

# The viability of the crustacean *Eury cercus lamellatus* (Branchiopoda, Cladocera) in a high mountain area in southern Norway

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The branchiopod *Eury cercus lamellatus* is widely distributed in Norwegian lakes, ranging from coastal to alpine areas. On the Hardangervidda mountain plateau in southern Norway, *E. lamellatus* was searched for in 144 lakes in 11 catchments in the western and 16 catchments in the central and eastern areas. The occurrence of *E. lamellatus* is mainly based on the diet of brown trout *Salmo trutta*. *Eury cercus lamellatus* was recorded in 25% and 70% of the lakes in these two areas, respectively. This may be due to striking differences in the environmental conditions, with more dilute water and lower water temperatures in western areas, and hence shorter growing seasons. The occurrence of *E. lamellatus* in central and eastern catchments increased with lake size, being found in 65% and 85% of lakes with a surface area of <2.0 and ≥2.0 km<sup>2</sup>, respectively. In the western area, *E. lamellatus* occurred less frequently in lakes above 1000 m a.s.l., which was not the case in central and eastern catchments. In this central part of Hardangervidda, the relative abundance of *E. lamellatus* in the diet of brown trout was studied more thoroughly in five different lakes, showing that they were preyed upon throughout the growing season (June to October). When the two big crustaceans *Gammarus lacustris* and *Lepidurus arcticus* are at low densities in these lakes, *E. lamellatus* became the staple food item for brown trout, except for larger fish (>400 mm). However, under high predation pressure, *E. lamellatus* also contributed significantly to the diet of larger fish. The abundance of *E. lamellatus* seems to vary highly on a yearly basis in one of the lakes (Sandvatn). Even though *E. lamellatus* is described as a typical littoral species, it was commonly found down to depths of 15 m.

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## INTRODUCTION

The branchiopod *Eury cercus lamellatus* (O.F. Müller, 1776) is widely distributed in Norwegian lakes, being recorded in 37% of all localities investigated (Walseng 2015). It is frequently found in lakes from sea level up to 1355 m a.s.l. (Sandøy & Nilssen 1986; Walseng 2015). *Eury cercus lamellatus* occurs both in small fishless ponds and in larger lakes, although its occurrence appears to increase with lake size (Walseng 2015). Further, it also tolerates acid waters with low ionic content (Sandøy & Nilssen 1986; Walseng 2015).

Hardangervidda is the most extensive mountain plateau in Europe, where the brown trout *Salmo trutta* Linnaeus, 1758 is an almost allopatric fish species. The lakes on Hardangervidda are rated among the best brown trout lakes in Norway, hosting large fish of high quality (Sømme 1941). A rich supply of crustacean food items such as *Lepidurus arcticus* (Pallas, 1793) and *Gammarus lacustris* G.O. Sars, 1863 is regarded as the main reason for prolonged growth of brown trout to sizes of one to three kg and even more (Huitfeldt-Kaas 1911; Dahl 1917; Sømme 1941). However, the smaller *E. lamellatus* may also

be an extremely important food item for brown trout. In high mountain lakes, the life-cycle traits of *E. lamellatus* and its significance as fish food has been little focused on since the studies that were carried out on the north-eastern part of Hardangervidda in the early 1900s (Dahl 1917). He showed that fish predation had a major impact on these crustaceans. However, in lakes with good access to *G. lacustris* and *L. arcticus*, brown trout selectively graze on these two big food items rather than on the smaller *E. lamellatus* (Qvenild & Rognerud 2018).

So far, only 23 localities with *E. lamellatus* have been noted in this area (Norwegian Biodiversity Information Centre, Artsdatabanken.no). It has a highly skewed geographic distribution, with almost all records from the central and eastern areas. The western areas receive much higher snow depositions than central and eastern areas (Qvenild & Hesthagen 2019). This cause a delay in the ice break-up in western lakes, resulting in shorter growing seasons and lower water temperatures (Borgstrøm 2016). This, in addition to more electrolyte poor water low in calcium (Skjelkvåle & Henriksen 1998), may cause more hostile conditions for *E. lamellatus*, as has

been shown for *L. arcticus* (Qvenild & Hesthagen 2019) and *G. lacustris* (Qvenild et al. 2020).

Proximity to species refugia and an adequate activity pattern may be crucial in optimising the survival of *E. lamellatus* under high predation pressure from fish. Their diurnal pattern of activity was demonstrated in a study of juvenile perch *Perca fluviatilis* Linnaeus, 1758 and roach *Rutilus rutilus* (Linnaeus, 1758) (Tewson et al. 2016). The habitat preferences and their pattern of activity was experimentally tested using different food sources and fish cues (Beklioglu & Jeppesen 1999). Exposed to fish, *E. lamellatus* seeked to the bottom of the chambers (or to sediment), probably in an attempt to hide within the sediment to avoid predation. Low epiphyte abundance evidently increases their vulnerability to visually hunting fish.

Field studies have shown that *E. lamellatus* is a typical semi-benthic and littoral species, being most abundant in shallow vegetated areas along the shoreline (Dahl 1917; Smirnov 1962; Koksvik 1995; Aase 2000; Örnólfssdóttir & Einarsson 2004), but it is also common down to depths of 20 m (Dahl 1932). It is an efficient grazer on periphyton (Smirnov 1962; Koksvik 1995; Örnólfssdóttir & Einarsson 2004), and may accumulate in enormous densities, especially in vegetated areas (Dahl 1913).

The main goal of this study was to outline the occurrence of *E. lamellatus* in lakes on Hardangervidda and gain knowledge of its

environmental requirements in such high mountain lakes. Apparently, *E. lamellatus* is a viable species that is well adapted to a wide range of environmental conditions (Smirnov 1962, Aass 1969; Sandøy & Nilssen 1986; Walseng 2015). It may therefore be a more important food source for fish than has been documented earlier, with a substantial ability to withstand high predation pressure. This may be the case in high mountain lakes in particular, when *G. lacustris* and *L. arcticus* are absent or occur at low densities. Even in more dense fish populations, *E. lamellatus* seems capable of withstanding heavy predation pressure (Qvenild & Rognerud 2018). In lowland lakes in southern Norway, the big cladocerans *Sida crystallina* O.F.M. and *E. lamellatus* were heavily predated by introduced rudd *Scardinius erythrophthalmus* (Linnaeus, 1758) in the littoral zone, hence being a strong competitor to young native perch and brown trout (Walseng & Jensen 2018). The abundance of the littoral cladocereans >1mm were reduced but they were not exterminated. Also in Lake Takvatnet in North Norway, *E. lamellatus* comprised a comprehensive part of the littoral crustacean community despite of heavy fish predation (Aase 2000).

To elucidate the ability of *E. lamellatus* to withstand high predation pressure from brown trout, we analysed their diet from five lakes at the central part of the plateau throughout the growing season for 15 years (see Qvenild et al. 2018). In one of these lakes,

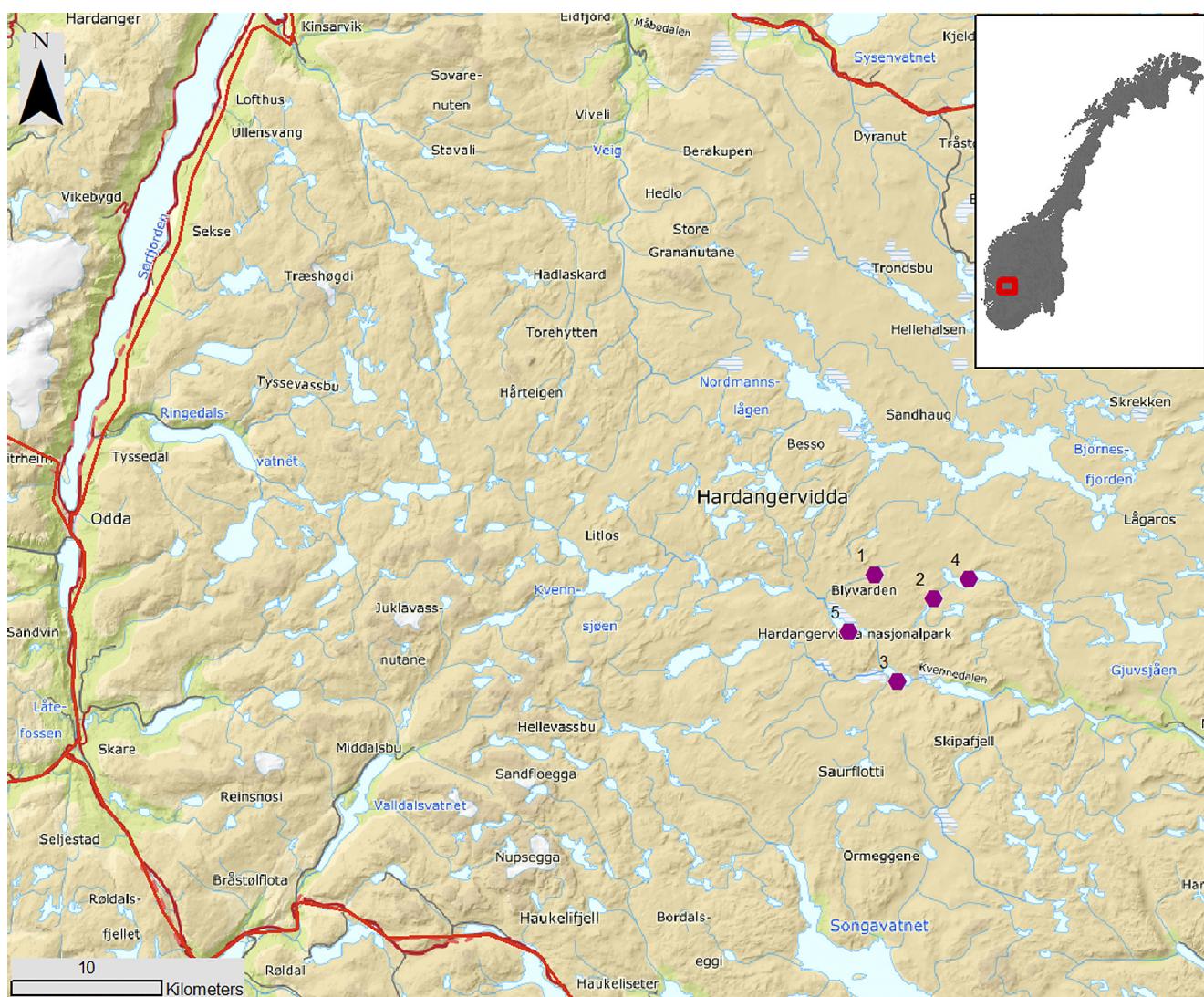


Figure 1. Map showing the location of the five study lakes on Hardangervidda: 1) Blånuttjørnane, 2) Dargesjåen, 3) Gunleiksuvatnet, 4) Fjellsjåen and 5) Sandvatn. Vital statistics for the lakes are given in Table 1. The Norwegian Mapping Authority CC BY 4.0.

