Large individuals in dense brown trout *(Salmo trutta)* populations: not always a paradox

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Samandrag

Store individ i tette bestandar av aure Salmo trutta: ikkje alltid eit paradoks. I 1958 hadde aurebestanden i Øvre Heimdalsvatn, 1088 m o.h., ein tettleik på 19.5 kg/ha, med individ som stagnerte i vekst før dei nådde 30 cm. I perioden frå 1958 til 1966 vart bestanden redusert ved intensivt garnfiske, noko som resulterte i auka individuell vekst, men få gamle fisk. På slutten av 1960-talet vart ørekyt etablert i vatnet, og auren vart ein delvis fiskeetar, med både ørekyt og aureungar på menyen. I dei seinare åra har det vore liten beskatning, og i perioden 2015-2021 har tettleiken i bestanden vore 19,3-26,8 kg/ha. Likevel har den asymtotiske lengda (L_∞) for auren vore den same som på sekstitalet då bestandstettleiken låg på 8-11 kg/ha. Både redusert rekruttering og førekomst av store individ kan vera eit resultat av at auren er blitt fiskeetar og kannibal. Fylgjeleg er store individ i ein tett aurebestand ikkje alltid eit paradoks.

Summary

In 1958, the brown trout population of the lake, Øvre Heimdalsvatn, 1088 m a. s. l., had a density of 19.5 kg/ha, with individuals stagnating in growth at lengths below 30 cm. During the period from 1958 to 1966, the population was reduced by intensive gillnet fishery, resulting in increased individual growth rate, but with few old fish. At the end of the 1960s, European minnow was established, and brown trout became partly a piscivore. In later years, the exploitation has been low, and during the years 2015-2021, the density has been in the range 19.3–26.8 kg/ha. However, the asymptotic lengths (L_∞) are still at the same size as during the 1960s, when population density was 8–11 kg/ha. Both reduced recruitment and the occurrence of large individuals may be a result of piscivory. Accordingly, large individuals in brown trout populations with high densities may not always be a paradox.

Introduction

Fish populations having high annual recruitment, combined with a low annual mortality, commonly consist of small, slow growing individuals, with growth stagnation at small size, as frequently seen in cyprinid, percid and salmonid species (Dahl 1917; Alm 1946; Burrough & Kennedy 1979; Langeland 1986; Amundsen 1988; 1989). Lacustrine brown trout *Salmo trutta* typically form such stunted populations (Dahl 1917; Huitfeldt-Kaas 1927; Jensen 1977; Langeland & Jonsson 1990). More than hundred years ago, Dahl (1917) demonstrated that annual growth rate in such dense allopatric brown trout populations could increase substantially after high exploitation by gillnetting, i.e., after a heavy reduction of population density. The dynamic changes in an allopatric brown trout population with stunted growth, after a period with high annual exploitation, was thoroughly described by Jensen (1977; 1986), based on a study in the subalpine lake, Øvre Heimdalsvatn in southern Norway. When his studies commenced in 1958, the brown trout population in this lake had a high density and low individual growth rate. Due to the following high annual exploitation by gillnetting, the population density was reduced from 19.5 kg/ha in 1958 to 8.2 kg/ha in 1963, and density continued to be low throughout the 1960s.

Brown trout was probably the only fish species in the lake during the first half of the 1960s. However, in 1969 European minnow *Phoxinus phoxinus* was observed in the western part of the lake (Lien 1978), and the minnow population increased during the next decades (Lien 1981; Museth et al. 2002). In an extensive study of the diet of brown trout during the years 1969 – 1972, fish were not at all found as a prey (Lien 1978), but in studies from 1993 to 2009, both European minnow and brown trout have been recorded as preys of brown trout (Borgstrøm et al. 2010). In the period 1993 - 2009, the annual number in age-class 4 years was estimated by mark-recapture to a mean of 1668 individuals, which was less than half the number of this age-class during the years without presence of European minnow (Borgstrøm et al. 2010).

After 2010, the gillnetting in the lake has been very modest, and together with a negligible sport fishery, the total annual capture has not exceeded 300–400 individuals (Knutsdatter Strand 2017). In the present study, population data of brown trout from the period 1958–1970, with heavy exploitation, have been analysed and compared with data from the years 2015–2021. Low annual exploitation is expected to give a population structure with a high proportion of old fish, early stagnation in growth and small maximum fish size, corresponding to the population status in 1958 (Jensen 1977; 1986). However, feeding on small-sized prey fish is a favourable strategy for several fish species, leading to higher individual growth rates and large body size (Aass et al. 1989; Næsje et al. 1998; Vehanen et al. 1998; Jonsson et al. 1999; Jensen et al. 2008). The outcome of a low fishing pressure on the brown trout population in Øvre Heimdalsvatn is accordingly highly open.

