroptera) in northern Norway, including confirmation of *M. alter* at the type locality after 90 years

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Klemetsen, A., Brittain, J. E. & Engblom, E. 2015. New records of *Metretopus alter* Bengtsson, 1930 and *Metretopus borealis* (Eaton, 1871) (Ephemeroptera) in northern Norway, including confirmation of *M. alter* at the type locality after 90 years. *Norwegian Journal of Entomology* 62, 117–128.

The type localities for the Holarctic mayflies *Metretopus borealis* (Eaton, 1871) and *Metretopus alter* Bengtsson, 1930 are in northern Norway, between Kautokeino and Karesuando in Finnmark County for *M. borealis* and along the small stream, Råvatnbekken, in Målselv, Troms County for *M. alter*. By combining new sampling, records in reports and theses and identification of museum material, new information on the distribution and ecology of both species is given. Larvae of *M. alter* were found in the type locality in 2012, 90 years after the initial collection, and in two other small streams in Balsfjord in 2012 and 2014. Råvatnbekken is a narrow, slow-flowing woodland stream with variable substrates and some macrovegetation. *M. borealis* was recorded in seven river systems throughout Troms and Finnmark, predominantly in the upper reaches. It was not collected in systems along the coast, indicating a continental distribution. While *M. alter* prefers smaller streams and avoids lakes, hard bottom substrates in moderately sized streams and lake littorals were typical *M. borealis* habitats. The streams had high diversities of mayflies and stoneflies and low abundance of *M. borealis*, while the lake littorals had low diversity and high abundance of *M. borealis*. This suggests less ecological interactions on lake shores allow high densities of *M. borealis*, although nutrient supply may also be important. The study confirmed two new localities for *M. alter* and many new localities for *M. borealis* in Norway.

Key words: Ephemeroptera, *Metretopus*, type localities, distribution, habitat preferences, North Norway.

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Introduction

Metretopus Eaton, 1901 in Norway.

There are 48 known species of mayflies (Ephemeroptera) in the Norwegian fauna (Kjærstad 2007, Artsdatabanken (2007–2012),

see also Brittain *et al.* 1996) and 369 known species in the whole of Europe (Bauernfeind & Soldan 2012). We follow the nomenclature of Bauernfeind & Soldan (2012) in this contribution. Four species: *Siphonurus aestivalis* (Eaton, 1903), *Metretopus alter* Bengtsson, 1930, *Metretopus borealis* (Eaton, 1871) and *Paraleptophlebia*

strandii (Eaton, 1901) have been described as *novae species* with type localities in Norway. *S. aestivalis* and *P. strandii* were found in southern Norway, but the type localities of the *Metretopus* species are both in the northern, subarctic part of the country. In this contribution, we present new information on the distribution and ecology of the two *Metretopus* species in northern Norway with emphasis on Troms and Finnmark, the two northernmost counties.

The mayfly family Metretopodidae has three genera and about 11 species (Bauernfeind & Soldan 2012). Two of the genera are found in Fennoscandia; the Palearctic *Metreplecton* Kluge, 1996 with a single species, *Metreplecton macronyx* Kluge, 1996, in Finland, and the Holarctic *Metretopus* with two species, *M. borealis* and *M. alter*. *M. borealis* is circumpolar and has its Palearctic distribution from Denmark to the Far East. *M. alter* has been recorded from 62° N in Sweden and sporadically to north-eastern Russia and Mongolia (Bauernfeind & Soldan 2012). It is also present in Alaska in the western Nearctic (McCafferty 1994). A third species, *Metretopus tertius* Tiunova, 1999 has also been described from the Russia Far East (Tiunova 1999). *M. alter* and *M. borealis* are very similar and several authors have considered them to be conspecific, but Engblom *et al.* (1993) stated this to be untenable as there are distinct morphological differences, especially in the male genitalia. The larvae are also very similar, and distinguishing characters were unknown until Engblom *et al.* (1993) described them from Sweden. Today they are accepted as close but distinct species (Engblom 1996, Bauernfeind & Soldan 2012). The family affiliation of the genus has been unclear until recently. Brittain *et al.* (1996) placed it in Amelotropodidae and Engblom (1996) placed it in Siphonuridae, but noted that this was for practical reasons while awaiting a critical review of the group. In the recent treatise on European mayflies (Bauernfeind & Soldan 2012) Metretopodidae are defined as a monophyletic family with several apomorphies including a characteristic bifurcation of the tarsal claws of the fore legs in the larvae (Figure 1).

