Research paper

A long-term study of the impact of the invasive species Eurasian minnow *Phoxinus phoxinus* on brown trout *Salmo trutta* production in a high mountain lake, Southern Norway

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The shallow Lake Skjerja was originally one of the most outstanding brown trout lakes on the Hardangervidda mountain plateau. During the period 1973–1985, the annual yield was on average 3.35 kg ha^{-1}. In the mid-1980s, Eurasian minnow established a dense population in the lake. Since 1994, 5304 kg of Eurasian minnow have been removed with baited traps, which correspond to an annual mean catch of 177 kg year^{-1} or 1.12 kg ha^{-1}. The competition for food, in addition to longer food chains, has had a strong negative impact on the brown trout production, with an annual yield reduced to 1.07 kg ha^{-1}, or 32% of the historical catches (1973-1985). The total removed biomass of the two fish species correspond to 65% of the brown trout yield before the invasion of the Eurasian minnow. In Lake Skjerja, the two crustacean species *Gammarus lacustris* and *Lepidurus arcticus*, have historically been staple food items for brown trout. Fishing with baited traps on the minnows, and the presence of a large fraction of predatory brown trout, may have reduced the predation pressure on the two crustacean species, and they are still a part of the brown trout diet. The availability of fish as food has resulted in a significant increase in the presence of large individuals of brown trout with maximum weights above four kg. Despite reduced annual yield of brown trout, Lake Skjerja is still a popular fish destination with nearly 200 big-sized brown trout (mean annual weight 1065 grams) landed annually. On Hardangervidda, an increase in air temperature has been observed since the 1980s, with a corresponding change in water temperature which may benefit Eurasian minnow. In warm summers, water temperature approaches 14°C which has proved to be near to the upper thermal threshold for *Lepidurus arcticus*.

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INTRODUCTION

Hardangervidda is the most extensive mountain plateau in Europe, where the brown trout *Salmo trutta* Linnaeus, 1758 is mainly the only fish species present. The lakes on Hardangervidda are rated among the best brown trout lakes in Norway, hosting large fish of high quality (Sømme 1941; Qvenild 2022). Lake Skjerja, situated on the north-eastern part of the plateau, is known as one of the most outstanding lakes providing high brown trout yields of large fish (Qvenild 2004). 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 into sizes of one to three kg and even more (Sømme 1941; Qvenild 2004; Borgstrøm 2016).

The freshwater organisms play important ecosystem roles in linking terrestrial detritus and periphytic algal production to higher trophic organisms such as brown trout. A study with stable isotopes in 14 lakes on Hardangervidda in 2001–2002, including Lake Skjerja, indicated that the food webs were grazer-dominated, and with short food chains (Rognerud *et al*. 2003). Most of the invertebrates, including *G. lacustris*, primarily grazed on periphytic algae. The exception was *L. arcticus* which had a more diverse diet. It is known to feed on detritus, bacteria, plants and algae, in addition to other crustacean species, including conspecifics (Lakka 2013, 2015). These two large and nutrient-rich crustaceans may be heavily grazed upon by fish, and at high abundances of brown trout, they may virtually be grazed near to extinction (Aass 1969; Qvenild & Hesthagen 2020).

Since the 1960s, the Eurasian minnow *Phoxinus phoxinus* (Linneus, 1758) has spread to many lakes and reservoirs in Norway (Museth *et al*. 2007). The success of introduced minnows into new localities, often at high altitudes, demonstrates their phenotypic and ecological plasticity. Viable populations are now frequently found in both lotic and lentic habitats in mountain areas up to 1400 m a.s.l. On Hardangervidda, Eurasian minnow was first observed in Ørteren Reservoir in 1973 (Borgstrøm 1973). From here it spread further upstream to Lake Skjerja, and to many other lakes on the north-eastern part of the plateau. In total, it has now established populations in at least 42 lakes on Hardangervidda (Qvenild & Hesthagen 2019).

As an omnivorous, opportunistic forager, Eurasian minnow introduced to high altitude lakes have been linked to decline in brown trout prey availability (Borgstrøm *et al*. 1985; Hesthagen 2005; Museth *et al*. 2007; Museth & Borgstrøm 2010; Borgstrøm *et al*. 2010).

The diet of brown trout changes with food availability (see Klemetsen *et al*. 2003 for references). By using stable isotopes, the trophic position can be quantified by the $\delta^{15}N$ signature (Rognerud *et al*. 2003). In the 14 investigated lakes, brown trout production was primarily based on grazer-dominated food webs and the $\delta^{15}N$ signature in brown trout ended up 3.5–5.0 ‰ higher than in its food organisms. This indicates a trophic level 1.0–1.5 above the true herbivore organism *Lymnea peregra* (O.F.Müller, 1774) which is normally used as a base line. However, in Lake Skjerja where Eurasian minnow was an available food item, brown trout had elevated $\delta^{15}N$ signatures which indicated longer food chains. Environmental contaminants as methylmercury accumulates in the food chain, and when feeding on Eurasian minnow the methylmercury concentrations in brown trout increased due to its elevated trophic position.

Since the 1980s, the climate on Hardangervidda has changed, owing to the secular trend in global climate. Both annual winter precipitation and temperature has increased (Qvenild 2022). The intrinsic relationship with air temperature makes mountain lakes very sensitive habitats to changes in climate. This widespread trend of warming lakes is anticipated to continue.

In Lake Skjerja, fish statistics reporting annual yield of brown trout are available since 1969, many years before Eurasian minnow was established. Our main aim in this paper is to combine the fish statistics with the results from the food web study in 2001–2002 (Rognerud *et al*. 2003) to quantify the long-term consequences of minnow introduction on brown trout production and food web dynamics in an increasingly warmer lake.

MATERIAL AND METHODS

Lake Skjerja (61.4199°N, 7.9712°E) is situated on the northeastern part of the Hardangervidda mountain plateau in the tributary Ørteråni in the Hallingdalselvi watercourse (Figure 1). This shallow lake (mean depth 1.7 m, maximum depth 6.0 m) has many small islets over a large part of the 1.57 km^2 lake area. With its small catchment (9.7 km^2), the retention time is approximately three years (nevina.nve.no).