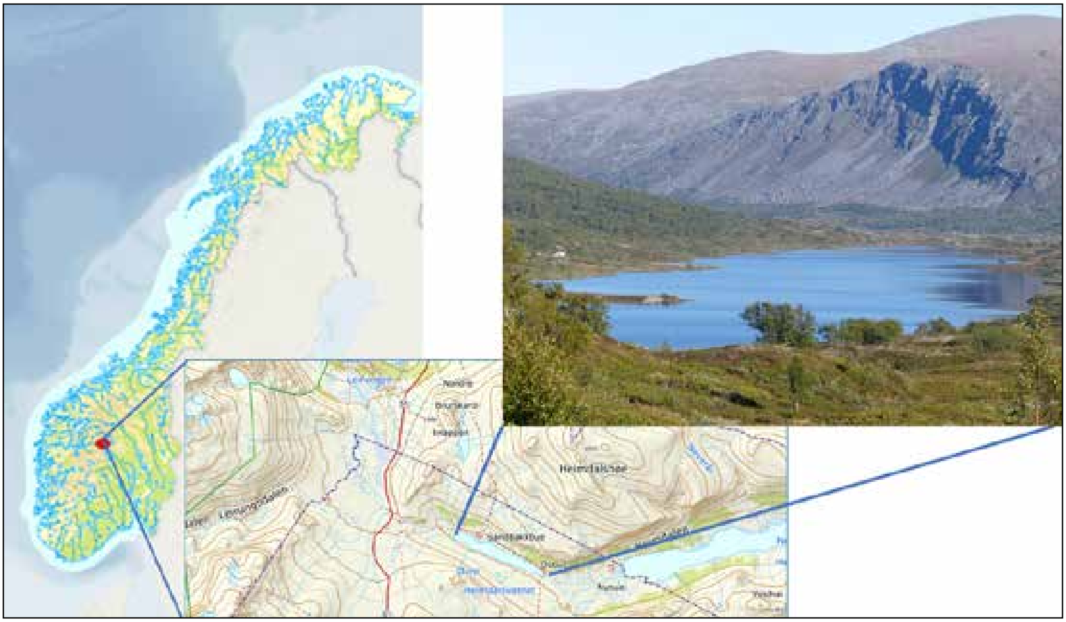

Figure 1. Geographic position of the lake, Øvre Heimdalsvatn, Øystre Slidre municipality, in southern Norway

Material and Methods

The lake, Øvre Heimdalsvatn is located in Øystre Slidre municipality, at 1088 m a.s.l. on the eastern slope of the Jotunheimen Mountains (Figure 1). The lake has a mean depth of 4.7 m, maximum depth of 13 m, and a surface area of 0.78 km^2 (Grøterud & Kloster 1978). It is ice-covered from mid or late October to early June (Kvambekk & Melvold 2010). Allochtonous input to the lake is significant, mainly consisting of fragments from dwarf willow, dwarf birch, and mountain birch, which nearly equals the primary production in the lake (Larsson et al. 1978).

Brown trout and European minnow are the only fish species in the lake. In 1977 and 1978, the estimated numbers of the newly established European minnow were 14 500 and 23 000 individuals ≥65 mm, respectively (Lien 1981), while in 1999 and 2000, the population had increased, with estimates of length-class ≥65 mm being 89 000 and 35 000 individuals, respectively (Museth et al. 2002). A short overview of the research activities connected to the lake until 2010 is given by Brittain & Borgstrøm (2010).

The total annual number of gillnet-nights during the period 1958–1972 was in the range 719–1550. A part of this effort consisted of a special gillnet fleet (called a pilot fleet), with eight gillnets with the mesh sizes 24, 26, 28, 30, 32, 34, 36, 38 mm (measured from knot to knot), which made up 88 – 136 gillnet nights annually during the period 1959–1970 (Jensen 1977). In all these years, except 1959, the gillnets in the pilot fleet were moved to new places every day during the samplings in August – September. Some of the mesh sizes used by Jensen in his 'pilot gillnet fleet' are not in ordinary sale today, and a corresponding gillnet fleet consisting of the mesh sizes 24, 26, 29 x 2, 32, 35 x 2, and 39 mm (knot to knot) was used in 2015-2021. According to data given by Jensen (1972; 1977), the two 'pilot gillnet fleets have overlapping relative selectivity for some length-classes (Figure 2). The total gillnet effort in the end of August – beginning of September 2015–2021, after sampling in all sections, has annually varied between 52 and 78 gillnet nights (Table 1). Regression models have been constructed between catch per effort by the pilot gillnet fleet used by Jensen (1977) and the estimated number of each

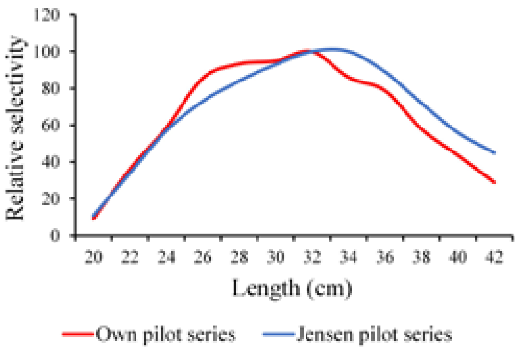

Figure 2. Relative selectivity of the pilot gillnet fleet (mesh sizes 24, 26, 28, 30, 32, 34, 36, 38 mm), used by Jensen (1977) in the lake Øvre Heimdalsvatn, 1958–1970, and the gillnet fleet (mesh sizes 24, 26, 29 x 2, 31, 35 x 2, 39 mm) used during the sampling in the years 2015-2021 according to selectivity data in Jensen (1972;1977). All mesh sizes measured from knot to knot.

Table 1. Number of gillnet nights used in connection with population estimation of brown trout in the lake, Øvre Heimdalsvatn in end of August – beginning of September in the years 2015 – 2021.

Mesh size (mm)	2015	2016	2017	2018	2019	2020	2021
24	8	7	7	8	9	9	9
26	8	7	7	8	9	9	9
29	8	7	8	8	13	12	12
31	12	12	14	8	12	15	15
35	10	12	14	16	16	19	21
39	7	7	7	8	12	10	12