The type locality for *M. borealis* is vaguely

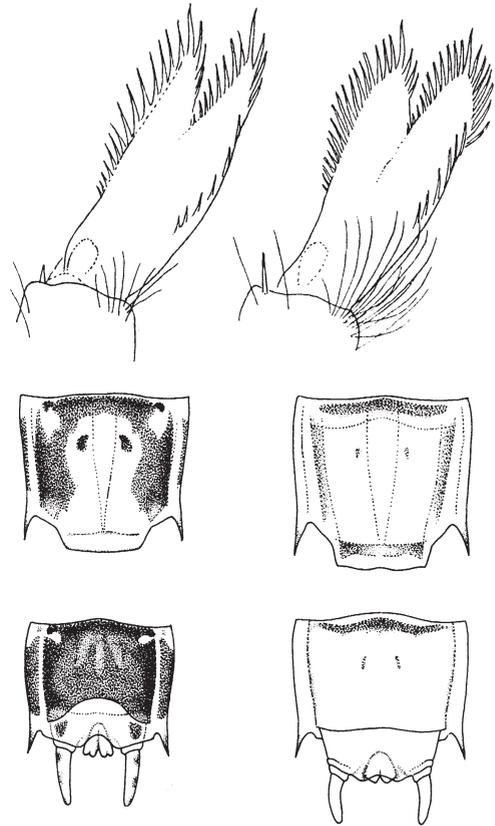


FIGURE 1. Distinguishing characters for mature larvae (> 7 mm) of *Metretopus borealis* (left) and *Metretopus alter* (right). Upper panel: bifid protarsal claws; anterior aspect; middle panel: female abdominal segment 9, ventral view; lower panel: male segment 9 with penis lobes, ventral view. After Engblom *et al.* (1993).

given as “Finmark (province), between Kautokeino and Karaswando” (Bauernfeind & Soldan 2012: 82), but the precise location will probably never be established. The type material is deposited in the Dale Collection, University Museum, Oxford, UK (Kimmins 1960). The type locality for *M. alter* is given as Raavand in “Nord-Norwegen, inneres Tromsø” by Bauernfeind & Soldan (2012: 81), clearly with reference to, but without direct citation from, Bengtsson (1930) where the species is described. Inneres Tromsø was a biogeographic region used by Bengtsson (1930) but for a reason not indicated, Bauernfeind & Soldan (2012: 81) wrongly placed the type

locality in Nord-Trøndelag County at 63° 31' N / 11° 13' E, not in Troms County close to 70°. The type material is deposited at Tromsø University Museum, UiT The Arctic University of Norway (hereafter Tromsø Museum).

A comprehensive field survey of insects in freshwater and humid habitats was recently undertaken in Finnmark County (see Ekrem *et al.* 2012). Our knowledge of the freshwater fauna is deficient in this very large county, with its high diversity of freshwater systems on the border between the European arctic and boreal climate zones. In this paper, we follow up the Finnmark initiative, and particularly the contribution on mayflies by Kjærstad *et al.* (2012), with new information on the distribution and ecology of the two species of *Metretopus* in Finnmark and Troms. In Norway *M. alter* was not found outside the type locality for a long time until one additional record came from the stream Gargiaelva in Alta, Finnmark in 1986 (Engblom *et al.* 1993). However, there were still only two localities, and *M. alter* was included in the Norwegian Red List from 1998 (Kjærstad 2007). In contrast, Engblom *et al.* (1993) mapped 69 and 31 localities for *M. alter* in Sweden and Finland, respectively, concluding that it has a more northern distribution than *M. borealis*. Several records of *M. alter* were close to the Norwegian border, suggesting that the species had a wider distribution in Norway than had been documented, and it was therefore excluded from the 2006 and 2010 revisions of the Norwegian Red List (Kjærstad *et al.* 2010).

Engblom *et al.* (1993) compared the habitats of these two species in Sweden and Finland. *M. borealis* was found mainly in streams, but occasionally also in lakes, while *M. alter* with a few exceptions in pools was restricted to running waters. Their lotic habitats overlapped considerably in chemical, physical and biotic characteristics, but there were significant differences in stream size. *M. borealis* occurred in streams up to 100 m wide and with a mean width of 13.4 m while *M. alter* streams had a mean width of 5.1 m and a maximum width of 16 m. There were no differences in water flow, but slight and significant depth differences between their preferred streams. We expected to find similar

differences between *M. borealis* and *M. alter* habitats in northern Norway.

Kjærstad (2007) noted that the probable reason for the lack of records in Norway was that potential habitats had not been investigated. In the present contribution, we intend to amend this lack of knowledge by: (1) making a systematic search for information on the genus in little known reports and theses on aquatic insects in northern Norway; (2) identifying *Metretopus* larvae in the collection of Tromsø Museum; and (3) sampling benthos in the type locality of *M. alter* and other localities in the Målselv river system, Troms County. We expected that these efforts would add new records for both *M. alter* and *M. borealis* in Norway and provide information on their distribution and habitats in the northern part of the country. We also wanted to document whether *M. alter* is still present in the type locality, 90 years after its initial discovery and provide a description of the type locality.

The description of M. alter.