**Table 1.** Vital statistics of the five study lakes. The statistics are given by the Norwegian Water Resources and Energy Directorate (NVE) and computed by the NEVINA procedure (NVE Atlas, [nve.no](#)), except for mean and maximum depth (own data). The lake area is included in the catchment which is computed with the outlet as set point in the NEVINA procedure. Lake number refers to the numbers given in Figure 1.

Lake no.	NVE ID no.	Locality	Altitude m a.s.l.	Area km <sup>2</sup>	°N	°E	Catchment km <sup>2</sup>	Mean depth (m)	Max depth (m)	Retention time (days)	References
1	18770	Blånuttjørnane	1313	0.31	60.0883	7.5020	3.7	6.1	31	179	Rognerud <i>et al.</i> 2005
2	18827	Dargesjåen	1209	0.64	60.0835	7.5866	15.7	4.7	15	66	Rognerud <i>et al.</i> 2006
3	14	Gunleiksbutvatnet	1076	1.29	60.0309	7.5655	434.6	2.9	12	2.5	Rognerud <i>et al.</i> 2003
4	39	Fjellsjåen	1197	2.31	60.0958	7.6566	37.4	8.1	26	175	Rognerud <i>et al.</i> 2006
5	17	Sandvatn	1112	1.57	60.0546	7.5111	288.2	2.6	13	3.9	Rognerud <i>et al.</i> 2005

**Table 2.** The number of stomachs sampled from the five study lakes. In total 4.334 brown trout stomachs were examined in 100 dated test-fishing events. For details, see Appendix 2.

Lake	Zone	Period	No. of events	No. fish with <i>Eurycercus lamellatus</i>				Frequency%	
				<250 mm	≥250 mm	<250 mm	≥250 mm	<250 mm	≥250 mm
Blånuttjørnane	Littoral	2004	2	19	21	4	0	21	0
Dargesjåen	Littoral	2003–2012	8	158	146	26	37	16	25
Fjellsjåen	Littoral	2006–2012	10	154	312	32	36	21	12
Gunleiksbutvatn	Littoral	2002	1	46	22	4	0	9	0
Sandvatn	Littoral	2001–2016	61	1709	1205	440	205	26	17
Sandvatn	Profundal	2001–2016	18	345	197	104	24	30	12
Total		2001–2016	100	2431	1903	610	302	25	16

comparative test-fishing was carried out in the littoral and profundal zones for 12 years to elucidate their attraction to different habitats (see Qvenild & Rognerud 2018).

## MATERIAL AND METHODS

### Study area

The Hardangervidda landscape is characterized by barren, treeless moorland interrupted by numerous pools, lakes, rivers and streams. The central part of this peneplain is a National Park. The main 27 catchments on the most central and remote parts of the plateau comprise an area of 6569 km<sup>2</sup> (Qvenild & Hesthagen 2019). In this area, 930 named lakes are identified (Norwegian Water Resources and Energy Directorate, NVE Atlas, [nve.no](#)), in which all the lakes are given their own NVE ID number. These localities also include 27 reservoirs for hydropower production that ranged in size from 0.39 to 78.77 km<sup>2</sup> (Appendix 1). Their water level fluctuation ranged from 0.5 to 91.9 m annually, most of them being regulated by more than 10 m (76%) and 60% more than 20 m (cf. NVE Atlas, [nve.no](#)). In addition, there are approximately 11,600 small unnamed lakes and ponds covering 157 km<sup>2</sup>.

The western area of Hardangervidda is dominated by rocky terrain and expanses of bare rock with thin or no moraine-covered bedrock of Precambrian gneisses and granites and sparse or no vegetation. Some catchments in the central part comprise bedrock of Cambro-Silurian sedimentary origin. The bedrock in the eastern areas also covers gneisses and granites but has deeper layers of moraine. The

water chemistry on Hardangervidda closely reflects the local bedrock geology (Skjelkvåle & Henriksen 1998). Hence, the lakes are highly variable in water chemistry, ranging from lakes being practically free of electrolytes to lakes with high ionic strength. The content of total organic carbon (TOC) is generally low, due to the sparse vegetation and thin soil, with TOC <1.6 mg C L<sup>-1</sup> in 75% of the lakes. In such clear-water lakes, calcium, magnesium and bicarbonate are the basic ions, reflected in pH, alkalinity and conductivity. From the data given by Skjelkvåle & Henriksen (1998) we estimated the relationship of conductivity  $\chi$  (in  $\mu\text{S cm}^{-1}$ ) and calcium concentration Ca (in  $\text{mg L}^{-1}$ ) to be:  $\text{Ca} = 1.7646 * \chi - 0.6774$  ( $r^2 = 0.987$ ,  $N=117$ ). The water quality in some of these lakes is repeatedly measured, and in such cases, the minimum values of calcium are used.

The climatic conditions on Hardangervidda are also highly variable (Qvenild & Hesthagen 2019). The winter and summer depositions are computed using the NEVINA procedure (NVE Atlas, [nve.no](#)) as mean values for the normal period 1961–1990. The winter deposition (October–April) differs substantially in a west to east gradient with an almost four-fold decrease from 1151 mm in Austdølo/Ljoso catchment to 292 mm in Uvdalselvi catchment. The mean summer deposition (May–September) in these two catchments varied less; being 614 and 332 mm, respectively. The mean winter and summer temperatures are computed similarly.

Brown trout is allopatric in most lakes on Hardangervidda. Arctic char *Salvelinus alpinus* (Linnaeus, 1758) occur in 3.1% and the European minnow *Phoxinus phoxinus* (Linnaeus, 1758) in 4.5% of a total of 930 named lakes (Qvenild & Hesthagen 2019).

## Distribution of *Eurycercus lamellatus* obtained from the literature

We searched for *E. lamellatus* in 144 lakes. (Appendix 1). Our main sources of information are technical reports and scientific papers. In most of these publications, the occurrence of *E. lamellatus* is mainly based on diet analyses of brown trout. In some lakes, other methods such as hauls and various types of bottom samplers, have also been used (Dahl 1917; Amundsen 1976; Halvorsen 1973; Walseng *et al.* 1994; Walseng *et al.* 1996; Fjellheim *et al.* 2007). The more basic fishery surveys provide detailed analyses of the different food items. In our context, the occurrence of *E. lamellatus* is noted as a positive finding when it is mentioned in the results of a survey. In lakes with negative findings, they may still occur (Dahl 1917). This is underlined by the results from lakes repeatedly examined that produced both positive and negative findings.

## Temporal variation in the abundance of *Eurycercus lamellatus*

Field studies in five lakes in the Kvenna catchment in the central part of Hardangervidda were performed between 2001 and 2016 (Figure 1); Sandvatn, Fjellsjåen, Dargesjåen, Kringsesjåen and Blånuttjørnane (Qvenild & Røgnedal 2018; Qvenild *et al.* 2018). These lakes are situated at altitudes of 1076 to 1313 m a.s.l., being medium-sized with surface areas of 0.31–2.31 km<sup>2</sup> and shallow with mean depths of 2.6–8.1 m (Table 1). These lakes contain sparse populations of

allopatric brown trout. However, the 1997 year-class was extremely numerous, which caused a sharp rise in stock densities in the period 2004–2008, especially in Lake Sandvatn (Qvenild & Rognerud 2018). The main crustacean food items in these study lakes, in addition to *E. lamellatus*, are *L. arcticus* and *G. lacustris*. Between 2001 and 2016 the diet of 3792 brown trout stomachs from 100 fishing events in the littoral zone in these five study lakes was analysed (Table 2, Appendix 2). To analyse the predation pressure from brown trout on these three crustaceans, we focused on the August–October period, when all species are available to be preyed upon. From this period, we obtained autumn diet of 3362 brown trout from the littoral zone, ranging in size between 110 and 470 mm.

In one of the lakes, Lake Sandvatn, comparative test-fishing was performed both in the littoral (2–5 m depth) and profundal zones (12–15 m depth) in mid-August in 12 years from 2001 through 2016 (Table 5). From the littoral and profundal zones, 2914 and 542 brown trout stomachs were obtained, respectively (cf. Appendix 2).