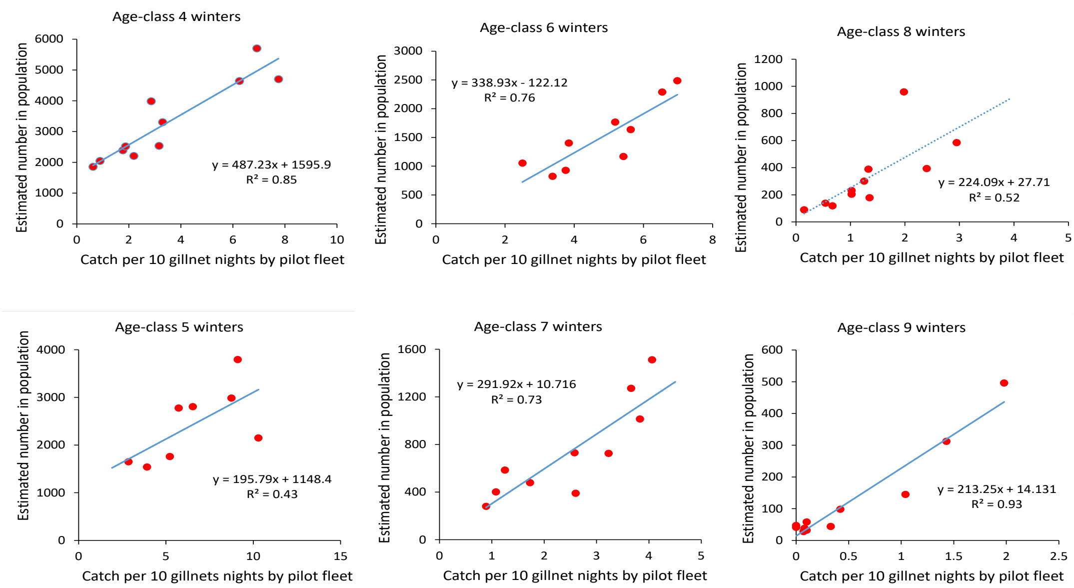

Figure 3. Estimated number of brown trout in age-classes 4–9 years in the lake, Øvre Heimdalsvatn in the years 1959-1970, plotted against catch per unit effort by the pilot gillnet fleet. All data adopted from Jensen (1977).

age class in the years 1960-1970 (Figure 3). The average number of fish in each age-class captured by each mesh size in 2015-2021 is used to obtain the total catch per unit of effort by the complete pilot fleet. Estimation of number in each age-class is thereafter carried out by use of the regression equations presented in Figure 3.

All captured trout were aged by otoliths, supplied with age determination and back-calculation of lengths by scales of fish younger than 10 years. By age determination, the otoliths were first cut in half through the center by use of a scalpel blade. Thereafter one of the otolith halves was placed on a spatula and burnt, until the winter zones turned distinctly brown (Christensen 1964; Power 1978), and age determined under a binocular microscope (Figure 4).

Jensen (1977) back-calculated fish length to growth start set to 1 June, and he presented population number, total biomass (kg) and population density (kg/ha) on 1 June in each year. For fish sampled in August-September 2015–2021, back-calculation of length to growth start (in June) has been carried out for the age-classes 5–9 winters by use of scales and the Lea-Dahl method (Lea 1910; Dahl 1910). Age-class 5 is not fully captured by the pilot fleet, and the mean length of this age-class in catches by the pilot fleet are with little doubt higher than the mean lengths of individuals in the entire cohort. Lengths at age 5 in year *t* have accordingly been obtained by back-calculation from six winter old individuals in year *t*+1 and *t*+2, respectively.

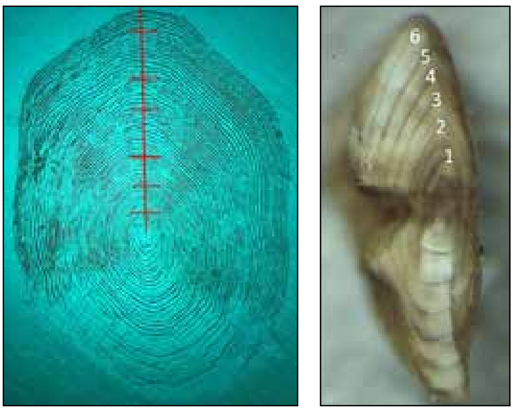

Figure 4. Scale and otolith of a six winter old brown trout, captured in the lake, Øvre Heimdalsvatn.

Jensen (1977) estimated the asymptotic length (L_∞) of the brown trout in Øvre Heim-