In 1930, Simon Bengtsson (Lund, Sweden) was invited to identify the collection of Ephemeroptera in Tromsø Museum (Bengtsson 1930). The material consisted of winged stages collected by curator T. Soot-Ryen in Troms and Finnmark in the 1920s, but also contained earlier samples from Johan Sparre Schneider. Bengtsson noted that this was not a small collection (“nicht geringe Material”, Bengtsson 1930: 4) and his work increased the number of mayfly species in north Norway from 7–8 to 22. Two species were described as new to science, *Paraleptophlebia tumida* Bengtsson, 1930, (later regarded a synonym of *Paraleptophlebia weneri* Ulmer, 1920; Landa 1969) and *Metretopus alter*. The description of *M. alter* included characters for imagines of males and females that separated it from *M. borealis*. Bengtsson (1930) applied the name *M. norvegicus* Eaton, 1901 for *M. borealis*, but these were later regarded as synonyms (Brekke 1938).

Soot-Ryen gave the locality where the first *M. alter* were collected as “Raavand längs dem dortigen Bach” (Bengtsson 1930: 18). This

implies that the collection took place along a stream connected to the lake, Råvatn in Målselv, and not at the lake itself. The lake has no inlet streams, so the only possibility is the outlet stream Råvatnbekken. Therefore, Råvatnbekken must be the type locality for *M. alter*.

Soot-Ryten collected only winged stages, never larvae. In mayflies, there is a greater chance of finding larvae as they live much longer than the adults. Here, the results of collecting efforts for *Metretopus* larvae in the type locality, and in several other localities in the Målselv river system, are reported.

Material and methods

There are many reports and theses, mostly in Norwegian, on invertebrate benthos from northern river systems at the University of Tromsø, The Arctic University of Norway (reports, e.g. Bergersen 1987, Huru 1980a, 1981d, 1982b in Tromsø Museum, theses e. g. Gabler 1994, 2000, M. Johansen 2005, K. M. S. Johansen 2014 in the Department of Arctic and Marine Biology). Most of the reports give results for benthos sampled in the 1970s and 1980s from river systems that were being considered for hydropower development. The theses are on diverse aspects of freshwater ecology but often contain substantial information on benthic insects. We searched all available reports and theses for information on presence or absence of *Metretopus* and, when present, on descriptions of the habitats and communities where it was found. After sorting and identification, parts of the material described in the reports were deposited at Tromsø Museum. *Metretopus* was never identified to species in the reports, presumably because the identification literature for larvae was inadequate at the time. Therefore, the samples in the museum were re-examined and identified by using the descriptions in Engblom *et al.* (1993) and Engblom (1996): *M. borealis* has distinct body colour patterns with dark markings on abdominal segments and femora while *M. alter* has diffuse patterns without markings. As shown in Figure 1, the shapes of the penis lobes and the bifid protarsal claws differ

between the species. The tuft of setae at the base of the protarsus is also shorter than the width of the tarsus in *M. borealis* and longer than the width of the tarsus in *M. alter*. In the treatment of the reports in the results section, the identity of *Metretopus* refers to this subsequent examination, not the reports themselves. Together, these sources provide knowledge on *Metretopus* from many of the large rivers as well as several smaller systems in northern Norway.

Qualitative kick-sampling (Johnson & Goedkoop 2002) was undertaken in the upper reach of the type locality Råvatnbekken in July 2011 but without finding *M. alter*. It was repeated on 12 August 2012 in a shallow pool, about 12 m long, up to 2.5 m wide, and 20–40 cm deep at Vestby, about half the way downstream from Råvatn. There was a thin layer of mud over gravel and small stones. The sediments, the vegetation in the pool and the riffle at the outlet were intensively sampled by aquatic kick sampling and sweeping through aquatic vegetation with nets with a mesh size of 0.45 mm. Sweep netting in the terrestrial vegetation alongside the stream was also carried out. Macroinvertebrates were picked by hand and conserved in ethanol. Kick sampling was also carried out along the shores of Råvatn in 2011 and 2012.

The northwest shore of the lake, Fjellfrøsvatn, including the inlet of the tributary stream, Andorelva, was sampled in July 2011 and again in July 2013. In July 2014, the Andorelva inlet and Luoppal, a large pool situated about 0.5 m above and ending about 20 m from the lake, were sampled. The pool is about 1100 m long and has a shallow lower end with dense vegetation of *Carex* and *Equisetum* along the margins and a substrate of mud and sand. In addition, four small streams in the Målselv system were also kick sampled: one flowing from the west into the tributary, Tamokelva, close to the Balsfjord/Målselv municipality border; one flowing from the tarn, Solvolltjørna, into the tributary, Fjellfrøselva; the stream, Geitbekken, flowing to the same tributary about 1 km northwest of Elvekrokneset; and one flowing into the lake, Lille Rostavatn, near the inlet of the tributary Rostaelva. All closely fitted the description given by Engblom *et al.* (1993) for

habitats preferred by *M. alter*.

Takvatn and Fjellfrøsvatn are large (15 and 6 km², respectively) and deep oligotrophic lakes situated in different tributaries of Fjellfrøselva. Most of the shores have wave-washed hard substrates with no macrophytes. The ecology of the lakes has been studied extensively (see Amundsen *et al.* (2013 and references therein). Klemetsen & Elliott (2010) carried out quantitative sampling for macroinvertebrates in the shallow shore zone in Takvatn in 2000–2003. As the larvae of *M. alter* and *M. borealis* can be difficult to distinguish (Engblom *et al.* 1993), the material from the lake was re-identified in 2013 by Eva Engblom, along with identification of kick samples from three new shore sites collected in 2011.