## RESULTS

## Geographical distribution of *Eurycercus lamellatus* on Hardangervidda

Of the 930 named lakes, 144 (15%) have been fully examined for

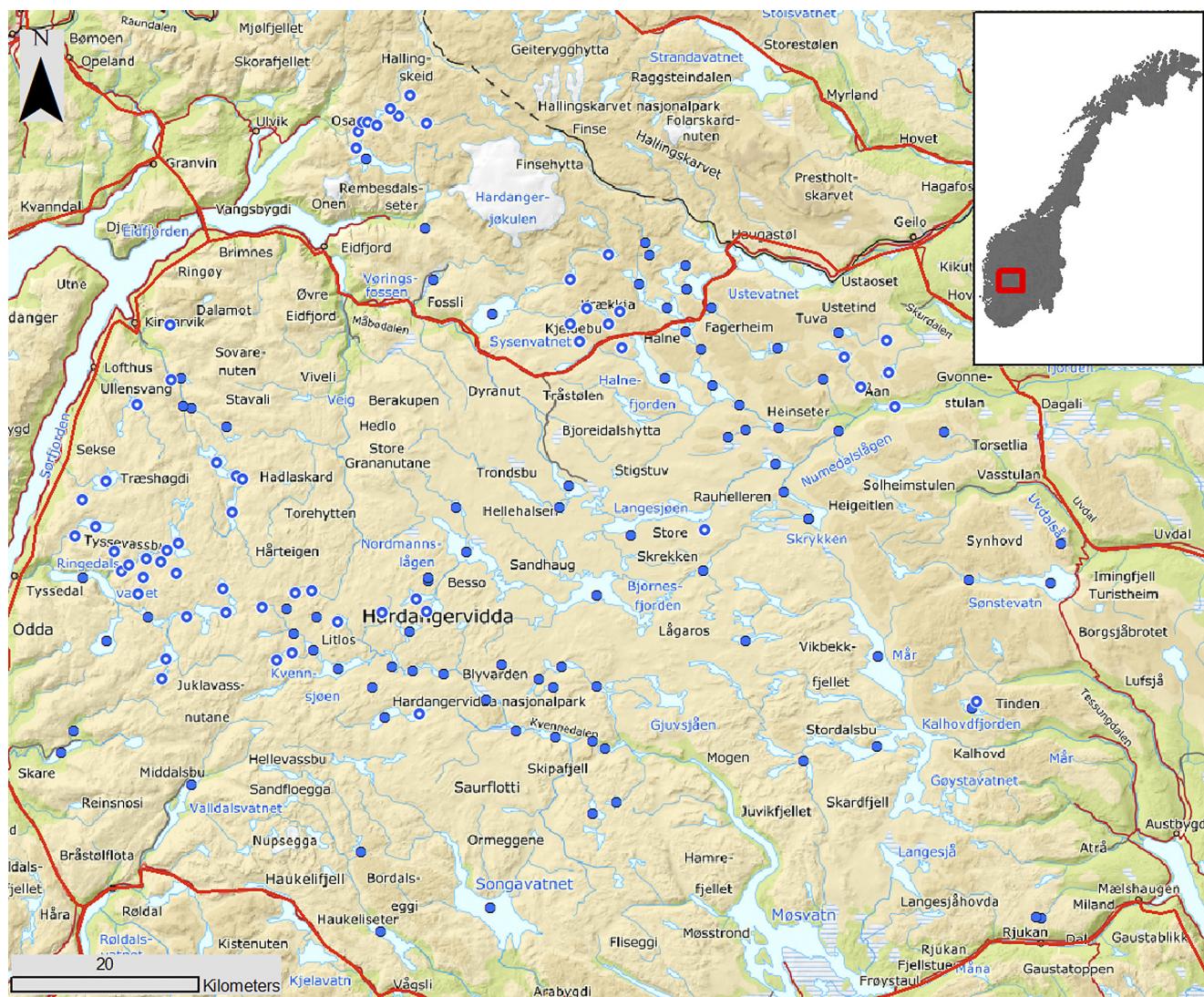


Figure 2. Lakes surveyed for the presence of *Eurycerus lamellatus* on Hardangervidda. Lakes with positive and negative findings are shown by filled and open dots, respectively. Details of the localities are given in Appendix 1. The Norwegian Mapping Authority CC BY 4.0.

*E. lamellatus*, of which 83 lakes (58%) produced positive findings (Figure 2, Appendix 1). Many of these localities have been repeatedly examined (Table 3). For example, Lake Sandvatn in the Kvenna catchment was studied for 15 years, all of which produced positive findings of *E. lamellatus* (Qvenild & Rognerud 2018).

In the 16 central and eastern catchments, *E. lamellatus* was recorded in 73 of 104 lakes (70%). In the lakes only sampled once, *E. lamellatus* was recorded in 52% of these cases. This fraction increased to 75% with two repeats. Lakes sampled more than two times, *E. lamellatus* was recorded in almost all (97%). In the diet of brown trout from 40 lakes in the 11 western catchments, *E. lamellatus* was only recorded in ten of them (25%). Many lakes in both areas have been repeatedly examined; i.e. a mean of 2.40 and 2.08 times, respectively.

Most of the named lakes are situated at altitudes of 1100–1399 m a.s.l. (85%), while 11% and 4% are located at lower and higher altitudes, respectively. In this interval, we related the occurrence of *E. lamellatus* to lake altitude. In the 16 catchments in central and eastern parts of Hardangervidda, where it is a common food item for brown trout, there were only small variations in their occurrence at different

altitudes (Table 4). In lakes located at 800 to 1099 m a.s.l. and at 1100 to 1399 m a.s.l., *E. lamellatus* was found in 85 and 68% of the lakes, respectively. *Eurycercus lamellatus* is a common species both in the lowest (Lake Isdalsvatnet at 832 m a.s.l.) and the highest located lake (Lake Vesle Meinsvatnet at 1353 m a.s.l.). Of the 755 lakes in this area, 53 are situated above 1353 m a.s.l., of which none was examined for *E. lamellatus*.

In the 11 western catchments, six of the ten lakes (60%) located at altitudes lower than 1000 m a.s.l. had *E. lamellatus*, compared to only four of the 30 lakes (13%) located higher than 1000 m a.s.l. (Table 4). In this area, Lake Nibbehølen is the highest situated lake (at 1191 m a.s.l.) with *E. lamellatus*. Of 155 lakes in this area, 93 of them are situated above 1191 m a.s.l. of which 16% were examined.

In the 95 natural lakes examined within the 16 central and eastern catchments, 75 had surface areas  $<2.0 \text{ km}^2$ , in which *E. lamellatus* were found in 64%. In the 20 lakes  $\geq 2.0 \text{ km}^2$ , 80% contained *E. lamellatus*. The species is also likely to occur in the remaining four lakes  $\geq 2.0 \text{ km}^2$  not examined in this area. However, the big lakes are more frequently investigated than the small ones. Of the lakes

Table 3. Percent of lakes examined for *Eurycercus lamellatus* in the 27 catchments studied on Hardangervidda. Only 144 lakes (15%) are properly examined for *Eurycercus lamellatus*, of which 58% had positive findings. Many of the lakes are repeatedly investigated given with a factor in the last column (= no. of examinations/no. of lakes).

No.	Catchment	No. of lakes	No. of lakes examined for <i>E. lamellatus</i>	% of lakes examined	No. of lakes with <i>E. lamellatus</i>	% of lakes recorded	No. of examinations	Repeatedly examined
1	Austdøla	22	10	45	1	10	15	1.50
2	Sima	14	1	7	1	100	2	2.00
3A	Isdølo	6	1	17	1	100	2	2.00
3B	Leiro	22	8	36	1	13	10	1.25
3C	Svinto	2	0	0	0		0	
4	Bjoreio	14	2	14	2	100	3	1.50
5	Veig	37	2	5	0	0	2	1.00
6A	Erdalsvassdraget	2	0	0	0		0	
6B	Bjotveitvelvi	2	0	0	0		0	
7A	Kinso	31	9	29	4	44	10	1.11
7B	Vivippo	4	1	25	0	0	1	1.00
8	Opo	10	1	10	0	0	1	1.00
9A	Espeelvi	1	1	100	0	0	1	1.00
9B	Vendo	2	1	50	0	0	2	2.00
10	Tysso	46	21	46	3	14	54	2.57
11	Austdøla/Ljoso	13	2	15	2	100	2	1.00
12	Suldalsvassdraget	7	1	14	1	100	2	2.00
13	Bora	34	2	6	2	100	4	2.00
14	Songa	44	1	2	1	100	6	6.00
15	Kvenna	99	29	29	23	79	102	3.52
16	Møsvatn	103	2	2	2	100	2	1.00
17	Mår/ Gøyst	156	6	4	5	83	10	1.67
18A	Uvdalselvi	39	4	10	4	100	8	2.00
18B	Ølmosåi	37	0	0	0		0	
19A	Lågen	154	33	21%	25	76	80	2.42
19B	Ufysja	10	3	30%	1	33	5	1.67
20	Ørteråni	19	5	26%	5	100	12	2.40
	TOTAL	930	146	16%	84	58	336	2.30

**Table 4.** Frequency percent of lakes with *Eurycerus lamellatus* at different altitudes in 16 catchments located in central and eastern areas and 11 western catchments on Hardangervidda.

Lakes with <i>Eurycerus lamellatus</i> from the 16 central and eastern catchments:				
Altitude m a.s.l	No. of lakes	Examined lakes	Lakes with <i>E. lamellatus</i>	Frequency of lakes with <i>E. lamellatus</i> (%)
<800	0	-	-	-
800-899	6	3	2	67
900-999	16	5	4	80
1000-1099	64	12	11	92
1100-1199	270	52	36	69
1200-1299	267	22	14	64
1300-1399	140	10	7	70
1400-1499	12	0	0	-
≥1500	0	-	-	-
	775	104	74	71
Lakes with <i>Eurycerus lamellatus</i> from the 11 western catchments:				
Altitude m a.s.l	No. of lakes	Examined lakes	Lakes with <i>E. lamellatus</i>	Frequency of lakes with <i>E. lamellatus</i> (%)
<800	6	5	4	80
800-899	5	2	2	100
900-999	10	3	0	0
1000-1099	14	5	0	0
1100-1199	34	10	4	40
1200-1299	46	9	0	0
1300-1399	34	6	0	0
1400-1499	5	0	0	0
≥1500	1	0	0	0
	155	40	10	25

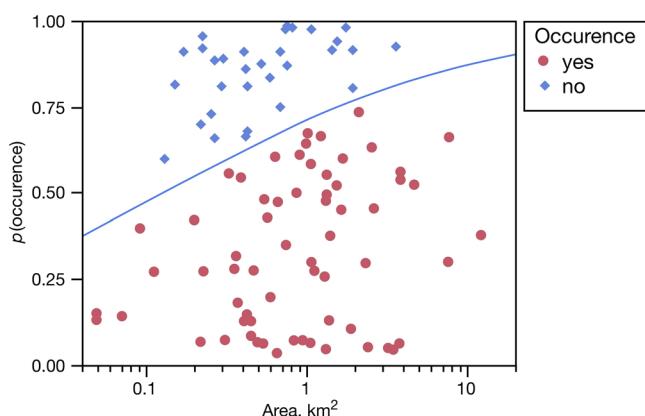
examined one to two times or more than two times, the mean area was 1.15 km<sup>2</sup> (N=68, SD±1.67) and 2.89 km<sup>2</sup> (N=27, SD±3.85), respectively.

The incidence of *E. lamellatus* increased significantly with lake size as shown by a logistic regression:  $p(\text{occurrence}) = (1 + \exp(0.848 + 0.910 \cdot \log \text{Area}))^{-1}$  (likelihood-ratio chi-square test:  $\chi^2 = 4.39$ ,  $p = 0.036$ ) (Figure 3).

The calcium concentration is assumed to be the most important water chemistry variable for crustacean growth (Rukke 2002). We have minimum measures of calcium concentration in 58 of 83 (70%) localities with positive findings of *E. lamellatus* of which 39% had calcium concentrations below 1.00 mg L<sup>-1</sup> (cf. Appendix 1).

In the central and eastern areas, 73 of 104 (70%) localities had positive findings of *E. lamellatus*. Of the 51 localities with calcium values, 18 (35%) had lower values than 1.00 mg L<sup>-1</sup>. The lowest value of 0.28 mg L<sup>-1</sup> was obtained in Lake Svartevatn in 1994, which was prior to the liming programme that started in 1994 (Fjellheim *et al.* 2002). During this early phase of acid precipitation, *E. lamellatus* was present in the lake. This is the lowest calcium concentration measured in any lake with positive records of *E. lamellatus* on Hardangervidda.