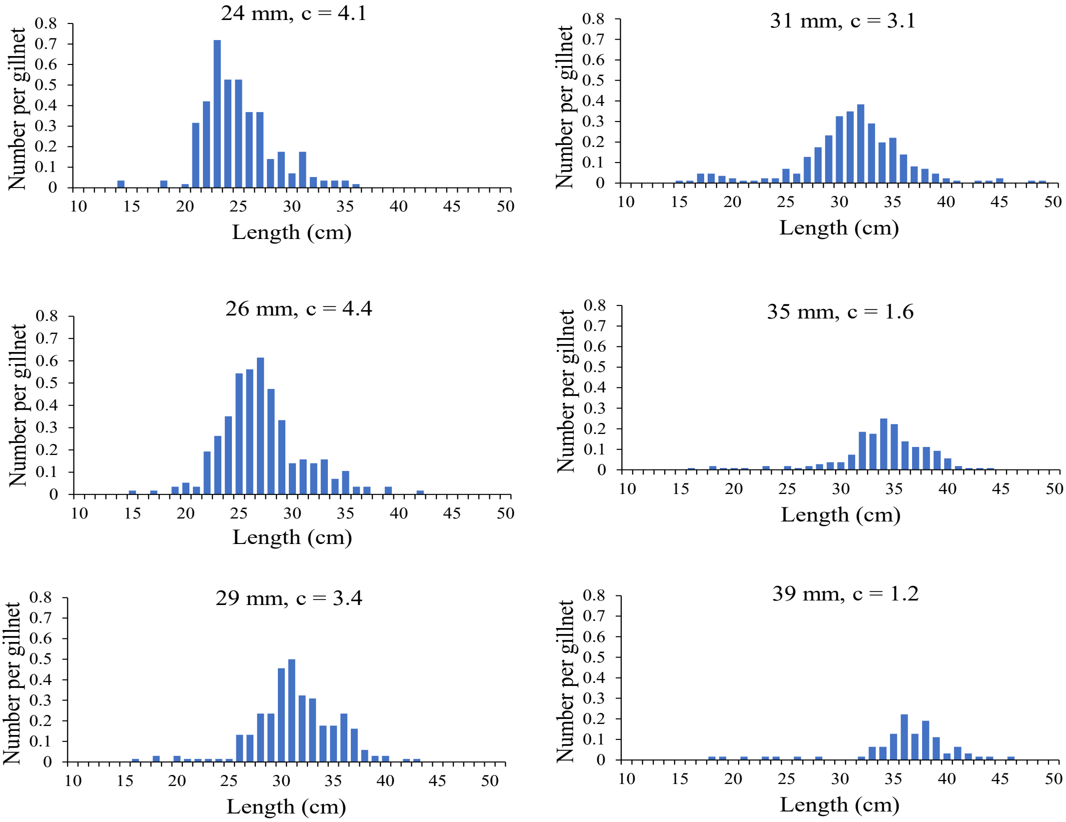

Figure 5. Length distribution of brown trout captured per gillnet/night by the mesh sizes 24, 26, 29, 31, 35, and 39 mm (knot to knot), in the lake, Øvre Heimdalsvatn 2015 – 2021. C = mean catch per gillnet/night

dalsvatn for the years 1958-1970, by use of the Walford plot (Walford 1946, Ricker 1975), where L_{t+1} is plotted against L_t, and L_{t+1} and L_t are back-calculated lengths to the last two annuli (in the scales) for age-class *t*. Corresponding calculation is carried out for both the period 1958-70 and for the material sampled in the years 2015-21, but for the age-classes 5 to 9 only, because of the small annual increase in length and missing formation of new annuli in scales of the majority of the older fish.

Results

Catch per unit effort (cpue) and age-class abundance

The gillnet fleet used in the years 2015-2021 captured brown trout from 14 to 49 cm in total length. The catch obtained by each mesh size consisted of fish from a relatively broad length interval, but with a distinct mode (Figure 5). From the smallest mesh size (24 mm) to the largest (39 mm), total catch per unit effort (cpue) declines, while the modes move to the right with increasing mesh size (Figure 5).

The mean cpue of four and five-year-old trout in 2015-2021 was lower than the mean cpue in the period 1960-1966. The cpue of age-class 6 winters was at the same level or even higher than in 1960-1966, and for older fish the cpue was much higher than in the 1960s (Table 2). In the years 1964-1966, the cpue of fish with age 8–9 years was in average 0.51, in contrast to the years 2015-2021, when the mean cpue of the same age-classes was 5.35 (Table 2). The catch of age-classes ≥ 10 years was likewise high during the years 2015-2021, with an annual mean cpue at 5.47. No data for these age-classes captured by the pilot gillnet fleet during the period 1960-

Table 2. Mean catch of brown trout per 10 'pilot' gillnets nights with i) a gillnet fleet consisting of nets with the following mesh sizes; 24, 26, 28, 30, 32, 34, 36, 38 mm (measured from knot to knot) during the sampling in the lake Øvre Heimdalsvatn in the years 1960 – 1966 (data from Jensen 1977), and ii) with a gillnet fleet consisting of nets with the mesh sizes 24, 26, 29 x 2, 32, 35 x 2, and 39 mm, in August – September in the years 2015 – 2021.

	Age-class						
Year	**4+**	**5+**	**6+**	**7+**	**8+**	**9+**	**≥ 10+**
1960	1.77	5,73	6,98	4,06	1,98	1,98	No data
1961	3.30	2.86	5,18	3,66	2,95	1,43	«
1962	2.19	10,30	3,75	3,23	2,40	1,04	«
1963	7.75	3,92	5,42	1,08	1,33	0,42	«
1964	6.92	8,75	3,37	2,60	0,67	0,10	«
1965	2.86	9,11	3,84	0,89	0,54	0	«
1966	3.16	6,54	6,54	1,25	0,15	0,07	«
Mean	**3.99**	**6.74**	**5.01**	**2.40**	**1.43**	**0.72**	**«**
2015	0,63	2,07	4,99	5,70	2,56	0,63	6,96
2016	0,89	3,17	3,99	5,22	3,62	1,83	5,92
2017	1,88	3,79	4,46	3,53	4,46	1,38	6,71
2018	6,41	6,88	6,41	4,69	2,66	3,91	4,22
2019	3,20	10,67	7,40	5,81	3,78	3,32	5,36
2020	2,51	6,28	10,18	4,91	3,69	1,15	4,81
2021	0,88	1,94	5,57	5,89	3,71	1,44	3,68
Mean	**2.34**	**4.97**	**6.14**	**5.11**	**3.50**	**1.95**	**5.38**

1966 are available.

Based on cpue of each age-class (Table 2) and use of the regression models from Figure 3, the number of individuals in each age-class ≥ 4 years has been estimated for the years 2015-2021 (Table 3). In 2015-2021, the mean estimated number of 4 winter old fish was 2745. In 1958–1966, the mean estimated number of this age-class was 3746 individuals. The difference in population age structure between the years 1964-1966 and the years 2015-2021 is summarized in Table 4. Although the number of 4 winter old recruits was lower in 2015-2021 than in the years 1964-1966, age-classes ≥8 years had a total estimated number of 2537 individuals in the years 2015-2021, in contrast to the average number of ≥8-year-old trout during the years 1964-1966 being 179 individuals (Table 4).

The annual capture of fish in the age-classes ≥10 years by the limited pilot gillnet fishery in 2015-2021 has been in the range 25–45, while in the years 1964-1966, the total number of individuals captured of age-classes ≥10 years was in the range 8–14, despite an annual effort of 1295–1495 gillnet nights, i.e., around 20 times higher effort compared to the period 2015–2021(Table 4).

Length at age

The mean back-calculated length at age is nearly identical during the years 1962-1971 and 2015-2021, i.e., in two periods with very different population densities (Figure 6). The mean back-calculated length of the age-classes 6–9 years in these periods is larger compared to the mean back-calculated lengths of the same age-classes in the years 1958-1961 (Figure 6).