Results

The type locality for Metretopus alter

Råvatn is a small (about 0.4 km²) oligotrophic lake situated 79 m a.s.l. in a flat forest landscape close to the main stem of the Målselv River. The catchment area is small (< 3 km²) and without inlet streams. The outlet stream, Råvatnbekken, Målselv, runs along a gentle slope first west, then northwest for c. 1.3 km, partly through agricultural land but mostly through mixed alder (*Alnus*) and birch (*Betula*) forest, to a long and narrow inlet to the stream Fjellfrøselva. It is a shallow, slow-flowing stream, up to c. 1 m wide, 10–20 cm deep in riffles and down to 0.5 m in pools. The sediments are sand, gravel and small stones in riffles and some mud in the pools. There are scattered debris of logs and branches of birch and alder in the water. The stream is partly vegetated along the banks, mainly *Carex* spp. but also *Menyanthes trifoliata*, *Caltha palustris* and *Comarum palustre*. The vegetation cover varies from zero to five on a six-graded scale. Grasses, ferns, *Filipendula ulmaria*, *Epilobium angustifolium* and *Salix* bushes dominate the vegetation on the banks. In some summers the stream may almost dry out (Jan-Tore Skjærvik, pers. comm.).

Three late instar larvae and two exuviae of *M. alter* were collected in the pool at Vestby (UTM 34WDB335573, Figure 2). Other mayflies collected were *Ameletus inopinatus* Eaton, 1887, *Baetis* (*Baetis*) *subalpinus* Bengtsson, 1917, *Baetis* (*Nigrobaetis*) *muticus* (Linnaeus, 1758), *Paracinygmula joernensis* (Bengtsson, 1909) and *Paraleptophlebia submarginata* (Stephens, 1836), while other macroinvertebrates included *Gyraulus acronicus* (Férussac, 1807) (Gastropoda), *Protonemura meyeri* (Pictet, 1841) (Plecoptera), limnephilids, simuliids and chironomids. No *Metretopus* were collected along the shores of Råvatn in 2011 and 2012.

The other Målselv localities

The material from Takvatn collected by Klemetsen & Elliott (2010) and the additional material from 2011 was confirmed as *M. borealis*. It was the third most abundant mayfly species on the stony shores after *A. inopinatus* and *Heptagenia dalecarlica* Bengtsson, 1912 and occurred at all new sampling stations in 2011. In a further study in 2012 (Johansen 2014) *M. borealis* was abundant on the stony shore, but, along with the other mayflies, it was not found deeper down in the littoral.

No *Metretopus* were found during the repeated sampling on the stony shores of Fjellfrøsvatn in 2011 and 2013, but a few *M. alter* larvae were collected in the stream, Andorelva, Balsfjord, just where it enters the lake (UTM 34WDB329664) in 2011, 2013 and 2014. This is the third locality for the species in Norway (Figure 2). The inlet flows gently under a bridge for only about 20 m from the upstream pool Luoppal. It is about 5 m wide and less than 0.5 m deep and the substrate is gravel and sand without vegetation. Several *Baetis* (*Baetis*) *fuscatus* (Linnaeus, 1761) and some *Siphonurus lacustris* Eaton, 1870 occurred along with *M. alter* in this short inlet stream. In 2014, *M. alter* was also collected in the un-vegetated reach of Luoppal close to the outlet of the short stream to the lake. Other benthos included oligochaetes, *Gammarus lacustris* G. O. Sars, 1863 (Amphipoda), dytiscids, limnephilids, and the mayflies *Siphonurus alternatus* (Say, 1824),