Of the 10 localities with *E. lamellatus* in the western area, water chemistry data are available from seven lakes, of which five had calcium concentration less than 1.00 mg L<sup>-1</sup>.



**Figure 3.** Logistic regression curve showing the probability of occurrence of *Eurycerus lamellatus* as a function of lake surface area. Of the 95 natural lakes studied within the 16 central and eastern catchments, *Eurycerus lamellatus* was found in 80% of the 20 lakes >2.0 km<sup>2</sup>, while the species was found in only 64% of 75 lakes <2.0 km<sup>2</sup>.

### The occurrence of *Eurycerus lamellatus* in reservoirs

Most of the 27 reservoirs within the study area have been repeatedly investigated, on average more than three times. *Eurycerus lamellatus* was searched for in 24 of these reservoirs, 67% of which had positive findings. In the central and eastern catchments, *E. lamellatus* was registered in all the nine reservoirs examined. In the western catchments, however, *E. lamellatus* was recorded in only seven of the 15 (47%) reservoirs examined. This included also Lake Ringedalsvatnet reservoir with a water amplitude of 91.9 m.

### *Eurycerus lamellatus* in the diet of brown trout

The diet of 3.792 brown trout from the littoral zone of the five study lakes was analysed, in which *E. lamellatus* was found in 784 (21%) of them (cf. Table 2). The earliest record was from Lake Dargesjåen on 17 June 2004. The water temperature on that date was 9.0°C, and only 56 degree-days since spring turnover at 4°C were achieved. In Lake Blånnutjørnane, *E. lamellatus* was noted on 18 June 2004, with a water temperature of 6.2°C and with only 44 degree-days since spring turnover. This was the earliest period of test-fishing. Six more fishing events were performed later in June in some of the lakes (cf. Appendix 2). However, no *E. lamellatus* were recorded, although most of the lakes had slightly higher water temperatures than the two localities with positive records. None of the lakes were fished in July, and most of the samples are from August and September, all with frequent records of *E. lamellatus*. The latest test-fishing in the fall was from Lake Fjellsjåen, on 2 October in 2006 and 2009, and both events recorded *E. lamellatus*.

As no test-fishing was performed in July, we used occurrence data for *E. lamellatus* from different published sources. Positive findings that month were registered in 25 different lakes within our study area (Amundsen 1976; Borgstrøm & Sporan 1998; Jensen 1975; Madsen 1970, 1971, 1980; Myrvang & Slettebø 2013; Qvenild 1978; Vasshaug 1970). The studies covered the following lakes (with NVE ID number): 23143 Ljosevatn, 393 Dragøyfjorden, 17040 Svartevatnet, 17411 Hetjørni, 17826 Flotatjørni, 391 Veslekrækkja, 17305 Inste Olavsbuvatn, 17908 Langesjøtjørni, 17402 Dyratjørnane, 17617 Store Selstjørn, 17322 Skardstjørnane, 67975 Lægreidvatnet, 17291 Dalboretjern, 553 Ørteren, 394 Geitsjøen, 17612 Vesle Selstjørn, 17289 Halnetjørni, 1906 Isdalsvatnet, 414 Øvre Hein, 18581 Ambjørsvatnet, 1907 Sysenvatn and 17583 Nedre Hein.

In the August–October period, when all species are available to be

Table 5. Frequency (%) of the three crustaceans *Eurycerus lamellatus*, *Gammarus lacustris* and *Lepidurus arcticus* in brown trout stomachs in the littoral and profundal zones of Lake Sandvatn sampled in mid-August from 2001 to 2016. Number of fish <25 cm and ≥25 cm is given. No test-fishing was carried out in the profundal zone in 2002, 2003, 2010 and 2014.

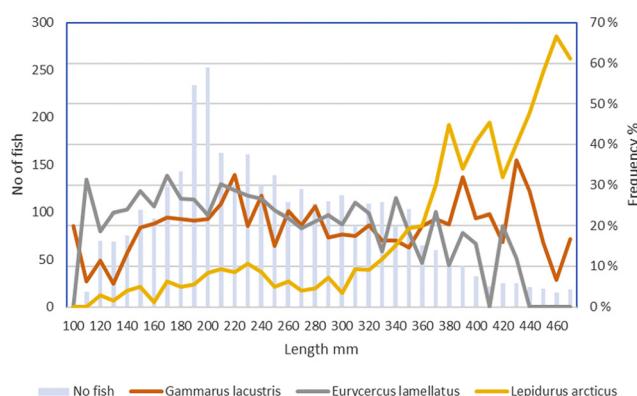


Figure 4. The frequency percent of *Eury cercus lamellatus*, *Gammarus lacustris* and *Lepidurus arcticus* in the diet of 3.362 brown trout from the littoral zone, ranging in size between 110 and 470 mm, from the five study lakes sampled during the period 8 August to 2 October in 2001–2016.

preyed upon, *E. lamellatus* was an important food item among most size-groups of brown trout, with an occurrence frequency of mainly 20–30% ( $F_{1,35}=54.75$ ,  $p<0.0001$ ,  $r^2=0.60$ ) (Figure 4). However, they became less important as food for fish with a length of 400–470 mm. The opposite trend was revealed for *L. arcticus*, which became more important as a food item as fish size increased ( $F_{1,35}=106.23$ ,  $p<0.0001$ ,  $r^2=0.74$ ). Only 4.3% of brown trout <200 mm (N=934) had preyed upon *L. arcticus*, as opposed to 48.0% of fish ≥400 mm (N=196). *Gammarus lacustris* was equally important as a food item for brown trout in all size groups ( $p>0.05$ ).

The comparative test-fishing in the littoral and profundal zones in Lake Sandvatn revealed that *E. lamellatus* and *G. lacustris* was common in the diet of brown trout in both zones (Table 5). However, their abundance varied substantially on a yearly basis in both zones; their mean occurrence ( $\pm SD$ ) were  $24\pm12\%$  vs.  $17\pm11\%$  and  $23\pm19\%$  vs.  $19\pm12\%$ , respectively. The variations in abundance in these two zones was not significantly different (independent-sampled t-test,  $p>0.05$ ). However, *L. arcticus* was more abundant in the profundal ( $11\pm12\%$ ) than in the littoral zone ( $4\pm4\%$ );  $F_{1,22}=10.34$ ,  $p<0.005$ ).

## DISCUSSION

*Eury cercus lamellatus* is widely distributed in Norwegian lakes, indicating that the species is well adapted to a wide range of environmental conditions (Walseng 2015). As a relatively large Cladocera (up to 4 mm), it has proved to be one of the most important food items for brown trout in the lakes on Hardangervidda, together with *G. lacustris* and *L. arcticus* (Dahl 1913, 1917; Sømme 1941). So far, there has been limited focus on *E. lamellatus*. In order to evaluate their occurrence on Hardangervidda, it was searched for in 144 lakes in 27 catchments covering an area of 6569 km<sup>2</sup>. On this mountain plateau, the environmental conditions are highly variable, with particularly harsh conditions in the 11 catchments in the western part, related to climatic conditions and water quality (Qvenild & Hesthagen 2019). The lakes on Hardangervidda are situated at a wide range of altitudes and sizes and included also 27 reservoirs. Thus, the distribution pattern of *E. lamellatus* in this mountain area may improve the knowledge of their environmental demands.

### The significance of the sampling method

The brown trout is an opportunistic feeder and its diet changes with the availability of food (Fjellheim *et al.* 2007; Qvenild &

Rognrud 2018). Thus, the complex variation in the aquatic organism community may be reflected in their diet. Since *L. arcticus* is a highly preferred food item, analysing brown trout stomachs appears to be the most sensitive method for detecting their existence, especially at low densities (Fjellheim *et al.* 2007; Qvenild & Hesthagen 2019). Thus, we employed the same method for detecting *E. lamellatus*. Even though the frequency some years was at low levels in Lake Sandvatn, the species was always detected.

One of the main constraints with regards detecting *E. lamellatus* is its small size (1–4 mm) compared to *L. arcticus* and *G. lacustris*. This makes it a less conspicuous species, easy to overlook when fish stomachs are checked in the field. In many studies focus is mainly given to *G. lacustris* and *L. arcticus* and *E. lamellatus* may be noted together with other semi-benthic species as “zooplankton” or only grouped to “cladocerans”. Thus, in less comprehensive studies, *E. lamellatus* may be omitted or not at all recorded.

The number of stomachs analysed in some lakes may also have been too few to detect *E. lamellatus*. In Lake Sandvatn, brown trout stomachs were repeatedly sampled in mid-August for 15 years, all with positive findings of *E. lamellatus* (Qvenild & Rognrud 2018). However, their occurrence showed high yearly variations (range 2–40%), indicating that sample size is crucial for a positive find. In 2015, 260 fish stomachs were analysed, and only five of them contained *E. lamellatus* (2%).

In the lakes in the central and eastern catchments examined only once, *E. lamellatus* was found in about 50% of them. When individual lakes were sampled more than two times, *E. lamellatus* was recorded in almost all cases. Repeated examinations therefore seem to be essential.

### *Eury cercus lamellatus* – a highly preferred food item for fish

The two large, nutrient-rich crustaceans, *G. lacustris* and *L. arcticus*, are known to be staple food items for brown trout in high mountain lakes, their preference reflecting the high quality of the fish (Dahl 1913, 1917; Sømme 1941). In this context, the smaller *E. lamellatus* is considered to be of secondary importance. To evaluate the effect of predation pressure on *E. lamellatus*, as well as on *G. lacustris* and *L. arcticus*, an extensive study of brown trout diet was carried out in five lakes by analysing 4.334 stomachs (cf. Qvenild *et al.* 2018). In these lakes, it was a heavy predation from smaller fish on *E. lamellatus*. However, larger fish also utilized them frequently. The relatively high importance for smaller fish has also been noted by Dahl (1932), Beklioglu & Jeppesen (1999) and Walseng & Jensen (2018). However, when densities of *G. lacustris* and *L. arcticus* are low, *E. lamellatus* may provide the staple food for brown trout, even for larger individuals. This was demonstrated in Lake Sandvatn in 2004–2008 when a dense brown trout population grazed the two big crustaceans to near extinction (cf. Appendix 2). This effect is best revealed when stomach fullness is checked. In this period, *G. lacustris* and *L. arcticus* accounted for 13 volume percent of the stomach content, compared to 41 volume percent for *E. lamellatus* (Qvenild & Rognrud 2018). When the brown trout population returned to its normal level in 2010–2016, the volume percent of *G. lacustris* and *L. arcticus* was 40%, compared to 20% for *E. lamellatus*. It is worth mention that *E. lamellatus* seemed to be capable to withstand the grazing at all brown trout densities in the study lakes. This was also noted by Dahl (1917) when he compared the crustacean communities in 12 lakes on the northern fells of Hardangervidda. When they were abundant, brown trout preferred *G. lacustris* and *L. arcticus* rather than *E. lamellatus*, even when the latter species was very abundant.