In the years 2015-2021, the empiric length of brown trout shows an annual increase until age 10-12 winters, but the annual increments in length of fish older than 9 years are small, usually less than 1 cm (Figure 7). Ten-year-old fish have a mean length at 34.7 cm (SD ±0.9 cm), while fourteen-year-old fish had a mean length

Table 3. Estimated number of brown trout in the age-classes 4+ to ≥ 15+in the lake Øvre Heimdalsvatn in i) the years 1959 – 1966 according to Jensen (1977), and ii) based on the cpue data from the years 2015 – 2021.

Age (years)											
År	**4+**	**5+**	**6+**	**7+**	**8+**	**9+**	**10+**	**11+**	**12+**	**13+**	**14+**	**≥15+**
1959	3857	3596	2418	1768	1174	639	267	28	1	1		
1960	2387	2775	2486	1511	959	496	286	108	7			
1961	3304	1649	1765	1271	585	312	155	103	14	4		
1962	2207	2149	928	724	394	145	70	29	36	6	3	
1963	4702	1540	1168	401	189	98	36	10	8	9		
|964	5698	2985	823	389	119	58	16	1	1	2	1	
1965	3983	3792	1401	279	138	41	8	2			1	
1966	2536	2806	2288	584	90	28	20	2				
Mean	**3584**	**2662**	**1660**	**866**	**456**	**227**	**107**	**35**	**11**	**4**		
År	**4+**	**5+**	**6+**	**7+**	**8+**	**9+**	**10+**	**11+**	**12+**	**13+**	**14+**	**≥15+**
2015	1914	1554	1569	1674	852	147	709	285	159	185	59	214
2016	2044	1769	1230	1535	838	405	392	338	103	316	74	153
2017	2519	1891	1391	1040	1028	309	490	204	366	109	224	170
2018	4714	2494	2049	1379	623	847	314	181	81	48	147	229
2019	3160	3238	2385	1708	875	723	508	300	103	103	47	194
2020	2829	2379	3328	1446	855	258	390	266	159	60	85	179
2021	2038	1528	1573	1732	858	320	342	139	137	119	57	88
Mean	**2745**	**2122**	**1932**	**1502**	**847**	**430**	**449**	**245**	**158**	**134**	**99**	**175**

Table 4. Mean estimated number of brown trout in the age-classes 4+ - ≥ 15+, in the lake Øvre Heimdalsvatn 1964 – 1966 (after heavy exploitation in the previous years)(After Jensen 1977), and based on cpue data from the years 2015 – 2021.

Age-class (years)												
Periode	**4+**	**5+**	**6+**	**7+**	**8+**	**9+**	**10+**	**11+**	**12+**	**13+**	**14**	**≥ 15+**
1964-66	4072	3194	1504	417	116	42	15	2	1	2	1	0
2015-21	2745	2122	1932	1502	847	430	449	245	158	134	99	175

at 37.7 cm (SD ±1.7 cm), i.e., an average annual increase of 0.8 cm per year from age 10 to 14 years.

Temperature and annual growth

There is a significant positive relationship between the June temperature in the outlet of Øvre Heimdalsvatn and the annual growth increments of brown trout during the years 1992–2020, as shown for age-class 6 years (Linear regression, df=15, R^2=0.46, $P<0.05$)(Figure 8).

The positive relationship between June air temperature at Vågåmo and the annual length increments in brown trout from Øvre Heimdalsvatn found in the 1960s, seems to be valid even when observations from 1993 to 2020 are included in the regression analysis (Figure 9a). The mean temperature at Vågåmo shows large annual variations, but without any specific trend (Figure 9b).

Asymptotic length and population density

The annual asymptotic length (L_∞) calculated by length of the age-classes 5 – 9 of brown trout presented in Table 5, gives a mean L_∞ at 45.6 cm for the years 1962-1970, and L_∞ at 44.8 cm for