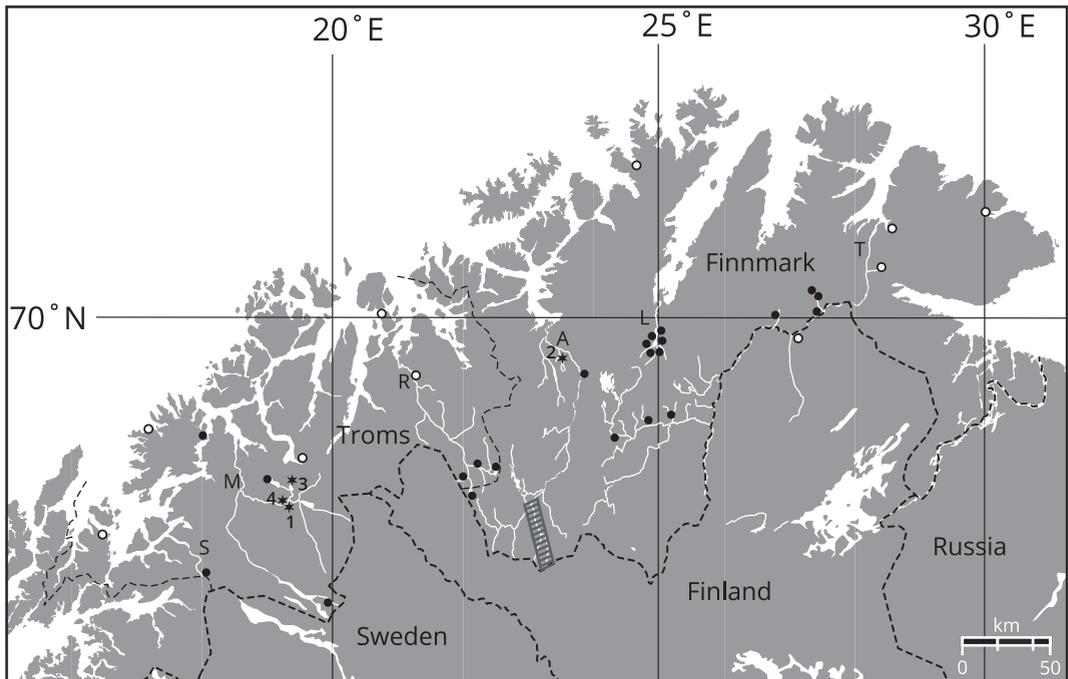


FIGURE 2. Map of new localities for *Metretopus alter* and *Metretopus borealis* larvae in Troms and Finnmark. Numbered asterisks: *M. alter*; 1: the type locality Råvatnbekken, Målselv (1922), 2. Gargiaelva, Alta (1986), 3 and 4: new localities in Balsfjord (2011, 2014). Black dots: new localities for *M. borealis*. Open dots: river systems without records of *Metretopus*. S: Spansdalselva, M: Målselva, R: Reisaelva, A: Altaelva, L: Lakselva, T: Tanaelva. Hatched area: region with the type locality of *M. borealis*.

S. lacustris, *Arthroplea congener* Bengtsson, 1908 and *Paraleptophlebia weneri*. *S. alternatus* and *A. congener*, but no *Metretopus*, were found in the dense vegetation belts further up in the pool.

M. alter was found in Geitbekken, Balsfjord, one of the four additional small streams in the Målselv system in 2014. This stream drains a few small bogs and runs in a forest landscape for about 1.8 km before entering the tributary, Fjellfrøselva. The sampling was done about 100 m above the inlet to the tributary (UTM 34WDB333602, Figure 2). This is the fourth locality in Norway, about 3 km north of the type locality. There is an overhanging birch, alder and willow forest at the sampling site. The stream is up to 1.5 m wide and 0.5 m deep and without macrovegetation. The substrates are stones, gravel, sand, mud, and wood debris. In addition to *M. alter*, oligochaetes, limnephilids, simuliids, the plecopterans *Diura* sp., *Capnia* sp. and *Nemurella pictetii* Klapalek, 1900, and the ephemeroptans *S. lacustris*, *Baetis* (*Baetis*)

bundyae Lehmkuhl, 1973 (sensu Engblom (1996)) and *H. dalecarlica* were collected.

Localities in reports and theses

Larvae of *Metretopus* sp. were recorded in seven of the 14 reports from river systems in Troms and Finnmark archived in Tromsø Museum (Table 1). The re-examination of the material deposited at the museum showed that all were *M. borealis*. There were no *M. alter* larvae in the museum collections. *M. borealis* larvae were also recorded in two theses (Johansen 2005, Johansen 2014).

Most of the river systems without records of *Metretopus*, Sæterelva, Harstad (Johansen 1998), Fosselva, Berg (Huru et al. 1985), Nordkjøselva, Balsfjord (Huru 1982a), Kvitneselva, Skjervøy (Huru 1983), Snøfjordelva, Måsøy (Huru 1981b), Julelva, Tana (Huru 1981c) and Syltefjordelva, Båtsfjord (Huru 1981a) are located on islands or close to the coast (Figure 2). In contrast,

the localities with *M. borealis*, Spansdalselva, Lavangen (Huru 1980b), Barduelva, Bardu (Huru 1981d), Lysbotnelva, Lenvik (Huru 1985), Reisaelva, Nordreisa (Huru 1980a), Altaelva, Alta (Bergersen 1987), Lakselva, Porsanger (Huru 1982b) and Tanaelva, Tana (Johansen 2005) are located away from the coast and close to the border with Sweden and Finland. The Museum also houses reports on benthos from some river systems, most of them coastal, in Nordland county, Strielva, Sortland (Fagermo *et al.* 1985), Elvegårdselva, Narvik (Huru 1982c), Valneselva, Bodø and Beiarn (Huru 1982d) and Sundsfjordelva, Gildeskål (Bergersen & Rubach 1986), but there are no records of *Metretopus* in any of these reports.

The following treatment of localities with *M. borealis* is given with reference to Table 1 and Figure 2.