The bedrock in the area covers gneisses and granites with deep layers of moraine, and this influences the water chemistry. The catchment of this clearwater lake comprises 9.5% of bogs only (nevina.nve.no). The content of total organic carbon (TOC) is not measured, but is generally very low in almost all lakes on Hardangervidda (Skjelkvåle & Henriksen 1998). pH-values have frequently been measured and it has varied in the range 6.5–7.0 (N=10). Calcium concentrations in neighbouring lakes are in the range 1.5–3.5 mg L^{-1} (Tysse & Garnås 1995).

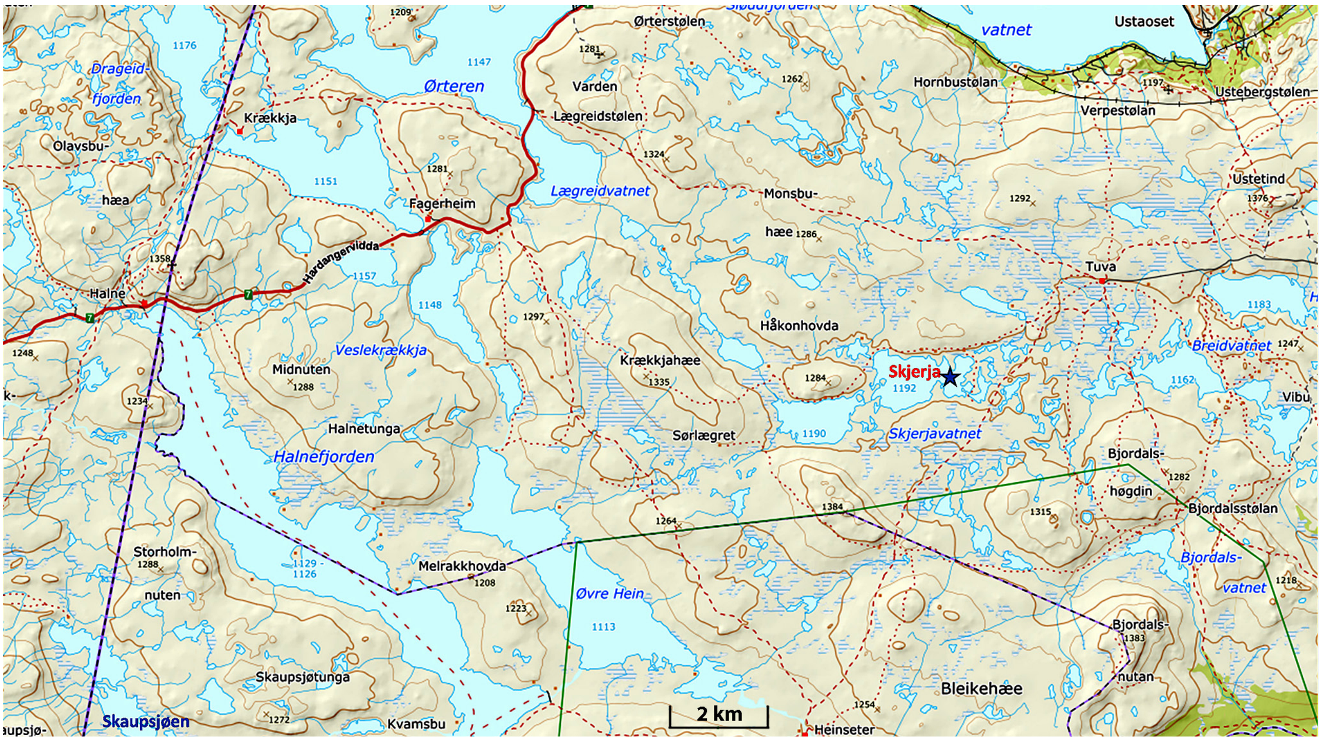

Figure 1. Lake Skjerja (61.4199°N, 7.9712°E) is situated at the north-eastern part of the Hardangervidda mountain plateau (red text and marked with blue star). Norwegian Mapping Authority CC BY 4.0.

The climatic conditions have proved to be important for production of brown trout on Hardangervidda (Qvenild 2022). In this context, the winter precipitation and summer air temperature and its significance to water temperature, is of special interest. They interact on the length and productivity of the ice-free summer period through variations in recruitment, growth and production of food organisms. On Hardangervidda, the winter precipitation (1 October – 30 April) differs substantially in a west to east gradient with an almost four-fold decrease. The Ørteråni catchment is located in the north-eastern and continental part with low winter precipitation of 369 mm, compared to more than 1100 mm in the western part with coastal climate (see Qvenild *et al.* 2021 where the climatic conditions in different watercourses on Hardangervidda are computed for the normal period 1961–1990 with the NEVINA-method (nevina.nve.no)).

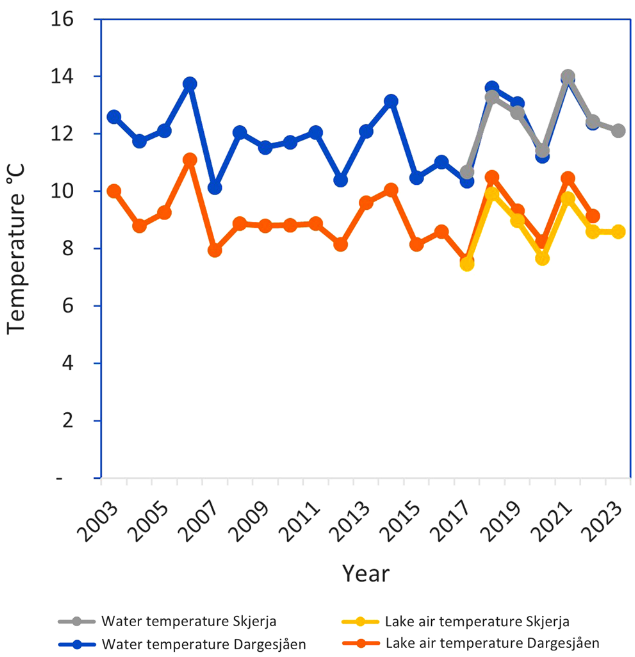

Figure 2. Littoral water temperature (1 July–15 September) in the lakes Skjerja compared with the Lake Dargesjåen. The water temperatures closely follow the lake air temperatures which are estimated from the meteorological stations 31620 Møsstrond and 25630 Geilo-Olderbråten (seklima.no)