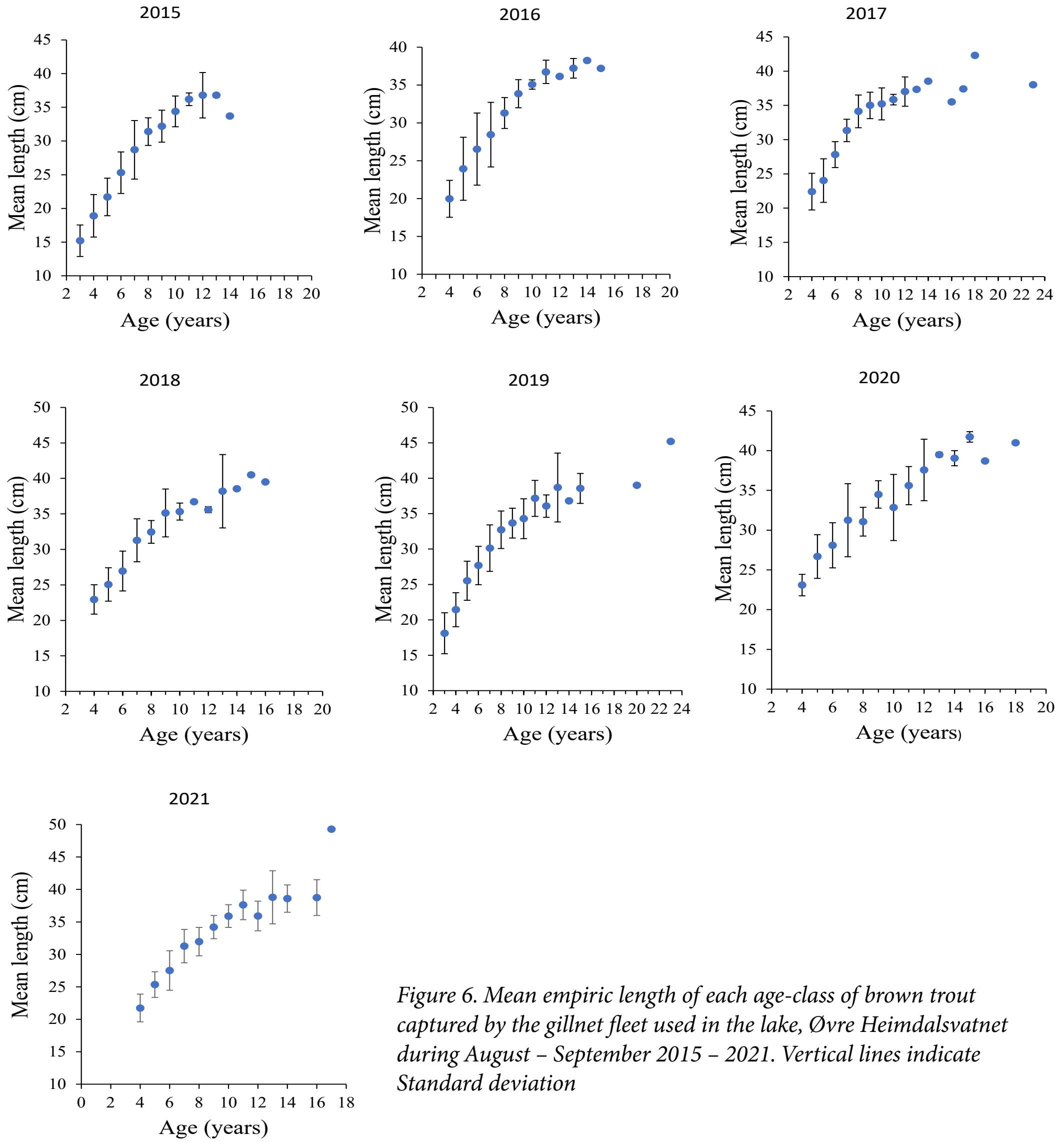

Figure 6. Mean empiric length of each age-class of brown trout captured by the gillnet fleet used in the lake, Øvre Heimdalsvatnet during August – September 2015 – 2021. Vertical lines indicate Standard deviation

the years 2015-2021. As expected, the L_∞ was at a minimum during the first year (1958), before the population density was heavily reduced. L_∞ increased considerably from the year 1963 onwards, with the low L_∞ in 1967 as an exception (Table 5).

Individual body weight and total biomass

The mean weights of age-classes 9–14 years in August-September 2015–2021 are generally at the same level or even higher than the corresponding mean weights in June 1962-66 (Appendix I, Appendix II). In these years, the estimated number of fish in age-classes ≥10 years varied between 770 (in 2018) and 1498 individuals (in 2017), which is considerably higher than in the period 1962-66, when the numbers varied between 11 and 144 (Table 3). Altogether, the estimated number of fish in each age-class during the years 2015–2021, with the corresponding mean weights, gives a total estimated biomass of ≥4 winter old fish in the range 1502–2090 kg, and a population density in the range 19.3–26.8 kg/ha (Appendix III). These

Table 5. Estimated brown trout population density (kg/ha) in the lake, Øvre Heimdalsvatn, and asymptotic length (L_∞ in cm) based on Walford plots for age-classes 5 – 9 years, 1958-1970 and 2015-2021.

Data after Jensen (1977)			Data from 2015-2021		
Year	**Density (kg/ha)**	**L_∞ (cm)**	**Year**	**Density (kg/ha)**	**L_∞ (cm)**
1958	19.5	31.8	2015	20.5	37.6
1959	16.8	35.9	2016	20.3	44.9
1960	15.0	36.8	2017	23.3	47.9
1961	11.7	37.0	2018	25.7	47.3
1962	8.6	35.3	2019	24.8	48.3
1963	8.2	45.9	2020	26.7	43.6
1964	10.0	50.5	2021	19.2	44.3
1965	11.0	47.0			
1966	10.4	52.7			
1967	9.2	39.7			
1968	8.0	45.0			
1969	9.3	44.9			
1970	14.6	49.2			

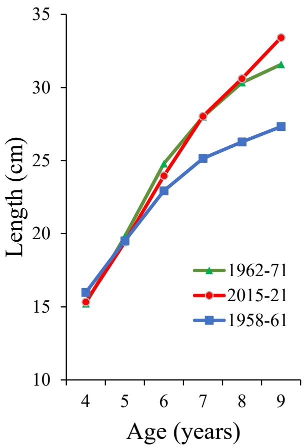

Figure 7. Mean back-calculated length to start of growing season for age-classes 4 – 9 years in the lake Øvre Heimdalsvatn for the years 1958-61, 1962-71 (Data after Jensen 1977), and from the sampling in 2015-2021

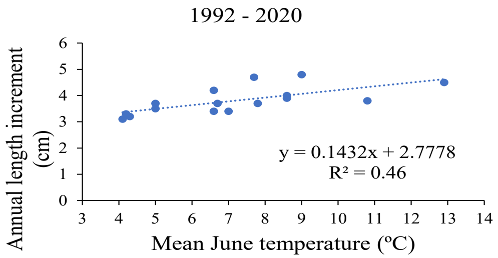

Figure 8. Annual growth increment of six year old brown trout from the lake, Øvre Heimdalsvatn during the period 1992 – 2020, plotted against annual mean June temperature in Hinøgla, the outlet from the lake (temperature data from sildre.nve.no)