The stream, Spansdalselva, is up to about 10 m wide and with substrate of stones, gravel and sand and scattered vegetation of algae, mosses and higher plants (Huru 1980b). *M. borealis* was found in low numbers (13 % of total benthos) in one out of 15 lotic stations, below the outlet of the lake, Lapphaugvatn (340 m a.s.l.), and *Metretopus* sp. (the specimens were badly preserved and could not be identified) also at Fosbakken (150 m a.s.l.). *Baetis (Acentrella) lapponicus* (Bengtsson, 1912) and *Baetis (Rhodobaetis) rhodani* (Pictet, 1843) were the most abundant species, out of a total of 13 mayfly species.

Several lakes and streams in the upper part of the Bardu river system were sampled by Huru (1981b) and *M. borealis* was found in low numbers in one stream, Gamasjokka (600 m a.s.l.). *B. (R.) rhodani* and *Ephemerella aurivillii* (Bengtsson, 1908) were the most common species out of a total of 15 mayfly species. Gamasjokka is up to about 5 m wide, has substrate of stones and gravel with little vegetation and dense shrubs of willow along the banks.

Huru (1985) sampled a few streams and one lake in the Lysbotnelva river system on the inner side of Senja. Two *Metretopus* larvae were recorded but not collected from the lake, Lysvatn. As they were found in a lake, they were probably *M. borealis*.

The Reisaelva river system had 19 species of mayflies Huru (1980a). *M. borealis* was found in the lakes Saitejavri (503 m a.s.l.) and Raisjavri (447 m) and the streams Njallajåkka and Askojåkka, all in the upper reaches of the system in a landscape of birch and willow shrubs. Both lakes have shallow littoral zones with substrates of stones and gravel and little or no macrovegetation. *M. borealis* was the most abundant (72 %) of six mayfly species in Saitejavri (four stations) and one of the three species in Raisjavri. Njallajåkka has substrate of stones and gravel and runs in rapids and shallow pools in a deep valley. There were nine mayfly species with *B. (R.) rhodani* the most abundant. *M. borealis* was found in low abundance (< 1 %) at one station, right below the tributary from Saitejavri. Askajåkka also has stony substrates. *M. borealis* was found in low numbers (4 %) in a mayfly community of 11 species dominated by *B. (R.) rhodani* and *B. (B.) subalpinus*. *Metretopus* has not been recorded in the main lowland stem of the Reisa River (Huru 1980a, Gabler 1994, 2000).

The main stem of the Alta river system is up to about 100 m wide and with substrate of stones and gravel. There is a mixed forest of birch, pine and alder along the banks. No upland stations in the system were sampled. Before hydropower regulation in 1987 there were 18 mayfly species, with *A. inopinatus*, *B. (R.) rhodani*, *B. (N.) muticus*, *H. dalecarlica*, and *E. aurivillii* being dominant (Huru 1984). *Metretopus* was sporadically found at four out of seven stations in the period 1980–86, but was not recorded after 1987 (Bergersen 1987, 1992). The specimens in the Museum collections were identified as *M. borealis*.

The overall mayfly richness was 21 in 29 running water and nine lake stations in the Lakselva river system (Huru 1982b). This is the highest mayfly diversity recorded for any river system in subarctic Norway. *B. (R.) rhodani* and *E. aurivillii* were the most abundant species and *A. inopinatus*, *B. (N.) muticus* and *H. dalecarlica* were also common. *Metretopus* was found in low numbers (2–4 % of the mayflies) in four out of seven river zones including tributary streams above and below the lake, Øvrevatn, and the outlets of Øvrevatn and Nedrevatn. The streams run in a birch-willow landscape, and the

substrates are mainly stones and gravel with little vegetation. *M. borealis* was also recorded from the hard bottom littoral in the lakes themselves, respectively in abundances of 12 (five other species) and 43 %. All museum specimens from Lakselva were identified as *M. borealis*.

No *Metretopus* were recorded from the Finnish river, Utsjoki, a tributary of the Tana River system (Herfindal 1997, Gabler 2000) but Johansen (2005) collected *M. borealis* in seven out of 13 tributary streams distributed along the entire system. The streams were sorted according to the riparian vegetation, *i.e.* willow, birch, mixed birch/pine and treeless alpine vegetation. The altitudes varied from 10 to 270 m a.s.l. They had mean widths of 2–8 m, mean depths from 11 to 34 cm and water currents around 30 cm s⁻¹. All had substrates of gravel, stones and small boulders, and some degree of moss cover. The combined mayfly richness was 17 with *B. (N.) muticus*, *B. (B.) rhodani*, *B. (B.) subalpinus* and *E. aurivillii* as the most abundant species. *M. borealis* were recorded in three birch streams, two birch/pine streams and two treeless streams, but not in the willow streams located in the lower part of the system (Figure 2). No *M. alter* were recorded.