As this study indicates, *E. lamellatus* tolerates heavy predation

pressure from brown trout. This may be due to an adequate antipredator behaviour such as diel changes in activity, combined with good access to suitable refugia (Tewson *et al.* 2016; Beklioglu & Jeppesen 1999). The preference for vegetated areas (Dahl 1913; Smirnov 1962; Koksvik 1995; Aase 2000; Örnólfssdóttir & Einarsson 2004; Walseng 2015) may also be an adaptation to improve their survival. However, there are no specific areas with dense vegetation in Lake Sandvatn, and variation in the stomach content of brown trout indicated that clusters of *E. lamellatus* occurred throughout the lake.

In our study, the occurrence of *E. lamellatus* increased significantly with lake size. This distribution pattern was also pointed out by Walseng (2015), and it demonstrates that lake size is of great importance for sustaining vital populations of *E. lamellatus*. We assume access to refugia are better in large and deep lakes than in small and shallow ones. It should be added that bigger lakes are more frequently investigated.

### Spatial distribution

In a national survey, *E. lamellatus* was frequently found in lakes from sea level up to 1355 m a.s.l. (Walseng 2015). However, at altitudes above 1000 m a.s.l., their occurrence was less than 30%. In another national study (Sandøy & Nilssen 1986), their occurrence was somewhat higher (41%). In the 16 catchments in the central and eastern parts of Hardangervidda, *E. lamellatus* was recorded in 70% of the lakes located higher than 1000 m a.s.l. Hence, their occurrence was much higher in this mountain area than revealed in the national surveys (Sandøy & Nilssen 1986; Walseng 2015). In the western part of the plateau, only 40 lakes were investigated. Here, the abundance of *E. lamellatus* in lakes at altitudes higher than 1000 m a.s.l. was only 13% (N=30), compared to 60% in lakes at lower altitudes (N=10). This indicates that *E. lamellatus* respond negatively to the harsher and more hostile conditions in this area. Thus, the environmental conditions in lakes in the central and eastern part seem to be more favourable for *E. lamellatus*. The highest locality with *E. lamellatus* on Hardangervidda was Lake Vesle Meinsvatnet at 1353 m a.s.l. They may also exist in higher altitude lakes in this area. However, only 7% of the lakes are located at higher levels. To date, none of these lakes has been examined.

The general drop in air temperature of about 0.6 °C 100 m<sup>-1</sup> altitude is reflected in the water temperature (Qvenild & Hesthagen 2019). Water temperature is crucial to all aquatic ectotherms. It has a significant impact on growth, development and generation time of cladocerans (Bottrell 1975; Gillooly 2000). This was shown in Lake Myvatn on Iceland, where *E. lamellatus* reached its maximum abundance later in the cold summer of 1992 than in the previous warmer summer (Örnólfssdóttir & Einarsson 2004). Delayed development was also indicated in our study, as *E. lamellatus* was barely noted in mid-August in the cold summer of 2015 (Table 5). There is a steep fall in snow deposition in a west to east gradient on Hardangervidda. Hence, the ice break-up will normally be significantly delayed in the western lakes, being colder and bringing a shorter ice-free season (Borgstrøm 2016; Qvenild & Hesthagen 2019). Even though *E. lamellatus* seems to tolerate a wide range of temperature conditions, the western parts of Hardangervidda may be more marginal to the development of *E. lamellatus*.

In the national-wide surveys, the distribution of *E. lamellatus* indicated a high tolerance to water temperature extremes (Sandøy & Nilssen 1986; Walseng 2015). It is noted that *E. lamellatus* may tolerate temperature well above 20°C (Smirnov 1962). However, there is a low probability of such extreme events in the lakes on Hardangervidda (Qvenild *et al.* 2018).

Besides the 930 named lakes on Hardangervidda, mainly with fish, there are a large number of small unnamed lakes and ponds, most of them without fish (Qvenild & Hesthagen 2019). The resting eggs of *E. lamellatus* tolerate both freezing and drying (Dahl 1913; Aass 1969). In addition, they also have a high tolerance to acid water and different temperature conditions. Hence, *E. lamellatus* should be well adapted to small lakes and ponds (Walseng 2015). On Hardangervidda, only 16 unnamed lakes and ponds have been studied, four with positive findings of *E. lamellatus* (Halvorsen 1973; Walseng *et al.* 1994; Walseng *et al.* 1996; Fjellheim 2004). Nevertheless, the potential for positive findings of *E. lamellatus* in such small fishless lakes and ponds should be substantial. When fish is present, the role of refugia became more relevant.

In Lake Sandvatn, the littoral and profundal zones were comparatively fished for 12 years (Table 5, Appendix 2). Both *E. lamellatus* and *G. lacustris* occurred frequently in both zones. On the other hand, *L. arcticus* was more abundant in the profundal zone, presumably due to intense predation pressure from a dense brown trout population (2004–2008). Lake Sandvatn is shallow, like many lakes in the central and eastern parts of Hardangervidda (Qvenild & Hesthagen 2019). In such lakes, *E. lamellatus* seems to be frequently abundant in different depth strata. This was also found in Lake Pålslbufjorden prior to the regulation in 1927 where *E. lamellatus* was commonly found down to depths of 20 m (Dahl 1932).

*Eury cercus lamellatus* seems to increase in abundance in reservoirs at a wide range of water amplitudes (Dahl 1926, 1930, 1932; Aass 1969). Within the study area on Hardangervidda, there are 27 reservoirs for hydropower production, ranging from 0.39 to 78.77 km<sup>2</sup> in size and with amplitudes of 0.5 to 91.9 m. In the reservoirs investigated (N= 24), 67% had positive findings of *E. lamellatus*. All the reservoirs (N=9) in the central and eastern catchments had *E. lamellatus*, as opposed to 47% of the reservoirs (N=15) in western catchments. *Eury cercus lamellatus* has also been recorded in the Lake Ringedalsvatnet reservoir, with an annual water amplitude of 91.9 m. This emphasises the remarkable capacity of *E. lamellatus* to adapt to new and unstable conditions (cf. Dahl 1926, 1932).

### Seasonal abundance of *Eury cercus lamellatus*

There is limited evidence regarding the seasonal abundance of *E. lamellatus* in Norwegian lakes. It survives the winter as resting eggs and is thus not available as fish food during the winter (Dahl 1913, 1926, 1932; Aass 1969; Koksvik 1995). *Eury cercus lamellatus* is assumed to hatch early in spring (Dahl 1913, 1926; Smirnow 1962; Koksvik 1995; Aase 2000; Örnólfssdóttir & Einarsson 2004). This is also confirmed by observations in two of our study lakes; detecting *E. lamellatus* on 17–18 June in 2004. In Lake Takvatnet, small *E. lamellatus* was observed near to ice break-up as early as 12 June at a temperature of 2.5°C (Aase 2000). Records of *E. lamellatus* in late June were also noted in Lake Mår in 2007, 2009, 2010 and 2011 (Rognrud & Fjeld 2014).

As revealed in our study, *E. lamellatus* is usually present from August until October. Of the 3362 brown stomachs, 770 (23%) contained *E. lamellatus* in this period. Many reports have also identified *E. lamellatus* as a common food item for brown trout in July on Hardangervidda. Throughout the summer, the abundance of *E. lamellatus* seem to increase until it culminates in late summer or early autumn on Hardangervidda. This was also the case in Lake Pålslbufjorden, an adjacent lake close to this mountain plateau, reaching maximum abundance in early September (Dahl 1932). The same pattern of seasonal abundance was also found in Lake Målsjøen (165 m a.s.l.) in central Norway (Koksvik 1995), in Lake Takvatn (214

m a.s.l.) in northern Norway (Aase 2000) and in Lake Myvatn (277 m a.s.l.) on Iceland (Örnólfssdóttir & Einarsson 2004). In all these lakes, *E. lamellatus* emerged early in June and reached maximum abundance from July until October. However, in colder high mountain lakes such as on Hardangervidda, we assume that *E. lamellatus* will reach their maximum abundance later than in low-land lakes.

### Environmental conditions may limit the distribution of *Eury cercus lamellatus*

On Hardangervidda, *E. lamellatus* revealed a skewed geographical distribution in the 144 lakes examined. In the 16 catchments in the central and eastern areas, only 14% of the 105 lakes are examined. In 70% of them, *E. lamellatus* was recorded. As pointed out above, this percentage may easily be increased by repeated investigations. In the 11 western catchments, *E. lamellatus* was recorded in only 26% of the 41 sites examined, in spite of repeated investigations in many of them. Thus, *E. lamellatus* seems to be far less common to this area.

The catchments in the western area are extremely barren, with only a thin layer of moraine or glacio-fluvial deposits on Precambrian bedrock, and almost without vegetation, where the water is dilute and low in calcium (Skjelkvåle & Henriksen 1998). On the other hand, the catchments in the central and eastern areas have a thicker moraine cover with more vegetation, providing water with a higher ionic content. The mean calcium concentrations in the lakes in western and central/eastern areas were 0.80 and 1.80 mg L<sup>-1</sup>, respectively (Qvenild & Hesthagen 2019). No threshold for the calcium demand of *E. lamellatus* has so far been established. In total, 40% of the 58 localities with positive findings of *E. lamellatus* had calcium concentration below 1.0 mg L<sup>-1</sup>. The lowest value was 0.28 mg L<sup>-1</sup>, which was obtained in Lake Svartevatn in 1994 prior to a liming programme (Fjellheim *et al.* 2002). Neither *G. lacustris*, *L. arcticus* nor *E. lamellatus* were detected in the diet of brown trout at that time. However, *E. lamellatus* quickly reappeared when the calcium level increased after liming (Fjellheim *et al.* 2002), demonstrating that *E. lamellatus* had survived this marginal water quality prior to this mitigation measure. This is the minimum level of calcium concentration measured in lakes on Hardangervidda hosting *E. lamellatus*.