Daily air temperatures were obtained from the meteorological stations 31620 Møsstrond (1980–2023) and 25630 Geilo-Olderbråten (2006–2023) (seklima.no). At the two stations, the mean air temperature (1 July – 15 September) for the normal period (1961–1990) were 9.37 and 9.94°C, respectively. On these stations, the temperature has increased by 1.13 and 1.44°C above the normal during the period 2000-2023. The temperatures on the two stations are highly correlated ($y=0.8926*x+1.9696$, $r^2=0.97$).

The air temperature is lowered by a linear adiabatic lapse rate with increasing altitude. An approximate lapse rate of 0.6°C 100 m^{-1} is widely accepted for the summer season in Fennoscandia and hence, we assume this to be a good proxy for calculating air temperature at specific lakes (see Qvenild *et al*. 2021 for references).

The surface water temperature (later noted as *water temperature*) was obtained by temperature loggers (mainly Hobo UA-002-64) which were placed in the littoral zone at a depth of 1-3 m. In this context the *summer period* was set to 1 July – 15 September, as the temperature loggers were mainly operated continuously in this period. The water temperature is closely correlated to what found in Lake Dargesjåen (60.0835°N, 7.5866°E) on the central part of the plateau. This lake has been monitored since 2003 (Figure 2).

During the period 2017–2023, the water temperature in Lake Skjerja varied interannually in the range 10.7–14.0°C, with an average of 12.4°C. As seen in the time series of Lake Dargesjåen, the summers 2006, 2014, 2018, 2019 and 2021 were warm with averages near to 14°C. Cold summers were experienced in 2007, and especially in 2015 where averages were close to 8°C. This pattern of warm and cold summers was a general picture of the water temperatures all over Hardangervidda (Qvenild *et al*. 2021).

The water temperature closely follows the air temperature at the lake (Figure 2). During the period 2017–2023 the average water temperature in Lake Skjerja was 3.67°C (range 3.23–4.26°C) above the lake air temperature, compared to 3.23°C (range 2.77–3.74°C) in Lake Dargesjåen for the same period. Water temperatures in the

Table 1. Fish surveys with test fishing fleets during the period 1970–2002. The test fishing fleet in 1970 and 1973 also contained 32 and 24 mm meshes.

Date	Effort (gillnet-nights)	No. fish	Weight (kg)	Mean weigth (gram)	Weigt series^{-1} (kg)	FC*	Max. size (gram)	No. fish net^{-1} 21–26 mm	No. fish net^{-1} 35–52 mm	Stomach content** *G.l*	*L.a*	*P.p*	References
26–27.07.70	42	124	50.00	403	9.60	1.12		3.43	2.43	2	3		Mollerud 1971
28–30.07.73	36	195	68.00	349	15.20	1.14		8.13	2.98				Mollerud 1973
1976	16	80	43.00	538	21.60	1.08		4.00	5.50				Smukkestad 1980
13–14.08.79	16	71	31.00	437	15.43	1.15		5.75	2.63	2	1		Smukkestad 1980
4–5.08.85	16	60	27.11	452	13.56	1.27	1960	5.50	2.13	2	2		Eriksen & Garnås 1985
3–4.08.88	16	67	18.24	272	9.12	1.16	2050	7.75	1.38	2	3		Eriksen & Garnås 1988
10–18.08.91	24	28	9.39	335	3.13	1.11	860	1.70	1.10	2	2	1	Eriksen 1991
18–19.08.92	16	36	10.32	287	5.16	1.05	910	2.75	1.83	1	3	1	Eriksen 1992
21–22.08.95	16	27	5.48	203	2.74	1.08	650	3.90	0.63	0	0	1	Eriksen 1995
22–23.07.02	16	45	13.02	289	6.51	1.15	1208	5.13	0.88	1	1	1	Rognerud *et al.* 2003

*FC - Fultons conditionfactor. **Stomach content: G.l - *Gammarus lacustris;* L.a - *Lepidurus arcticus*; P.p - *Phoxinux phoxinus*. The diet items are graded in categories (0-not recorded, 1-recorded, 2-significant part, 3-dominating part).

Table 2. Total catch of brown trout on different kinds of gears during the period 2013–2023 in Lake Skjerja. During the period, 1894 brown trout weighing 2 064 kg could be identified on the different kinds of gear.

Gear category	Gear	Total number	%	Total weight (kg)	%	Mean weight (gram)
Active gear	Convoy	197	10%	210	10%	1 066
Active gear	Flies	34	2%	37	2%	1 088
Active gear	Earthworms	132	7%	135	7%	1 023
Active gear	Otter	902	47%	925	45%	1 025
Active gear	Rappala/lures/wobblers	181	9%	185	9%	1 022
Passive gear	Gillnets	448	23%	572	28%	1 277
		1 894	100%	2 064	100%	1 090

Table 3. Gillnet catches during the periods 1970–1985 and 2013–2023.