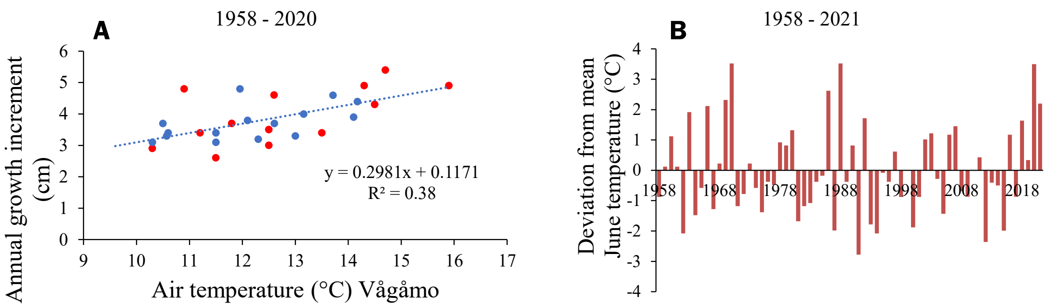

Figure 9. A) Length increment of brown trout from the lake Øvre Heimdalsvatn at age 6 plotted against recorded (1958-2004, in red) and estimated (2005 – 2020, in blue) June temperature at the meteorological station at Vågåmo. B): Deviation from mean June temperature (°C) at Vågåmo, 1958-2021. Temperature data from 2005-2021 estimated by data from Skåbu (all temperature data from seklima.met.no)

Appendix I. Mean weight (gram) of fish in age-classes captured by the pilot gillnet fleet in the lake, Øvre Heimdalsvatn during August-September 2015 – 2021.

Age (years)	2015	2016	2017	2018	2019	2020	2021
3	35				57		
4	67	79	114	115	98	109	96
5	101	141	135	150	162	171	147
6	157	185	208	187	210	223	194
7	229	235	308	304	271	259	285
8	318	318	403	345	348	323	295
9	328	417	444	443	381	471	356
10	407	447	466	458	387	381	421
11	488	518	505	534	501	420	470
12	506	555	537	438	440	511	396
13	520	536	572	508	544	327	561
14	346	536	609	600	518	610	478
15	603	584		699	487	647	
16	489	535		608		543	461
17		617		620			
18	473					620	
19							
20					519		
21							
22							
23					907		

Appendix II. Mean weight (gram) of 9 – 14-year-old brown trout from the lake, Øvre Heimdalsvatn 1. June 1962 – 1964, according to data in Jensen (1977). Number of individuals in parenthesis.

Year	9	10	11	12	13	14
1962	266 (145)	284 (70)	310 (29)	339 (36)	500 (6)	433 (3)
1963	301 (98)	428 (36)	340 (10)	363 (8)	533 (9)	
1964	329 (58)	388 (16)	400 (1)	500 (1)	300 (2)	550 (2)
1965	488 (41)	488 (8)	900 (2)			900 (1)
1966	382 (28)	665 (20)	450 (2)			

densities are considerably higher than in all years during the 1960s (Appendix III). Except in 2021, the population densities are even higher than in 1958, at start of the extensive exploitation.

Annual survival rate

The mean estimated number of each age-class of brown trout during the years 1964-66, i.e., after several years with population reduction, gives an annual survival rate at S=0.381 (instantaneous mortality, Z=0.9648), while the corresponding annual survival rate based on the material from the years 2015-21, is S=0.699 (Z=0.3585) (Figure 10). The estimated annual mortality rate in 2015-2021 thus becomes A=0.301, which is nearly equal to the natural mortality rate during the 1960s (A=0.266). In the 1960s, the annual gillnet catch varied from

***Appendix III.** Biomass (kg) of age-class 4 to ≥13 years, and total biomass (kg) and density (kg/ha) of brown trout in the lake, Øvre Heimdalsvatn from 1958 to 1970 (after Jensen 1977), and in the years 2015-2021, based on the population estimates in the present study.*

	Age										
Year	4+	5+	6+	7+	8+	9+	10+	11+	12+	≥13+	Biomass (kg)	Density (kg/ha)
1958	207.5	234.0	278.1	301.4	267.7	181.0	32.8	3.3	4.6	-	1510.4	19.5
1959	140.0	252.4	255.6	259.9	205.8	122.5	55.9	7.3	0.2	0.4	1300.0	16.8
1960	87.1	187.3	282.7	226.5	175.3	105.4	67.2	29.1	2.1	-	1162.7	15.0
1961	125.6	117.7	194.3	206.5	115.7	71.6	39.3	29.0	4.4	1.4	905.5	11.7
1962	91.8	174.3	116.7	121.1	82.1	38.5	19.9	9.0	12.2	4.3	669.9	8.6
1963	189.0	121.5	144.8	80.8	44.7	29.5	15.4	3.4	2.9	4.8	636.8	8.2
1964	222.2	268.1	125.9	87.8	40.3	19.1	6.2	0.4	0.5	1.7	772.2	10.0
1965	149.0	325.7	233.3	71.1	45.3	20.0	3.9	1.8	-	0.9	851.0	11.0
1966	90.3	217.2	316.2	125.6	28.7	10.7	13.3	0.9	-	-	802.9	10.4
1967	73.0	129.9	231.0	201.9	60.5	11.5	4.4	2.4	0.5	-	715.1	9.2
1968	115.2	112.6	139.2	149.4	80.1	14.7	3.7	1.2	-	0.6	616.7	8.0
1969	151.3	166.0	221.9	111.7	55.0	12.6	1.1	-	-	0.6	720.2	9.3
1970	326.3	354.7	188.4	164.4	68.5	20.1	6.0	-	-	-	1128.4	14.6

Year	4+	5+	6+	7+	8+	9+	10+	11+	12+	≥13+	Biomass (kg)	Density (kg/ha)
2015	66.4	91	181.4	302.9	239.1	46.8	254.5	121.5	71.8	208.7	1584.1	20.3
2016	60.4	116.4	131.4	301.8	181.2	137.6	158.9	159.6	45.4	275.6	1568.3	20.1
2017	85.8	117.5	180.8	221.5	336.9	120.7	213.7	93.7	180.8	274.1	1825.5	23.4
2018	195.5	211	259.7	309.7	192.7	335.9	135.1	85.5	34.3	240.1	1999.5	25.6
2019	143.1	215.3	441.7	295.1	262.1	88.5	148.1	126.2	65.9	158.7	1944.7	24.9
2020	147.5	261.6	519.7	314.6	237.5	118.2	139.3	106.1	77.4	168.3	2090.2	26.8
2021	71.8	115.5	221.4	404.6	217.2	104.7	128.6	58.0	51.2	129.1	1502.1	19.3

981 (in 1969) to 2934 brown trout (in 1961), while the annual gillnet catch during the years 2015–2021 has varied between 253 trout (in 2015) and 175 trout in (2021).