These results indicate that *E. lamellatus* tolerates waters low in calcium. However, Sandøy & Nilssen (1986) noted a preference for electrolyte-rich waters for their survival. As calcium is the major cation in lakes on Hardangervidda, there is a very close relationship between conductivity and calcium concentration as estimated from the data in Skjelkvåle & Henriksen (1998). This reveals calcium concentrations <1 mg Ca L<sup>-1</sup> to be equivalent to conductivities <9 µS cm<sup>-1</sup>. This places 40% of the localities in the lowest conductivity category in the national-wide survey of Sandøy & Nilssen (1986), resulting in a consistently lower probability of supporting *E. lamellatus*. Rapid postmolt calcification of the exoskeleton is essential to all crustaceans (Rukke 2002). Hence, we can assume that low calcium concentrations also impede the process of ecdysis in *E. lamellatus*.

In spite of the apparently high tolerance of *E. lamellatus* to low water temperature and dilute waters, we assume that the combination of these two environmental factors contributes to their sparse occurrence in the lakes in the western areas of Hardangervidda compared to that in central and eastern parts of the mountain plateau. This may be reinforced in high altitude lakes with even lower temperatures as documented in western areas. Thus, this small crustacean seems to be more viable in harsh conditions compared to *L. arcticus* and *G. lacustris* earlier reported from the same area (Qvenild & Hesthagen 2019; Qvenild *et al.* 2020).

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Appendix I. Specific information of the 144 lakes examined in the 27 catchments with 11 catchments in the western region (W) and 16 catchments in the central and eastern region (C/E). The number of examinations is specified together with any associated positive records. Reg indicates that the lake is regulated. The numbered references are specified below the table.

Region	Catchm. no.	Catchment	NVE ID no.	Lake	Reg	Altitude m a.s.l.	Area km <sup>2</sup>	ESPG: 25833			No. of exam.	Pos. rec.	pH	Ca mg L <sup>-1</sup>	References
W	1	Austdøla	1917	Austdølnutvatnet	Reg	1040	0.63	70 590	6 742	742	2	0			28, 74
W	1	Austdøla	1918	Rundavatnet	Reg	1040	1.28	72 020	6 744	428	2	0			28, 74
W	1	Austdøla	1921	Langvatnet	Reg	1158	6.40	69 287	6 739	016	2	1	6.4	0.56	26, 28, 55, 74
W	1	Austdøla	1922	Kvilinganutvatnet		1140	0.53	74 117	6 745	937	1	0	5.8	0.4	28, 74
W	1	Austdøla	16656	Austdalsvatnet		1059	0.08	72 907	6 743	724	1	0			28
W	1	Austdøla	16664	Austdalsvatnet		1163	0.32	75 886	6 742	930	1	0	6.9	1.2	26, 28, 74
W	1	Austdøla	16677	Rossevatni		954	0.09	69 545	6 743	018	1	0			28, 74
W	1	Austdøla	16682	Rossevatni		936	0.06	68 971	6 743	002	2	0			74
W	1	Austdøla	16712	Austdølvatnet		907	0.13	68 552	6 742	080	2	0			28, 74
W	1	Austdøla	16787	Grasbotntjørn		1107	0.12	68 354	6 740	315	1	0			28
W	2	Sima	17050	Skykkjedalsvatnet		837	0.43	75 584	6 731	638	2	2	6.65	1.48	38
C/E	3A	Isdølo	1906	Isdalsvatnet		832	1.07	76 533	6 726	176	2	2	6.52	2.12	28, 34, 74
C/E	3B	Leiro	1907	Sysenvatn	Reg	880	10.42	82 835	6 722	461	3	2	6.6	0.88	28, 34, 51, 74
C/E	3B	Leiro	17070	Finsbergvatnet		1190	1.23	95 280	6 728	945	1	0	6.02	0.82	13, 55
C/E	3B	Leiro	17149	Langavatnet		1124	0.74	91 211	6 726	281	1	0	6.03	0.62	13
C/E	3B	Leiro	17289	Halnetjørn		1259	0.16	96 421	6 722	876	1	0			42
C/E	3B	Leiro	17291	Dalboretjern		1153	0.12	92 974	6 723	206	1	0	6.38	0.85	13, 42
C/E	3B	Leiro	17305	Inste Olavsbuvatn		1175	0.64	95 206	6 721	531	1	0			42
C/E	3B	Leiro	17322	Skardstjørnane		1125	0.29	91 140	6 721	561	1	0	6.51	1.91	13, 42
C/E	3B	Leiro	17402	Dyratjørnane		1173	0.25	92 219	6 719	647	1	0	5.93	0.75	13, 42
C/E	4	Bjoreio	17865	Kleivshovdtjørnane		1215	0.82	89 929	6 701	871	1	1			42, 44
C/E	4	Bjoreio	27430	Tinnhølen		1213	4.54	90 972	6 704	204	2	2	7.05	4.16	12, 13, 55
C/E	5	Veig	18409	Grøndalsvatn		1268	0.56	63 593	6 693	034	1	0			23, 42, 45
C/E	5	Veig	18434	Grøndalsvatn		1281	0.22	61 784	6 692	865	1	0	7.15	3.08	23, 42, 45, 55
C/E	7A	Kinso	1912	Veivatnet		1172	4.68	53 384	6 706	672	1	0			3.16
C/E	7A	Kinso	1913	Omkjelsvatnet Nedre		1199	2.39	55 086	6 701	409	1	0			42, 74
C/E	7A	Kinso	17878	Kinsevatnet		1184	0.26	56 181	6 704	912	1	0			3.32
C/E	7A	Kinso	27476	Rjuvavatnet		889	0.30	48 598	6 715	537	1	0			2.24
C/E	7A	Kinso	27478	Stavalivatnet		900	0.69	49 566	6 715	667	2	1			2.12
C/E	7A	Kinso	27500	Kinsevatnet		940	0.21	49 818	6 712	693	1	1			42
C/E	7A	Kinso	27510	Fodnastølsvatnet		955	0.33	50 687	6 712	409	1	1	7.22	3.89	42, 55
C/E	7A	Kinso	27523	Austmannavatnet		1170	0.19	54 407	6 710	520	1	1			42
C/E	7A	Kinso	27573	Sperrådalsvatn		1179	0.14	55 531	6 705	279	1	0			2.44
W	7B	Vivippo	27450	Grytingsvatn		700	0.24	48 434	6 721	377	1	0			42
W	8	Opo	1904	Opesjovatnet		1014	1.25	44 930	6 712	854	1	0	6.65	0.76	42, 55, 74
W	9A	Espeelvi	27611	Mostjørn		1238	0.25	39 059	6 702	750	1	0			47
W	9B	Vendo	1903	Store Vendevatnet	Reg	1268	3.64	41 667	6 704	733	2	0	6.8	1.28	34, 36

## Appendix I. Continued.

Region	Catchm. no.	Catchment	NVE ID no.	Lake	Reg	Altitude m.a.s.l.	Area km <sup>2</sup>	ESPG: 25833			No. of exam.	Pos. rec.	pH	Ca mg L <sup>-1</sup>	References
W	10	Tysso	1890	Øvre Tyssevatn	Reg	1333	2.92	49 307	6 698 163	3	0	6.38	0.64	34, 36, 47	
W	10	Tysso	1892	Nonskardvatnet		1284	1.39	54 087	6 693 281	2	0	6.67	0.95	47, 55	
W	10	Tysso	1893	Øvre Bersåvatnet	Reg	1106	3.37	40 547	6 699 937	3	0			34, 47	
W	10	Tysso	1894	Nibbehølen	Reg	1191	2.06	46 031	6 690 183	4	2	6.4	0.64	34, 36, 47	
W	10	Tysso	1897	Øvre Nybuvatnet		1191	0.68	50 202	6 690 302	3	0			34, 47	
W	10	Tysso	1898	Nedre Håvardsvatnet	Reg	1264	5.46	54 458	6 690 703	5	0	6.67	1.03	36, 47	
W	10	Tysso	1900	Nedre Bersåvatnet	Reg	1029	0.88	38 299	6 698 844	3	0			34, 47	
W	10	Tysso	1901	Langevatnet	Reg	1190	6.36	41 622	6 687 621	5	1	6.28	0.53	34, 35, 36, 47	
W	10	Tysso	1902	Breidavatn	Reg	1232	3.35	47 989	6 685 761	3	0			34, 47	
W	10	Tysso	27650	Nedre Tyssevatn		1317	0.43	48 130	6 697 391	3	0			34, 47	
W	10	Tysso	27661	Hadletgrøna		1264	0.35	42 541	6 697 205	1	0			47	
W	10	Tysso	27663	Holmevatn		1271	0.84	45 895	6 696 516	4	0	6.36	0.64	34, 36, 47	
W	10	Tysso	27669	Nedre Veidedalsvatn		1312	0.15	47 503	6 696 107	1	0			47	
W	10	Tysso	27672	Stednesvatnet		1213	0.15	44 070	6 695 812	2	0			34, 47	
W	10	Tysso	27677	Øvre Veidedalsvatn		1333	0.22	49 095	6 694 926	1	0			47	
W	10	Tysso	27680	Tyssehølen		1162	0.11	43 332	6 695 188	1	0			34	
W	10	Tysso	27682	Reinakolltjørn		1359	0.18	45 595	6 694 481	1	0			47	
W	10	Tysso	27693	Langtjørn		1305	0.27	45 054	6 692 759	1	0			47	
W	10	Tysso	27758	Hattasteinsvatnet		1287	0.92	47 553	6 683 669	1	0			47	
W	11	Austdølo/ Kjølo	1702	Reinsnorsvatnet		594	3.35	36 722	6 675 691	1	1			42	
W	11	Austdølo/ Kjølo	23143	Ljosevatn		630	0.57	38 106	6 678 046	1	1			42	
W	12	Suldalsvassd	1866	Valldalsvatnet	Reg	745	7.33	50 628	6 672 273	2	2	6.33	0.63	34, 37	
W	13	Bora	55	Bordalsvatnet	Reg	891	7.69	70 888	6 656 673	3	2	6.5	2.62	11, 25, 41, 43, 60	
W	13	Bora	12118	Åremotvatni	Reg	1180	1.13	68 743	6 665 138	1	1	5.9	0.9	25, 56, 61	
C/E	14	Songa	10	Songa	Reg	974	30.01	82 524	6 659 180	6	6	6.4	0.97	1, 11, 25, 59, 62, 65	
C/E	15	Kvenna	12	Vollevatnet		1030	1.66	94 853	6 676 114	4	2	6.2	1.33	30, 51, 56, own data	
C/E	15	Kvenna	13	Briskevatnet		1068	2.62	89 550	6 677 403	3	2	6.6	3.74	25, 30, own data	
C/E	15	Kvenna	14	Gunleiksbu- vatnet		1071	1.29	85 362	6 678 032	5	5	6.62	1.59	30, 51, 55, 75, 76, own data	
C/E	15	Kvenna	15	Nedre Bjørnavatnet		1136	2.13	75 023	6 679 965	1	0	6.7	2.13	33, 45, 55, 75, 76	
C/E	15	Kvenna	16	Øvre Bjørnavatnet		1147	2.92	71 335	6 679 440	4	3	6.53	1.46	32, 33, 45, 55, 75, 76	
C/E	15	Kvenna	17	Sandvatn		1112	1.57	82 122	6 681 359	15	15	6.4	1.15	25, 30, own data	
C/E	15	Kvenna	18	Nedre Krokavatn		1141	1.16	77 610	6 684 108	1	1	6.7	2.73	32, 75	