Year	Days	Gillnets night^{-1}	Gillnet-nights	No. fish	Weight (kg)	Mean weight (gram)	CPUE no. fish gillnet^{-1}	CPUE kg gillnet^{-1}	Mesh size mm 39	Mesh size mm 45	Mesh size mm 52	References
1970	10	6	60	112	122.0	1 089	1.9	2.03			6	Eriksen 1985
1971	11	6	66	70	75.8	1 083	1.1	1.15			6	Eriksen 1985
1972	9	20	180	220	155.5	707	1.2	0.86		14	6	Eriksen 1985
1973	7	23	161	283	185.3	655	1.8	1.15	3	14	6	Eriksen 1985
1976	2	14	28	113	99.0	876	4.0	3.54	2	8	6	Eriksen 1985
1977	4	16	64	306	260.8	852	4.8	4.07	2	8	6	Eriksen 1985
1978	3	30	90	235	219.6	935	2.6	2.44	4	14	12	Eriksen 1985
1979	6	30	180	346	352.5	1 019	1.9	1.96	4	14	12	Eriksen 1985
1980	8	30	240	325	283.8	873	1.4	1.18		15	14	Eriksen 1985
1981	5	50	250	337	270.3	802	1.3	1.08		28	20	Eriksen 1985
1982	5	50	250	349	291.7	836	1.4	1.17		28	20	Eriksen 1985
1983	4	50	200	391	294.3	753	2.0	1.47	4	26	18	Eriksen 1985
1984	4	50	200	328	277.8	847	1.6	1.39	4	26	18	Eriksen 1985
1985	3	50	150	269	218.7	813	1.8	1.46	4	26	18	Eriksen 1985
2013	26	3	78	56	63.7	1 137	0.7	0.82	x	xxx	x	Geilo fha
2014	7	3	21	15	19.8	1 317	0.7	0.94	x	xxx	x	Geilo fha
2015	27	3	81	71	80.4	1 133	0.9	0.99	x	xxx	x	Geilo fha
2016	23	3	69	67	98.8	1 475	1.0	1.43	x	xxx	x	Geilo fha
2017	18	3	54	40	56.3	1 408	0.7	1.04	x	xxx	x	Geilo fha
2018	12	3	36	38	50.8	1 338	1.1	1.41	x	xxx	x	Geilo fha
2019	16	3	48	45	50.2	1 115	0.9	1.05	x	xxx	x	Geilo fha
2020	26	3	78	61	80.0	1 311	0.8	1.03	x	xxx	x	Geilo fha
2021	7	3	21	22	27.4	1 244	1.0	1.30	x	xxx	x	Geilo fha
2022	3	3	9	6	5.8	960	0.7	0.64	x	xxx	x	Geilo fha
2023	3	3	9	11	14.2	1 295	1.2	1.58	x	xxx	x	Geilo fha

During 2013-2023 the effort was mainly two gillnets pr. night, some nights complemented with one single or one doble net. In the table, three gillnets pr. night are used which is an overestimate. Mesh size used: x – used, xxx – mostly used.

two lakes are closely correlated ($y=0.8564*x+1.7887$; $r^2=0.9749$). Hence, we can back-calculate the water temperatures both from air temperatures and/ or from water temperatures in Lake Dargesjåen.

Until mid-1980s, brown trout was the only fish species present in Lake Skjerja. The population has been surveyed with test fishing at ten occasions with "Jensen-series" (Table 1). The mesh-sizes used, with some exceptions, was 52, 45, 39, 35, 29, 26 and 2*21 mm (knot to knot). The use of multiple mesh sizes is assumed to document major changes in the size distribution of the brown trout population, and we used the weight on a series as a proxy of the fish biomass (Jensen 1972).

To supplement the natural recruitment, the lake has regularly been stocked with brown trout of the local strain. Before 1990, fry was stocked each year (range 500–3500 fish year^{-1}). Thereafter, stocking of one-summer old (range 400–1600 fish year^{-1}) and one-year old brown trout (range 200–1000 fish year^{-1}) became dominant. The effect of the stockings is unknown.

A fishery with baited traps to reduce the population of the minnows has been conducted yearly since 1993 (Appendix 1). The fishery is operated through the summer season, mostly with 45 traps. Approximately 80% of the total catch are taken in the spawning period of the minnows early in the season (Rolf Mykkeltvedt, pers. comm.).

The brown trout diet in Lake Skjerja has been analysed in the different surveys regarding the occurrence of *L. arcticus* and *G. lacustris*. They have been recorded in all years, except in 1995. In the last test fishing in 2002, the diet was analysed in detail. Also, smaller crustacean species, especially the branchiopod *Eurycercus lamellatus* (O.F. Müller, 1776), was an important food item. In addition, the gastropod *L. peregra* was frequently found. In Lake Skjerja, Eurasian minnows was recorded in a brown trout stomach in 1991 (Eriksen & Garnås 1991). In the subsequent years, Eurasian minnow has been regularly documented in the brown trout stomachs (Table 1).

The area is owned by Hol municipality. The fishery has since 1967 been administrated by Geilo hunting- and fishing association. The association has obtained detailed statistics of annual catches back to 1969 (see Appendix 1). The fishery has mainly been a recreational fishery with most of the catches taken by active gears as rods with spinners, flies, lures, wobblers, etc. Convoy which consists of spinners combined with hooks baited with earthworm, is a very popular method. However, the far most used fish equipment is the otter which is easy to handle in the shallow lake. Since 2013, every single fish taken on different gears are noted with weight and length by the local fishing guard (Table 2). The effort of active gears is not possible to estimate, but the fishing activity may be characterised as active to very active in mostly all years (Ivar Sygnabere, pers. comm.). However, in 1986 the activity was at a low level due to radioactive deposition after the Chernobyl accident.

A supplementary annual fishery with gillnets is conducted by the fishing association (Table 3). Statistics of the gillnet fishery (numbers, weight and fishing effort) is available during the period 1970–1985 (Eriksen 1995). The dominating mesh sizes were 45 (52%) and 52 mm (40%). Since 2013, gillnet catches are available only with daily catches. This is mainly taken on two gillnets pr. night, but some nights one or two more nets are added (not specified). The dominating mesh size used is 45 mm (Rolf Mykkeltvedt, pers. comm.). The annual catches on active gears and gillnets are given in Appendix 1.