Discussion

We had expected to add several new localities for *Metretopus alter* in Norway, but this was not the case. It was confirmed at the type locality and found in two new localities in the Målselv river system: the stream, Andorelva, flowing into Fjellfrøsvatn and the stream, Geitbekken, flowing to the tributary, Fjellfrøselva. However, all other records of *Metretopus* in Troms and Finnmark were *M. borealis*. This was surprising because *M. alter* is found in many localities northern Sweden and Finland (Engblom *et al.* 1993). Kjærstad (2007) suggested that the paucity of records from Norway was due to a shortage of collections in suitable habitats. Therefore, we sampled four small streams in Målselv with characteristics that matched the description of *M. alter* habitats given by Engblom *et al.* (1993). We found *M. alter* in one of them but not in the other three. It is most

likely that it is not there but we cannot rule out that the collection efforts were not thorough enough, although several stations were sampled in each stream and the timing should be right for a univoltine summer species. There were, however, never many larvae in the samples and it was not found in the type locality in 2011 in spite of quite extensive sampling. These observations indicate that *M. alter* is neither common nor abundant in the region and therefore may be overlooked even if it is present. It is worth mentioning that Soot-Ryen collected adult mayflies from many localities in Målselv in the 1920s but only found *M. alter* at Råvatnbekken (Bengtsson 1930).

It was also surprising that it was not found in any of the river systems described in the reports and theses from Nordland, Troms and Finnmark, especially since larvae had been collected in Gargiaelva in Alta (Engblom *et al.* 1993). Some of the reports may not be thorough but most of them are, and the theses were all based on rigorous collections at the right time and at several stations. However, as many lakes were sampled and most of the lotic habitats were possibly larger than preferred by *M. alter*, it is likely that many localities were not suitable. In any case, our results indicate that it may be present but not abundant in suitable habitats and that more extensive and focussed sampling is needed in order to show if *M. alter* is more widely distributed in Norway.

Nevertheless, it was positive that *M. alter* still survives in the type locality, Råvatnbekken, 90 years after its initial discovery. The population does not appear to be large, but it clearly has been able to survive for a long time in quite harsh conditions, as this is a rather small stream that may nearly dry up in some summers (Jan-Tore Skjærvik, pers. comm.) and probably also freeze to the bottom in cold winters. This agrees well with the conditions in Vargbäcken in Västerbotten, Sweden where Anders N. Nilsson (Engblom *et al.* 1993) studied the phenology of the species. In general, Engblom *et al.* (1993) found that *M. alter* has a preference for smaller streams with substrates of stones and sand. Stream widths were from below 1 to 16 m, depths 10 cm to 1 m and currents up to 1.5 ms⁻¹. pH values were around neutral and water colour varied but tended towards

clear water. Vegetation cover varied, but was generally low. The type locality comes quite close to this description and several of the insects listed with *M. alter* in Sweden (the mayflies *Siphonurus lacustris*, *Baetis* (*B.*) *subalpinus*, *Paracinygmula joernensis*, and the stonefly *Leuctra digitata* Kempny, 1899) are present. In addition to *M. alter*, Bengtsson (1930) found *Siphonurus aestivalis* Eaton, 1903, *Centropilum luteolum* (Müller, 1776) and *Leptophlebia vespertina* (Linnaeus, 1758) in the material collected along Råvatnbekken.

In contrast, *M. borealis*, appears to be widespread in Troms and Finnmark. The identification of the larvae in Tromsø Museum and the re-identification from Takvatn added a number of new localities in both counties. This supports the general conclusion of Kjærstad *et al.* (2012) that it is found in all Strand provinces in Finnmark. The old material of adults in Tromsø Museum also shows this, as it comprises collections from Målselv, Porsanger and Karasjok (all leg. T. Soot-Ryen) and Sør-Varanger (leg. A. Wessel). With the present contribution, it is now documented from the majority of the large river systems in Troms and Finnmark (Spansdalselva, Barduelva, Målselva, Reisaelva, Altaelva, Lakselva and Tanaelva). However, the records indicate a pattern of occurrence away from the coast (Figure 2). Almost all localities are inland and often in the upper parts of the river systems. Reisaelva and Tanaelva illustrate this well. In Reisaelva, *M. borealis* is found in several localities high up in the system (Huru 1980a), but not in downstream stations (Huru 1980a, Gabler 1994, 2000). In Tanaelva, the species was found in all upper streams but not in the two downstream tributaries (Johansen 2005). The location of the type locality (between Kautokeino and Karesuando, Figure 2) fits this pattern. This may reflect a general pattern of distribution of aquatic insects in subarctic Norway as the inland systems with *M. borealis* had many (13–21) mayfly species while the coastal systems without it had only 2–12 species (Table 1). The inland systems also tend to have high diversities of stoneflies (Table 1), explained by the greater degree of continentality away from the coast (Lillehammer 1985).