## Appendix I. Continued.

Region	Catchm. no.	Catchment	NVE ID no.	Lake	Reg	Altitude m a.s.l.	Area km <sup>2</sup>	ESPG: 25833		No. of exam.	Pos. rec.	pH	Ca mg L <sup>-1</sup>	References
								X	Y					
C/E	15	Kvenna	38	Skardvatnet		1149	0.97	93 901	6 682 778	1	1			31
C/E	15	Kvenna	39	Fjellsjåen		1195	2.31	90 148	6 684 863	7	5	6.31	0.74	25, 31, 55, 75, 76, own data
C/E	15	Kvenna	40	Urdevatnet		1329	1.55	93 521	6 669 198	3	3	5.81	0.44	55, 56, 64, 75, 76
C/E	15	Kvenna	42	Valgardsvatni		1319	1.84	74 012	6 688 631	3	3	6.36	1.42	42, 45, 55, 63, 75, 76
C/E	15	Kvenna	43	Litlosvatnet		1170	1.52	63 673	6 686 656	7	4	6.56	1.19	23, 32, 45, 54, 55, 75, 76
C/E	15	Kvenna	11836	Vesle Meinsvatnet		1353	0.57	96 007	6 670 387	2	2	6.05	0.46	75, 76
C/E	15	Kvenna	18495	Grottjørnanene		1322	0.44	71 055	6 690 732	1	0	6.6	3.46	75
C/E	15	Kvenna	18545	Sledalsvatnet		1288	0.43	58 269	6 691 313	1	0			33
C/E	15	Kvenna	18558	Krokavatnet		1236	0.42	60 847	6 691 012	3	1	6.8	2.57	33, 45, 57, 75
C/E	15	Kvenna	18581	Ambjørsvatnet		1269	0.81	66 343	6 689 682	2	0	6.6	2.33	9, 23, 45, 55
C/E	15	Kvenna	18597	Skavatn		1249	0.47	64 063	6 690 187	4	1	6.7	5.04	23, 24, 33, 45, 75
C/E	15	Kvenna	18700	Kollsvatnet		1182	0.61	61 644	6 688 435	9	6	6.7	1.5	23, 24, 33, 45, 49, 55, 57
C/E	15	Kvenna	18770	Blånuttjørnane		1310	0.31	83 830	6 685 129	1	1	6.72	2.3	55, own data
C/E	15	Kvenna	18773	Krokavatn		1150	1.21	72 085	6 684 881	1	1			32, 42
C/E	15	Kvenna	18782	Vassdalsvatnet		1282	0.45	61 466	6 686 400	2	0	6.26	1.25	23, 33, 55
C/E	15	Kvenna	18827	Dargesjåen		1205	0.64	87 775	6 683 553	8	7	6	0.67	25, 31, 63, 64, 75, 76, own data
C/E	15	Kvenna	18831	Vassdalsvatnet		1299	0.74	59 870	6 685 608	1	0			33
C/E	15	Kvenna	18854	Kringlesjåen		1255	0.72	89 249	6 682 690	5	2	6.1	0.64	25, 31, 55, 75, 76, own data
C/E	15	Kvenna	18919	Tuevatn		1282	0.36	69 955	6 682 678	1	1			45
C/E	15	Kvenna	19079	Honserudvatnet		1045	0.38	93 458	6 676 917	2	1			Own data
C/E	15	Kvenna	66946	Midtre Krokavatn		1141	0.93	74 249	6 684 438	1	1			32, 42
C/E	16	Møsvatn	12178	Landsetvatnet		1077	0.22	140 859	6 658 142	1	1			7
C/E	16	Møsvatn	12188	Middøltjønne		1072	0.06	141 341	6 658 117	1	1			7
C/E	17	Mår/ Gøyst	36	Mår	Reg	1121	20.55	123 922	6 685 973	3	3	6.2	1.02	1, 25, 29, 51, 52, own data
C/E	17	Mår/ Gøyst	75	Gøystvatnet	Reg	1087	31.26	123 821	6 676 361	2	2	5.6	0.67	11, 25, 29, 51, own data
C/E	17	Mår/ Gøyst	92	Rosjå		1174	2.03	134 023	6 680 450	1	1	6.6	3.16	7, 25
C/E	17	Mår/ Gøyst	107	Store Saure		1120	1.63	115 955	6 674 870	2	2	5.8	0.79	25, 39
C/E	17	Mår/ Gøyst	109	Viuvatnet		1324	3.03	109 773	6 687 654	1	1	5.88	0.47	25, 55, 56, 63
C/E	17	Mår/ Gøyst	18721	Ljostjørn		1178	0.42	134 529	6 681 268	1	0			7
C/E	18A	Uvdalselvi	427	Store Ormetjørn		1187	0.71	130 989	6 709 879	3	3			21, 22
C/E	18B	Uvdalselvi	409	Vikvatn		1064	1.22	133 668	6 694 102	1	1	6.8	2	68
C/E	18B	Uvdalselvi	426	Damtjørn		1223	0.44	143 460	6 698 024	1	1			68
C/E	18B	Uvdalselvi	17949	Sønstevatnet	Reg	1060	12.53	142 350	6 693 775	3	3	6.85	1.7	65, 68
C/E	19A	Lågen	390	Orsjoren		951	2.37	125 791	6 712 627	2	0	6.8	1.5	2, 12, 67

## Appendix I. Continued.

Region	Catchm. no.	Catchment	NVE ID no.	Lake	Reg	Altitude m a.s.l.	Area km <sup>2</sup>	ESPG: 25833			No. of exam.	Pos. rec.	pH	Ca mg L <sup>-1</sup>	References
								X	Y						
C/E	19A	Lågen	392	Storekrekka		1151	4.18	101 435	6 723 196	3	3	5.91	0.7	63, 64, 69	
C/E	19A	Lågen	393	Dragøyfjorden		1180	3.33	98 419	6 725 710	3	2	5.49	0.65	17, 51, 69, 72	
C/E	19A	Lågen	394	Geitsjøen		1112	3.22	113 050	6 706 544	4	3	6.9	1.32	2, 12, 74	
C/E	19A	Lågen	395	Langesjøen		1210	11.04	97 530	6 698 934	4	4	6.61	1.56	4, 12, 46, 55, 66	
C/E	19A	Lågen	396	Geitvatnet		1197	1.55	105 307	6 695 177	1	1			14	
C/E	19A	Lågen	414	Øvre Hein		1113	6.33	106 335	6 714 906	3	3	6.62	1.32	2, 69, 74	
C/E	19A	Lågen	415	Halnefjorden	Reg	1130	13.70	101 185	6 715 697	8	8	6.3	1.76	1, 27, 51, 69, 74	
C/E	19A	Lågen	416	Langevatn		1158	5.09	116 530	6 700 686	1	1			2, 12	
C/E	19A	Lågen	416	Skrykken		1158	5.09	116 530	6 700 686	1	1			2, 12	
C/E	19A	Lågen	418	Bjornesfjorden		1223	18.38	93 966	6 692 522	4	3	6.69	1.7	3, 5, 6, 51, 66	
C/E	19A	Lågen	420	Nordmannslågen		1244	10.88	79 991	6 697 139	1	1	6.87	2.4	13, 42, 44	
C/E	19A	Lågen	421	Dimmedalsvatnet		1334	1.70	75 845	6 690 862	1	0	5.9	2.53	13, 45, 75	
C/E	19A	Lågen	17018	Svartevass-tjørni		1237	0.40	99 168	6 730 136	6	5	5.74	0.28	17, 71	
C/E	19A	Lågen	17040	Svartevatnet		1233	1.13	99 538	6 728 768	10	7	5.69	0.35	17, 42, 71	
C/E	19A	Lågen	17366	Nedre Bjørkevatn		1161	0.84	120 435	6 717 924	3	0			2, 51	
C/E	19A	Lågen	17366	Øvre Bjørkevatn		1161	0.84	120 435	6 717 924	1	0			2, 51	
C/E	19A	Lågen	17397	Heinumgen		1138	0.37	105 066	6 718 724	2	2	6.34	0.83	2, 69, 74	
C/E	19A	Lågen	17411	Hetjørni		1162	0.22	96 712	6 718 971	1	0			42	
C/E	19A	Lågen	17454	Bjordalsvatn		1121	0.52	118 134	6 715 599	1	1	7.15	4.04	2, 55	
C/E	19A	Lågen	17460	Orsjøtjørni		1079	0.43	122 190	6 714 827	1	0			2	
C/E	19A	Lågen	17583	Nedre Hein		1075	1.23	113 349	6 710 330	4	4	6.6	1.48	2, 27, 69, 74	
C/E	19A	Lågen	17591	Halstjørni		1022	0.08	119 782	6 710 045	1	1			2	
C/E	19A	Lågen	17612	Vesle Selstjørni		1128	0.10	109 866	6 710 191	1	1			2	
C/E	19A	Lågen	17617	Store Selstjørni		1135	0.49	107 988	6 709 350	2	2	7.19	2.44	2, 55, 74	
C/E	19A	Lågen	17898	Nordvatnet		1256	1.02	78 918	6 701 916	1	1	6.52	3.3	13, 42, 44, 55	
C/E	19A	Lågen	17908	Langesjøtjørni		1209	0.26	105 566	6 699 604	1	0			46	
C/E	19A	Lågen	18289	X-tjørn		1326	0.04	75 897	6 694 381	1	1			44	
C/E	19A	Lågen	18305	Y-tjørn		1330	0.04	75 917	6 693 986	1	1			44	
C/E	19A	Lågen	18374	Bismarvatnet		1331	1.88	74 729	6 692 150	1	0	6		13, 42, 45	
C/E	19A	Lågen	66935	Heintjonne		1112	0.58	109 162	6 712 787	1	1	6.6	0.8	2, 74	
C/E	19A	Lågen	66954	Holen		1157	0.47	113 891	6 703 571	1	1			12	
C/E	19B	Ufysja	17281	Holværvatnet		1183	1.43	119 750	6 720 539	2	1			2, 12	
C/E	19B	Ufysja	17297	Svantjern		1129	0.21	124 886	6 719 724	1	0			2	
C/E	19B	Ufysja	17401	Ljosevatnet		1182	0.90	125 104	6 716 355	2	0			2	
C/E	20	Ørteråni	553	Ørteren	Reg	1147	9.44	103 584	6 725 146	3	2	6.48	1.1	15, 16, 50	
C/E	20	Ørteråni	17104	Øvre Trestiklan	Reg	1149	0.48	103 408	6 727 693	2	1	6.43	0.7	15, 16, 50	
C/E	20	Ørteråni	17371	Skjerjavatnet		1192	1.57	113 282	6 718 885	2	1			51, 58, own data	
C/E	20	Ørteråni	67975	Lægreidvatnet	Reg	1147	1.74	106 124	6 723 166	3	3	6.77	2.3	15, 16, 50	

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Appendix 2. The catch of brown trout and the crustacean species *Eury cercus lamellatus*, *Gammarus lacustris* and *Lepidurus arcticus* in the 100 fishing events in the five study lakes (cf. Qvenild *et al.* 2018).