RESULTS

In the 1970s, Lake Skjerja was intensively exploited with high catches. During the period 1973–1985, when brown trout was the only species present, the mean annual yield was 3.35 kg ha^{-1} (SD±0.75 kg ha^{-1}, range 2.35–5.10 kg ha^{-1}). The catches are presented as mean annual yields (Figure 3).

In 1993, the first fishing of minnows with baited traps was conducted, with 20 kg removed (Figure 3). During the following 30 years, a total of 5304 kg has been taken out, which corresponds to an annual mean of 177 kg year^{-1} or 1.12 kg ha^{-1}. During the same period, 4895 kg of brown trout has been caught (data missing for 1989), which corresponds to an annual mean of 169 kg year^{-1} or 1.07 kg ha^{-1}. Hence, the Eurasian minnow has had a strong negative impact on brown trout production, reducing the annual yield to 32% of the original potential. The combined yield of the two species (2.17 kg ha^{-1}) was reduced to 65% of what the allopatric brown trout population produced (3.35 kg ha^{-1}).

The population structure has been followed by multiple test fishing (Table 1). Some of the surveys contain population characteristic analyses of the population. The individual growth rate of brown trout

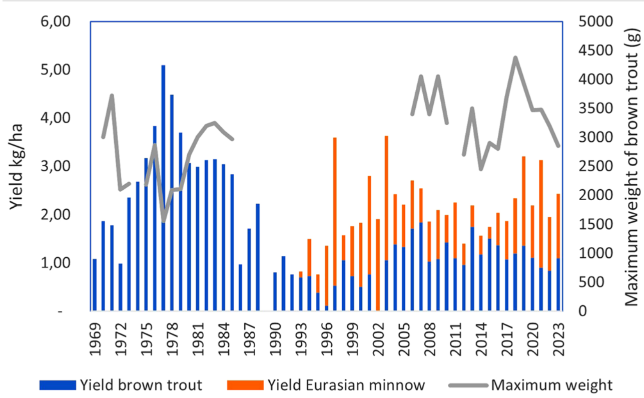

Figure 3. Yield estimates of brown trout in Lake Skjerja during the period 1969–2023 (blue bars). The removed biomass of Eurasian minnow since 1993 is indicated by red bars. The annual yield of brown trout has diminished to almost one third after the introduction of the Eurasian minnow. The maximum size of brown trout has increased after the invasion of Eurasian minnow and is assumed to be an effect of the increased food supply from fish.

is normally above 6 cm year^{-1}, and female maturation is reached at an age of 6 years and at a length of 36-40 cm (Smukkestad 1980; Eriksen 1992). The size structure of the population has varied a lot (Table 1). Before 1988, it was a high fraction of large fish taken on mesh sizes 35-52 mm (37%). During this period, the catches was on average 15.08 kg series^{-1} (range 9.60–21.60 kg series^{-1}). In the following years, the catches of fish on mesh sizes smaller than 35 mm were more dominating. After the establishment of Eurasian minnow, the total catch has decreased by approximately 70% to an average of 4.39 kg series^{-1} (range 2.74–6.51 kg series^{-1}).

During the period 2013–2023, most of the fish captured on the different fishing gears were noted with weight and length. Fulton's condition factor was on average 1.16 (N=1828; SD±0.13), which indicates fish in good nutritional state. In total, 1894 brown trout with a total weight of 2064 kg were individually measured (Table 2). The most used method was otter which caught 47% and 45% of the total catch in numbers and weight, respectively. During the period 1970–1985, 46% of the catches was taken on gillnets compared to 26% in 2013-2023 (see Appendix 1). The mean weights on active and passive gears were 1031 and 1287 grams, respectively. There were only minor differences

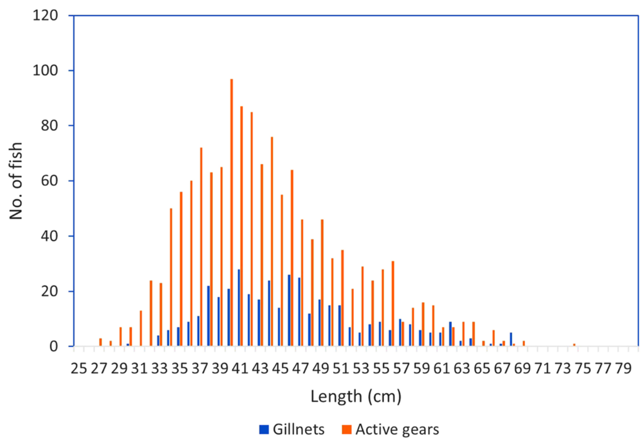

Figure 4. Length distribution of brown trout in the catches with active (N=1406) and passive gears (N=401) during the period 2013–2023. The length distribution in the active gears is assumed to be equal to the length distribution in the brown trout population. The gillnet fleet consisting of gillnets with mesh sizes 39, 45 and 52 mm is fishing more selective on the larger sizes of the population.

in mean weight on the different kinds of active gears, indicating a rather similar gear selectivity (Table 2). Hence, the length distribution may give a representative and comparable picture of the population structure of the brown trout population (Figure 4).

The gillnet-fishery in Lake Skjerja has changed. The average annual effort during the period 1970–1985 was 151 gillnet-nights year^{-1} (range 28–250 gillnet-nights year^{-1}) (Table 3). During 2013-2023, the effort was reduced to an average of 46 gillnet-nights year^{-1} (range 9–81 gillnet-nights year^{-1}). The CPUE (catch pr. unit effort) was high in the first period, providing an average of 2.05 fish and 1.78 kg gillnet^{-1}, respectively. The effort used in the second period (2013–2023) was more than two and less than three gillnet day^{-1}, giving a CPUE 0.88–1.33 fish gillnet^{-1} or 1.11–1.67 kg gillnet^{-1}. However, the mean weight in the catches has increased. This indicates a population with a lower density, but with larger fish.