M. borealis shows adaptation to a wide range

of habitats in subarctic Norway. Moderately sized streams were the most common habitat and it was also found on the stony shores of several large lakes. It was not found in the rivers Reisaelva and Utsjoki in spite of extensive sampling but the sporadic reports from Altaelva show that it can live in large rivers. The streams were up to about 10 m wide and 1 m deep and had substrates of stones and gravel and little vegetation. The habitats in Tanaelva are probably typical, with mean values for width, depth and current of up to 8 m, up to 34 cm and about 30 cm⁻¹, respectively (Johansen 2005). It was always found in stream communities with high diversities of other mayflies and stoneflies (Table 1). *Baetis* (*B.*) *rhodani* was common in all the systems and *Ephemerella aurivillii* in most of them. In Sweden, *M. borealis* has a strong preference for meandering rivers with sandy bottoms, an abundance of submerged fallen trees, algae, mosses and higher plants, as well as diverse insect communities (Engblom *et al.* 1993). Stream sizes (width and depth) of the present localities are within the ranges given for Sweden and the insect diversities appear to be similar, although the localities in Troms and Finnmark tend to have coarser substrates than the Swedish streams and had almost no fallen trees and little macrovegetation. The coarser substrates indicate swifter streams and the other differences are probably related to latitude and altitude, as many of the Norwegian streams are in areas with sparse or no trees and poor conditions for macrophytes.

M. borealis occurred in high abundance in several large lakes. It was the third most abundant mayfly (after *Ameletus inopinatus* and *Heptagenia dalecarlica*) on the stony shore of Takvatn (Klemetsen & Elliott 2010, Johansen 2014). Johansen (2014) concluded that it was absent deeper down in the littoral as it seems to prefer the stony shore habitat and avoid the macrovegetation of the lower littoral. High numbers were also found in Saitejavri (Huru 1980a) and Nedrevatn (Huru 1982b). The shores of these large lakes are wave-washed habitats with substrates of rocks, stones, gravel and sand and no macrophytes. These habitat characteristics resemble the streams of the region in many ways. Mayfly and stonefly richness in the shore communities of lakes, such

TABLE 1. New localities for *Metretopus borealis* in Troms and Finnmark counties. Region: Strand-system geographical regions, Year: sampling years, Habitat: habitats with records of *M. borealis* (L: lake, S: stream, R: river; with number of localities indicated), Ephem: Ephemeroptera richness, Plecop: Plecoptera richness.

River system	Region	Year	Habitat	Ephem	Plecop	References
Spanselva	TRI	1978	S (1)	13	14	Huru (1980b)
Lyselva	TRY	1984	L (1)	5	8	Huru (1985)
Barduelva	TRI	1980	S (1)	15	14	Huru (1981d)
Målselva	TRI	2012	L (1)	7	3	Johansen (2014)
Reisaelva	TRI	1987	L (2), S(2)	19	22	Huru (1980a)
Altaelva	FV	1980–1986	R (1)	18	20	Huru (1984), Bergersen (1987, 1992)
Lakselva	FI	1977–1978	L (2), S (4)	21	18	Huru (1982b)
Tanaelva	FI	2000–2002	S (7)	17	20	Johansen (2005)

as Takvatn (Klemetsen & Elliott 2010), Saitejavri (Huru 1980a) and Nedrevatn (Huru 1982b) was, however, much lower than for the streams where *M. borealis* was recorded. This indicates not only that the stony shores of large lakes in the region provide suitable habitats for *M. borealis*, but also suggests that the shore habitat allows high densities, presumably because of the lower degree of ecological interactions, although food supply may also be important.

The ecological niches of the two *Metretopus* species appear to be similar. Söderström (1991) and Engblom *et al.* (1993) found that in Fennoscandia *M. borealis* is a univoltine species with winter eggs. The life cycle of *M. alter* is poorly known but is probably similar. They are presumably detritus and biofilm feeders like many species in related families. Engblom *et al.* (1993) found them together in a Swedish stream and Bauernfeind & Soldan (2012) note that they are often syntopic. This seems natural as their habitat requirements overlap considerably. However, there are differences, with *M. borealis* tending towards larger streams and wave-washed lake shores while *M. alter* prefers smaller streams and avoids lakes. This may be related to temperature as it is suggested that eggs of *M. alter* need a water temperature close 10° C to hatch (Engblom *et al.* 1993) and small streams tend to be warmer during summer.

Although the present combination of new collections, information from reports and theses and identification of material at Tromsø Museum

demonstrated two new localities for *M. alter* and many new localities for *M. borealis* in Norway, the study showed that many aspects of the distribution and ecology of *M. alter* and *M. borealis* are insufficiently known. Therefore, this pair of closely related mayflies, both of them described from northern Norway, offer challenges to provide more information on both, but particularly on the still poorly known *Metretopus alter*.

Acknowledgements. We thank Randi Brenn Skjærvik and her late husband Jan-Tore Skjærvik, who tragically died in an avalanche in 2013, for their hospitality when sampling on their land. We are also grateful to Robert Bergersen at Tromsø Museum for his help with providing *Metretopus* samples and a series of little known reports from the magazines of the museum, and to Frøydis Strand for drawing Figure 2. The editor and reviewers are also thanked for constructive comments.

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Received: 23 March 2015

Accepted: 5 June 2015