Locality	Zone	Date	No. of fish		No. of fish with <i>E. lamellatus</i>		No. of fish with <i>G. lacustris</i>		No. of fish with <i>L. arcticus</i>	
			<25 cm	≥25 cm	<25 cm	≥25 cm	<25 cm	≥25 cm	<25 cm	≥25 cm
Blånuttjørnane	Littoral	18.06.04	10	9	4	0	4	8	0	0
Blånuttjørnane	Littoral	17.08.04	9	12	0	0	4	9	2	2
Dargesjåen	Littoral	10.08.03	37	32	2	2	10	3	16	12
Dargesjåen	Littoral	13.08.03	17	6	7	1	2	3	7	3
Dargesjåen	Littoral	14.08.03	0	25	0	1	0	14	0	14
Dargesjåen	Littoral	17.06.04	49	13	9	2	10	9	0	0
Dargesjåen	Littoral	28.06.07	36	25	0	0	5	6	0	0
Dargesjåen	Littoral	29.09.07	19	13	8	8	11	6	5	2
Dargesjåen	Littoral	29.09.11	0	12	0	9	0	1	0	4
Dargesjåen	Littoral	28.09.12	0	20	0	14	0	2	0	1
Fjellsjåen	Littoral	02.10.06	0	50	0	1	0	3	0	42
Fjellsjåen	Littoral	27.06.07	32	35	0	0	19	15	0	0
Fjellsjåen	Littoral	29.09.07	13	29	0	1	7	10	9	28
Fjellsjåen	Littoral	27.09.08	21	31	2	0	4	1	17	23
Fjellsjåen	Littoral	21.06.09	5	22	0	0	3	18	0	0
Fjellsjåen	Littoral	02.10.09	13	33	5	1	4	7	5	9
Fjellsjåen	Littoral	26.06.10	22	21	0	0	10	15	0	0
Fjellsjåen	Littoral	29.09.10	18	21	6	4	11	3	7	5
Fjellsjåen	Littoral	29.09.11	16	44	5	21	6	7	2	7
Fjellsjåen	Littoral	28.09.12	14	26	14	8	4	4	3	5
Gunleiksbuvatnet	Littoral	13.08.01	46	22	4	0	10	3	2	3
Sandvatn	Littoral	12.08.01	48	30	7	3	3	3	0	1
Sandvatn	Littoral	14.08.01	0	25	0	0	0	5	0	11
Sandvatn	Littoral	12.08.02	20	55	3	0	3	15	1	27
Sandvatn	Littoral	16.08.04	21	28	8	10	0	2	0	0
Sandvatn	Littoral	15.08.05	64	21	15	5	4	2	0	0
Sandvatn	Littoral	16.08.05	0	25	0	1	0	5	0	0
Sandvatn	Littoral	17.08.05	0	32	0	4	0	6	0	1
Sandvatn	Littoral	19.08.05	11	1	1	0	0	0	0	0
Sandvatn	Littoral	14.08.06	47	31	25	2	3	8	0	0
Sandvatn	Littoral	16.08.06	7	25	2	3	0	0	0	0
Sandvatn	Littoral	27.06.07	44	39	0	0	13	15	0	0
Sandvatn	Littoral	12.08.07	43	52	17	18	2	0	0	0
Sandvatn	Littoral	13.08.07	7	30	3	10	0	0	0	0
Sandvatn	Littoral	14.08.07	41	7	20	4	6	0	0	0
Sandvatn	Littoral	15.08.07	8	88	0	10	1	2	0	0
Sandvatn	Littoral	30.09.07	10	36	3	16	0	5	0	3
Sandvatn	Littoral	10.08.08	70	16	17	5	6	0	0	0
Sandvatn	Littoral	11.08.08	109	14	26	3	0	0	1	2
Sandvatn	Littoral	13.08.08	1	37	1	30	0	1	0	1
Sandvatn	Littoral	14.08.08	0	4	0	1	0	0	0	1
Sandvatn	Littoral	15.08.08	0	10	0	3	0	1	0	0
Sandvatn	Littoral	16.08.08	0	2	0	0	0	0	0	1
Sandvatn	Littoral	28.09.08	22	11	1	1	0	2	0	0

## Appendix 2. Continued.

Locality	Zone	Date	No. of fish		No. of fish with <i>E. lamellatus</i>		No. of fish with <i>G. lacustris</i>		No. of fish with <i>L. arcticus</i>	
			<25 cm	≥25 cm	<25 cm	≥25 cm	<25 cm	≥25 cm	<25 cm	≥25 cm
Sandvatn	Littoral	09.08.09	52	12	16	6	5	2	0	0
Sandvatn	Littoral	10.08.09	94	4	16	2	6	0	1	0
Sandvatn	Littoral	12.08.09	5	33	3	18	0	0	0	2
Sandvatn	Littoral	14.08.09	5	21	2	3	2	8	1	7
Sandvatn	Littoral	26.06.10	20	24	0	0	12	16	0	0
Sandvatn	Littoral	08.08.10	77	10	24	0	14	3	0	0
Sandvatn	Littoral	09.08.10	30	9	5	1	5	3	2	2
Sandvatn	Littoral	10.08.10	6	12	0	0	2	6	1	3
Sandvatn	Littoral	11.08.10	20	13	6	3	4	9	0	0
Sandvatn	Littoral	30.09.10	39	36	13	5	16	11	0	0
Sandvatn	Littoral	14.08.11	29	12	4	0	11	4	1	0
Sandvatn	Littoral	15.08.11	33	12	4	1	13	7	0	2
Sandvatn	Littoral	16.08.11	64	2	14	0	19	0	2	0
Sandvatn	Littoral	18.08.11	9	25	0	0	4	8	0	2
Sandvatn	Littoral	19.08.11	2	15	0	2	1	6	0	3
Sandvatn	Littoral	30.09.11	17	15	13	2	12	13	0	0
Sandvatn	Littoral	13.08.12	10	7	7	2	6	1	0	0
Sandvatn	Littoral	14.08.12	20	4	7	2	9	0	0	0
Sandvatn	Littoral	15.08.12	43	0	6	0	8	0	0	0
Sandvatn	Littoral	16.08.12	19	27	9	9	3	3	0	1
Sandvatn	Littoral	17.08.12	0	15	0	1	0	2	0	5
Sandvatn	Littoral	11.08.13	33	5	12	0	11	1	2	0
Sandvatn	Littoral	12.08.13	18	19	6	3	6	7	1	3
Sandvatn	Littoral	13.08.13	42	10	15	1	12	6	3	1
Sandvatn	Littoral	15.08.13	82	5	48	0	16	2	9	2
Sandvatn	Littoral	10.08.14	66	14	7	0	28	7	7	2
Sandvatn	Littoral	11.08.14	28	6	5	0	9	4	5	1
Sandvatn	Littoral	12.08.14	4	5	0	0	2	4	0	0
Sandvatn	Littoral	09.08.15	58	16	1	1	29	3	0	0
Sandvatn	Littoral	10.08.15	21	31	0	0	10	13	0	0
Sandvatn	Littoral	12.08.15	4	59	1	2	0	12	0	0
Sandvatn	Littoral	13.08.15	29	0	0	0	7	0	0	0
Sandvatn	Littoral	14.08.15	5	37	0	0	2	5	0	0
Sandvatn	Littoral	14.08.16	45	19	19	3	5	8	1	4
Sandvatn	Littoral	15.08.16	52	17	12	5	11	8	3	1
Sandvatn	Littoral	16.08.16	19	0	4	0	1	0	0	0
Sandvatn	Littoral	17.08.16	0	6	0	1	0	1	0	2
Sandvatn	Littoral	18.08.16	36	29	12	3	3	2	3	3
Sandvatn	Profundal	17.08.01	8	3	1	1	0	0	0	1
Sandvatn	Profundal	18.08.04	1	41	0	0	0	11	0	1
Sandvatn	Profundal	19.08.04	20	0	5	0	3	0	0	0
Sandvatn	Profundal	18.08.05	1	21	0	1	0	4	0	7
Sandvatn	Profundal	19.08.05	1	6	0	0	0	2	0	3
Sandvatn	Profundal	15.08.06	12	10	3	0	2	2	0	1
Sandvatn	Profundal	17.08.06	0	2	0	1	0	0	0	0
Sandvatn	Profundal	13.08.07	12	0	12	0	1	0	0	0

## Appendix 2. Continued.

Locality	Zone	Date	No. of fish		No. of fish with <i>E. lamellatus</i>		No. of fish with <i>G. lacustris</i>		No. of fish with <i>L. arcticus</i>	
			<25 cm	≥25 cm	<25 cm	≥25 cm	<25 cm	≥25 cm	<25 cm	≥25 cm
Sandvatn	Profundal	14.08.07	29	11	18	8	2	2	0	0
Sandvatn	Profundal	12.08.08	60	18	17	5	3	3	2	5
Sandvatn	Profundal	11.08.09	51	5	9	0	7	4	2	3
Sandvatn	Profundal	16.08.11	4	22	0	3	1	8	0	3
Sandvatn	Profundal	17.08.11	16	8	0	0	9	3	5	1
Sandvatn	Profundal	15.08.12	9	3	3	0	1	0	0	0
Sandvatn	Profundal	16.08.12	6	0	2	0	1	0	0	0
Sandvatn	Profundal	14.08.13	39	5	13	1	9	1	11	2
Sandvatn	Profundal	11.08.15	19	22	3	0	12	4	0	0
Sandvatn	Profundal	15.08.16	56	21	18	3	9	1	8	8