During the period 1973–1985, the mean maximum weight of brown trout was 2602 grams (N=12, SD±550 grams, range 1560–3250 grams). After the introduction of Eurasian minnow, this increased to 3367 grams (N=18, SD±522 grams, range 2450–4380 grams) (Figure 3). The proportion of fish larger than one, two and three kg in the total catch (N=1809) were 46, 9 and 1%, respectively.

DISCUSSION

In the beginning of the 20th century, brown trout contributed economically and nutritionally in the local households in the nearby communities of the Hardangervidda mountain plateau. The first to report on the fisheries on Hardangervidda was Huitfeldt-Kaas (1911). His preliminary investigation on the fishery statistics contributed to an overall analyses of a better resource utilization plan for the plateau ("Fjeldbeitekomitéen" 1911). In this early period, the activity in harvesting the mountain lakes was limited and the average annual yield in the 43 lakes he examined was only 0.64 kg ha^{-1}. In a later investigation, Knut Dahl and Iacob Sømme added 72 annual yield data from 23 specific lakes (Dahl & Sømme 1934). The yield varied from 0.09-4.06 kg ha^{-1}, with a mean of 1.17 kg ha^{-1}. Earlier, Dahl (1913) had reflected on the low yields obtained from these mountain lakes and thought it was due to the difficult logistics at the plateau. However, long-term studies in the Norwegian reference lake Øvre Heimdalsvatn in the Jotunheimen area in the 1960s, confirmed levels lower than 5 kg ha^{-1} to be normal in comparable brown trout mountain lakes (Jensen 1977). Jensen also claimed yields to be lower than this in lakes with high proportions of large individuals. A recent study has confirmed the low yield estimates in the lakes on Hardangervidda (Qvenild 2022). From 69 lakes, 575 annual yields of brown trout are in line with the early findings of Dahl & Sømme (1934). Only 10% of the yield estimates exceeded 3 kg ha^{-1}, reaching 5.53 kg ha^{-1} as the maximum value achieved.

The morphometric and physicochemical conditions in Lake Skjerja are excellent for brown trout production. Grazer-dominated food webs comprising *L. arcticus* and *G. lacustris* will have a high potential for brown trout production. This is confirmed by the exceptional high catches on the initial test fishing surveys. When allopatric, the catches reached values varying from 9.06 to 21.06 kg series^{-1} which is very high values compared to other allopatric populations on Hardangervidda, and in other Norwegian lakes (Ugedal *et al*. 2005). This is also reflected in high historical yields. In the 1970s, the lake was harvested by a private tenant who estimated an annual yield of approximately 300 kg or 2 kg ha^{-1}. With a more active use in the following years (1973–1985), the annual yield was on average 3.35 kg ha^{-1} which is a high yield compared to other lakes on the plateau (Qvenild 2022). All of these 13 yearly catches from Lake Skjerja are in the uppermost part of this fish yield statistics.

Effect of Eurasian minnow introduction on brown trout production

Many brown trout populations on the eastern part of Hardangervidda has been negatively impacted by Eurasian minnow (Rognerud *et al*. 2003; Borgstrøm 2009). The minnow probably reached Lake Skjerja in the mid-1980s (Eriksen & Garnås 1991), and in 1993 Geilo hunting and fishery association initiated the first fishing with baited traps to reduce the abundance of this unwanted species. Due to a high effort during the following 30 years, 5304 kg have been removed (177 kg year^{-1}). During the same period 4895 kg of brown trout has been taken. The mean annual yield of brown trout has been reduced to 32% of the original potential (1973–1985), indicating a serious decline in brown trout production. In a study of gillnet catches from 73 lakes in Southern Norway, the abundance of brown trout was on average 35% lower in lakes where minnow was present compared to lakes with allopatric brown trout populations (Museth *et al*. 2007). This indicates that the effect of the minnow introduction in Lake Skjerja has been more severe than the average.

Test fishing with "Jensen-series" is assumed to give a representative picture of the population structure and relative abundance of brown trout populations in high mountain lakes (Jensen 1972). This method was most frequently used prior to 2000. From Hardangervidda we have obtained 218 test fishing data from 107 specific lakes with this series (own material). The weight of fish caught on a series may be used as a proxy of the biomass of the brown trout population. During the period with allopatric brown trout (1970–1985) it was taken on average 15.08 kg series^{-1} (range of 9.6–21.6 kg series^{-1}). All the values are among the 15% highest in the test fishing series and may be considered as high values (Ugedal *et al*. 2005). After Eurasian minnow had established in the lake (1991–2002), the weight series^{-1} declined to an average of 4.39 kg series^{-1} (range 2.74–6.51 kg series^{-1}), i.e. 29% of the original level. This emphasizes the severe effect on brown trout production seen in the reported annual yields from the fishing statistics.

However, some of the reduced yield may be explained by reduced fishing. From the test fishing results with Jensen-series, an average of 15.08 kg gillnet-series^{-1} was taken during 1979–1985 compared to 4.39 kg gillnet-series^{-1} during 1991–2002 (see Table 1). The yield was reduced from 473 kg to 106 kg, respectively (see Appendix 1). As the catches on the Jensen-series may be relative expressions of the biomass, there will be a direct proportional relationship between the yields (Y) and the product of biomass (B) and fishing mortality (F) in the two periods ($Y_1=F_1*B_1$ and $Y_2=F_2*B_2$). Hence, the estimated fishing mortality was 23% lower in the last period due to a lower effort.

The population density of Eurasian minnow increased from the mid-1980s. We assume that the high abundance strongly increased the competition for food and lowered the biomass of brown trout. From 1994, the effort with baited traps has been at a rather constant level (Rolf Mykkeltvedt, pers. comm.). Hence, the catches may reflect the relative biomass of minnows. Both predation and competition from brown trout in addition to temperature are reflected in the catches of minnows (see Appendix 1). Warm summers acts directly on the catchability of the traps and may also result in increased recruitment. The intense fishing with baited traps obviously gave the wanted effect. In the following years after 2005, the yield of brown trout doubled to an average of 198 kg year^{-1} (range 133–290 kg year^{-1}). The increased annual yield was also followed by high mean weights of brown trout in this period. Sustained fishing with traps, and the increased predation pressure and competition for food from brown trout, have kept Eurasian minnow at a lower level. Despite reduced population size of minnow, it still impacts negatively on brown trout production.