Discussion

Brown trout in mountain lakes in Norway may reach ages at least up to 34-38 years (Svalastog 1991; Borgstrøm 2016). Fish aged 14-18 years have been regularly captured in the lake Øvre Heimdalsvatn during the last years, with the oldest individual sampled in the period 2015-2021 being 23 years. This is in contrast to the period 1958–1970, when brown trout older than

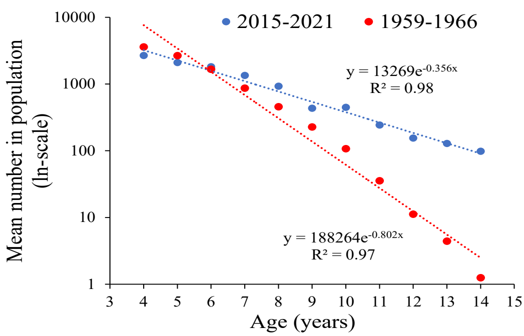

Figure 10. Mean estimated number of brown trout in the age-classes 4–14 winters in the lake Øvre Heimdalsvatn from the years 1964-1966 (After Jensen 1977) and from the years 2015-2021. The regression models and R^2 are given for both periods.

14 years was not identified during the whole study period (Jensen 1977; 1986). Gunnerød (1966) demonstrated that the annulus formation in scales of brown trout presuppose an annual growth in length of at least 1-1.5 cm per year, which is more than the average length increment of old fish in Øvre Heimdalsvatn during the period 2015-2021, and probably also in 1958-1959. Low annual length increments leading to missing formation of annuli in scales, and thereby an underestimation of age by scale reading, is also stated in other studies of brown trout (e.g., Jonsson 1976; Závorka et al. 2014), and likewise observed in age determination of other fish species such as Arctic charr, whitefish, and cisco (Nordeng 1961; Aass 1972; Skurdal et al. 1985). Accordingly, the occurrence of old fish in Øvre Heimdalsvatn was most probably heavily underestimated during the first years from 1958 and onwards, because Jensen (1977) used scales only for the age determination.

In 1966, fish aged ≥9 years contributed with only 24,9 kg to the total population biomass of 802,9 kg that year (Jensen 1977), in contrast to the estimated biomass of age-classes ≥9 winters at 480-992 kg in 2015-2021 (Appendix III). Despite a gillnet effort corresponding to less than one gillnet night per ha in this latter period, the total catch of age-classes ≥9 years was nearly the same as the total biomass of these age-classes in the population in 1966. According to Jensen (1986), an effort of five gillnet nights per ha in the lake, Øvre Heimdalsvatn would have given a catch mortality of 21 %. An effort of one gillnet night may accordingly correspond to a catch mortality of an order of 4%. Given a total biomass of 605 kg of age-classes ≥9 years in 2020, the fishing effort used in 2020 is expected to give a catch of around 24 kg of age-classes ≥9 years. The actual catch was 19.8 kg, or nearly as expected. Similar results were obtained in the other years during the period 2015–2021, being a strong indication of a high number and biomass of old fish in the population during these years.

The high contribution of old fish in the lake Øvre Heimdalsvatn, is as described from other high mountain brown trout populations where annual exploitation is low (Borgstrøm & Museth 2005; Borgstrøm et al. 2015). Such population structures are also described from more or less unexploited fish populations in Arctic lakes, with accumulation of a high number of age-classes within a relatively narrow length interval (Johnson 1976; Svenning & Borgstrøm 1995). Power (1978) and Ricker (1975) explained this population structure by low and stagnating growth and low annual mortality of old fish.

Although the estimated number of fish with age ≥10 years in the period 2015–2021 is substantially higher than in the 1960s, the mean weights of fish in age-classes 10–14 in August-September are in general higher than for the same age-classes in the 1960s (see Appendix I and II). The sustained annual growth in length of the brown trout from Øvre Heimdalsvatn after 2015 is hard to explain based on the observed low annual growth rates when population biomass was high during the years 1958-1960 (Jensen 1977). Lien (1978) examined the stomach content of 1594 brown trout from the lake, Øvre Heimdalsvatn captured throughout the years 1969-1972, without finding European minnow or brown trout as prey items. After the establishment and population increase of European minnow, this species became an important part of the brown trout diet (Museth et al. 2003; Hagen 2003). Even brown trout juveniles became a prey, admittedly in a low frequency in brown trout stomachs, but still this predation may partly explain the reduced recruitment to the population (Borgstrøm et al. 2010). In general, piscivory may strongly influence the population abundance of potential prey fish (Amundsen 1995; Sandlund & Forseth 1995, Svenning & Borgstrøm 1995; 2005), and may also result in a faster growth rate of the piscivorous individuals. The predation on minnows and young life stages of brown trout may likewise have contributed to the sustained annual growth rate of the brown trout, despite the large population biomass.

Conclusion

The present exploitation of the brown trout population of the lake Øvre Heimdalsvatn is very low, resulting in low annual mortality, and an accumulation of old fish. The frequent occurrence of body weights in the range 400–600 gram or even higher, and asymptotic lengths at the same level as in the period 1962-1970, despite considerably higher population densities, is apparently a paradox due to traditional knowledge. However, a major change has occurred in the lake by the establishment of a European minnow population. A contemporary shift towards partly piscivory in brown trout seems to have taken place in this alpine lake and should be regarded as a common situation in such alpine lake ecosystems rather than a paradox. This piscivory may have reduced the recruitment to the brown trout population, as well as maintained the annual growth rate of old individuals at the same level as during the period when population density was low.

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