Although the brown trout yield has been strongly reduced, Lake Skjerja is still a popular fish destination with nearly 200 big-sized brown trout annually landed during the period 2013-2023. The Eurasian minnow is frequently found in the brown trout stomachs through the fishing season. However, we assume that the minnow is most heavily preyed on during its spawning period early in the season as recorded in Lake Øvre Heimdalsvatn (Museth *et al*. 2003). Even though cannibalism is not documented in Lake Skjerja, young brown trout may also be an important surplus to the diet as shown in Lake Øvre Heimdalsvatn (Borgstrøm *et al*. 2010; Borgstrøm 2022). In addition, high levels of methylmercury and an elevated $\delta^{15}N$ signature indicate fish eating (Rognerud *et al*. 2003). The mean weights taken on different sportfishing gears exceeds one kilo (1031 grams), and the fraction of large fish landed is substantial with frequent catches of individual brown trout passing one (46%) and two (9%) kg and even more. Thus, there is still a high probability for a good fish experience in Lake Skjerja.

Effect of Eurasian minnow introduction on the two crustacean species *Gammarus lacustris* and *Lepidurus arcticus*

Gammarus lacustris and *L. arcticus,* are known to be staple food organisms for brown trout in high mountain lakes, and they may be heavily preyed upon by fish (Qvenild 2022). At high population densities of brown trout, they may be grazed near to extinction (Aass 1969; Qvenild & Hesthagen 2020). With introduction of Eurasian minnow, the increased predation pressure has been linked to decline in brown trout prey availability (Borgstrøm *et al*. 1985; Museth *et al*. 2007). In Lake Øvre Heimdalsvatn, *G. lacustris* and *L. arcticus* were originally a major part of the brown trout diet (Lien 1979). Some decades after the introduction of Eurasian minnow, *G. lacustris* seem still to be an important food item (Borgstrøm *et al*. 2010). However, predation from brown trout and Eurasian minnow has obviously had a negative effect on the occurrence of *L. arcticus*. An even more devastating effect of Eurasian minnow introduction was observed in the high-altitude mountain lake, Lake Sylvetjønne in Jotunheimen (Hesthagen 2005). Originally populations of *L. arcticus* and *G. lacustris* provided extraordinary catches of large brown trout. After an accidently introduction of Eurasian minnow in the 1980s, this outstanding fishery has been strongly reduced.

Before the invasion of Eurasian minnow, *L. arcticus* and *G. lacustris* were important prey items in Lake Skjerja (Smukkestad 1980; Eriksen & Garnås 1985, 1988; Eriksen 1991,1992). In 1995 they were virtually grazed to extinction (Eriksen 1995). A high effort with baited traps started in 1994, and it is assumed that the sustained effort with traps has reduced the predation pressure from the minnow. In 2002, the two crustacean species were again present (Rognerud *et al.* 2003). Stomach content is regularly checked by the local fish guard who confirms that *L. arcticus* and *G. lacustris* still seem to be important in the lake (Ivar Sygnabere, pers. comm.). Good individual condition of brown trout (Fultons condition factor = 1.16), and the red flesh colour, give the impression of fish of high quality with good access to important crustacean food items. In contrast, *L. arcticus* and *G. lacustris* no longer seem to be important in the brown trout diet in the nearby Lake Skaupsjøen where no systematic reduction of Eurasian minnow is performed (Borgstrøm 2009). A large fraction of big-sized brown trout in Lake Skjerja may also be crucial in regulating the abundance of Eurasian minnow as experienced in Lake Øvre Heimdalsvatn (Museth *et al*. 2003).

Climate change implications

A near relationship between air temperature and water temperature is generally accepted (Kvambekk & Melvold 2010). The pattern with warm and cold summers is reflected in a variety of other lakes, both on Hardangervidda and elsewhere (Qvenild 2022). On Hardangervidda, an increase in air temperature has been observed since the 1980s (seklima.no). Hence, this trend is also assumed to be reflected in warmer aquatic habitats as seen in the long-term series in Lake Øvre Heimdalsvatn (Sildre.no). This perpetuating trend of warmer lakes is anticipated to continue and will most likely affect the future status of the lakes.

The brown trout has proved to be sensitive to the change in climatic conditions on Hardangervidda, with populations ranging from near collapse in the first decades of the 20th century, to an almost instantaneous change to very rich fisheries in the 1930s (Qvenild 2022). Climate induced strong year classes dominated the fisheries in the 1930s. A similar strong year-class appeared in 1997. In the last decade, the warm summers 2014 and 2018 seem to have produced strong year-classes. Such climatic induced variations in recruitment and growth pattern may be stronger with a warmer, wetter and more unpredictable climate. Such a climate may also induce increased productivity in lakes and rivers and with an increased nutrient input from terrestrial habitats.

Due to the removal of Eurasian minnow, *G. lacustris* and *L. arcticus* are still available food organisms in Lake Skjerja. Even though these two crustaceans can survive water temperatures above 20°C for shorter periods of time, it should not exceed 16 and 18°C for longer periods, respectively (Lakka 2020; Wilhelm & Schindler 2000). During the period 2017–2023, the water temperatures have sporadically exceeded 18°C in Lake Skjerja, but only for short periods. In the warm summer 2018, the maximum temperature was 18.5°C. Hence, harmful high temperatures do not seem to be any threat for the existence of the two species at this point.

A study of the distribution of *L. arcticus* in the Fennoscandia Mountain range, indicated that an average water temperature (1 July – 15 September) of 14°C is close to the upper thermal threshold for the species (Qvenild *et al*. 2021). In lakes with higher temperatures, *L. arcticus* seem to suffer, likely because of life cycle mismatches. In some years (2018 and 2021), the mean water temperature approached this limit in Lake Skjerja. However, the lake still seems to have a viable population of *L. arcticus*. Lake Skjerja is a very shallow lake and thus, it lacks proximity to a colder refugia in the hypolimnion. However, extreme year to year variations may be problematic for a species like *L. arcticus*, which has proved to be very sensitive to various environmental disturbances (Lakka 2020; Qvenild 2022).

A warming of lakes may be tolerated by *G. lacustris* through its phenotypic plasticity in the reproduction traits (Qvenild *et al.* 2020). The water temperature in Lake Øvre Heimdalsvatn has also increased in recent years, and the summer average temperature has exceeded 14°C in some years. Despite the invasive Eurasian minnow, *G. lacustris* is still an important food item for brown trout (Brittain *et al.* 2019). In contrast, *L. arcticus* seem to suffer, likely due to the combined effect of a high predation pressure from Eurasian minnow reinforced by the warmer water, which likely is beneficial for the minnows. *Lepidurus arcticus*, both being a prey and a predator, is assumed to have structural effects of the freshwater ecosystem (Jeppesen *et al*. 2001). Hence, a collapse of the *L. arcticus* may have severe effects on the food web dynamics in the lake.

As indicated by catches of Eurasian minnow with baited traps in Lake Skjerja, a higher water temperature may benefit this species by increased recruitment and individual growth. This can cause increased predation pressure on the two crustacean species, in addition to a stronger competition for these food items with the brown trout. Increased periphytic production and its effect on the grazer dominated ecosystem, may be in favour of Eurasian minnow. Hence, warmer freshwater ecosystems can be an additional challenge in managing sympatric brown trout and Eurasian minnow populations in the future.

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Appendix 1. Fishery statistics of brown trout and Eurasian minnow in Lake Skjerja during the period 1969–2023.

	No. of fish	Total weight (kg)	Average weight (gram)	Maximum size (gram)	% taken on gillnets	Removed minnows (kg)*	References
1969		170			-		Skogheim, letter 7 Feb 1970
1970	365	294	806	3 000	55%		Skogheim, letter 21 Nov 1970; Mollerud 1971
1971		280		3 720	37%		Mollerud, letter15 Feb 1972
1972		156		2 100	100%		
1973	771	370	480	2 200	51%		Skogheim, letter 3 Dec 1973; Smukkestad 1980
1974	811	422	520		-		Skogheim, letter 1 Mar 1975; Smukkestad 1980
1975	912	498	546	2 180	-		Skogheim, letter 27 Feb 1976; Smukkestad 1980
1976	787	505	642	1 570	20%		Skogheim, undated
1977	1059	801	756	1 560	33%		Skogheim, letter 7 Jan 1978
1978	889	705	793	2 090	31%		Smukkestad 1980
1979	683	582	853	2 105	61%		Smukkestad 1980
1980		483		2 710	59%		Eriksen 1985
1981		470		3 000	57%		Eriksen 1985
1982		492		3 200	59%		Eriksen 1985
1983		494		3 250	60%		Eriksen 1985
1984		478		3 090	58%		Eriksen 1985
1985		446		2 970	52%		Eriksen 1985
1986		153					Eriksen & Garnås 1988
1987		270					Eriksen & Garnås 1988
1988		350					Eriksen & Garnås 1991
1989							Eriksen & Garnås 1991
1990		127					Eriksen & Garnås 1991
1991		180					Eriksen & Garnås 1991; Eriksen 1992
1992		120					Eriksen 1992
1993		110				20	Eriksen 1995
1994		115				120	Geilo hunting- and fishing association
1995		60				60	Eriksen 1995
1996		19				195	Geilo hunting- and fishing association
1997		83				482	Geilo hunting- and fishing association
1998		166		4 250		82	Geilo hunting- and fishing association
1999		115				163	Geilo hunting- and fishing association
2000		79				210	Geilo hunting- and fishing association
2001		120				320	Geilo hunting- and fishing association
2002						300	Geilo hunting- and fishing association
2003	207	166	802	3 100		405	Geilo hunting- and fishing association
2004	206	218	1 058			163	Geilo hunting- and fishing association
2005	211	210	995			137	Geilo hunting- and fishing association
2006	230	270	1 174	3 400		155	Geilo hunting- and fishing association
2007	217	290	1 336	4 050		110	Geilo hunting- and fishing association
2008	122	162	1 328	3 400		130	Geilo hunting- and fishing association
2009	170	170	1 000	4 050		160	Geilo hunting- and fishing association
2010	236	224	949	3 250		90	Geilo hunting- and fishing association
2011	201	173	861			180	Geilo hunting- and fishing association
2012	175	152	869	2 700		69	Geilo hunting- and fishing association
2013	279	274	983	3 500	23%	70	Geilo hunting- and fishing association
2014	171	186	1 086	2 450	11%	60	Geilo hunting- and fishing association
2015	218	237	1 089	2 900	43%	37	Geilo hunting- and fishing association
2016	175	214	1 226	2 800	46%	106	Geilo hunting- and fishing association

Appendix 1. Continued.

	No. of fish	Total weight (kg)	Average weight (gram)	Maximum size (gram)	% taken on gillnets	Removed minnows (kg)*	References
2017	137	169	1 230	3 700	35%	125	Geilo hunting- and fishing association
2018	158	187	1 187	4 380	26%	180	Geilo hunting- and fishing association
2019	199	214	1 075	3 930	23%	290	Geilo hunting- and fishing association
2020	144	175	1 213	3 470	46%	170	Geilo hunting- and fishing association
2021	159	133	833	3 480	21%	350	Geilo hunting- and fishing association
2022	144	142	986	3 200	4%	175	Geilo hunting- and fishing association
2023	154	168	1 089	2 850	8%	210	Geilo hunting- and fishing association

*Removed minnows are noted in litres which is approximated to be equal to kilos.