Crustacean zooplankton trophic position, food item origin and relationship to fish in the temperate, subalpine Lake Savalen, central Norway, compared with similar lake ecosystems

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Sammendrag

Trofisk nivå til krepsdyrplankton og deres relasjon til fisk i Savalen sammenlignet med beslektede økosystemer. Savalen er en subalpin, oligotrof, dimiktisk og regulert innsjø i Norge, Nord-Europa. Den ligger mellom 703-708 meter over havet i den sentrale delen av Norge. Innsjøen har et maksimalt overflateareal på 15.2 km^2. Dyreplankton ble studert siden det utgjør en avgjørende kobling i akvatisk næringsnett. Energi og materiale akkumulert gjennom primærproduksjon blir inkorporert i konsumenter og overført til planktivor fisk via dyreplankton. Forholdene mellom de stabile isotoper av nitrogen (^{15}N:^{14}N) og karbon (^{13}C:^{12}C) ble analysert. Stabilt karbonisotopforhold gjenspeiler tilførselen av karbon som avslører bidragene til forskjellige matkilder, og nitrogenisotop indikerer organismenes trofiske plassering. I Savalen viste dyreplanktonartene markante forskjeller i deres trofiske nivåer, med de høyeste δ^{15}N-verdiene i den mest uttalte rovdyrarten *Bythotrephes longimanus*. Litt lavere var δ^{15}N-verdiene i de omnivore artene *Arctodiaptomus laticeps* og *Heterocope saliens*, som begge har et mindre karnivort matvalg enn *B. longimanus*. De laveste δ^{15}N-verdiene i dyreplanktonartene ble funnet hos filtratoren *Daphnia galeata* med et betydelig inntak av alger, bakterier og muligens en liten mengde protister. En storflom i mai/juni 1995 demonstrerte på en overbevisende måte viktigheten av alloktont materiale for dyreplanktonsamfunnet i naboinnsjøen Atnsjøen. Dyreplanktontettheten økte tre ganger og biomassen ble det dobbelte etter flommen sammenlignet med referanseår. Viktige stikkord i denne undersøkelsen er; næringsnett, krepsdyr, artsøkologi, stabile isotoper og allokton påvirkning.

Summary

Lake Savalen is a subalpine, oligotrophic, dimictic and regulated lake situated in Norway, north Europe. It is located between 703-708 meters above sea level in the central part of Norway. The lake has a maximum surface area of 15.2 km^2. The zooplankton was studied since it forms a crucial link in the aquatic food web. Energy and matter accumulated through primary production are incorporated into consumers and transmitted to planktivorous fish via zooplankton. The ratios of the stable isotopes of nitrogen (^{15}N:^{14}N) and carbon (^{13}C:^{12}C) were analysed. Stable carbon isotope ratio reflects the input of carbon revealing the contributions of different

food sources, and nitrogen isotope indicates the trophic role of the organisms. In Lake Savalen the zooplankton species showed marked differences in their trophic levels, with the highest $\delta^{15}N$ values in the most pronounced predator species *Bythotrephes longimanus*. Slightly lower $\delta^{15}N$ values were found in the omnivorous species *Arctodiaptomus laticeps* and *Heterocope saliens*, both of which probably have a less carnivorous food choice than *B. longimanus*. The lowest $\delta^{15}N$ values found in zooplankton species logically fall in with the filtrator *Daphnia galeata* with a significant intake of algae, bacteria and possibly a small amount of protists. A major spring flood in May/June 1995 in the closely situated Lake Atnsjø demonstrated in a most convincing way the importance of allochthonous material for the zooplankton community. The zooplankton density increased three-fold and the biomass two-fold after the flood, compared with reference years. Important key words in this study are; food web, crustaceans, species ecology, stable isotopes and allochthonous input.

Introduction

Zooplankton forms a crucial link in the aquatic food web; energy and matter accumulated through primary production are incorporated into consumers and transmitted to planktivorous fish via zooplankton. While the evidence for terrestrial contributions to the nutrient and carbon cycles of lakes have been stressed for many decades (Wetzel 1983), the allochthonous support to zooplankton production has been more ambiguous. However, numerous studies performed before the use of stable isotopes reported the use of detritus in humic lakes where phytoplankton was limited (Hessen et al. 1990, Jones 1992, Hessen 1998). Several recent studies suggest significant terrestrial support to zooplankton (Cole et al. 2011; and ref. herein) but this interpretation is debatable for several reasons (e.g. Brett et al. 2017) and it is hard to quantify gut content in zooplankton (e.g. Fryer 1957, Rautio & Vincent 2007). Further, it is problematic to measure the isotopic signature of phytoplankton (e.g. Taipale et al. 2016) and especially for carbon; phytoplankton isotopic footprint can be similar to terrestrial organic matter (France 1997). Stable isotopes are often used to identify pathways of organic matter through food webs (e.g. Matthews & Mazumder 2007, Francis et al. 2011, Piscia et al. 2018). The basic theory is that the isotope ratio of a consumer depends on its diet measured by the ratios of the stable isotopes of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$). Stable carbon isotope ratio reflects the input of carbon revealing the contributions of different food sources, and nitrogen isotope ratio indicates the trophic role of the organisms (e.g. Post 2002, Layman et al. 2012).

In the present study the crustacean zooplankton of the subalpine Lake Savalen has been studied with respect to trophic structure and food items origin, with special reference to the influence of terrestrial allochthonous input. This lake is a typical Norwegian lake similar to a number of lakes in that region as dimictic, oligotrophic with medium fish predation (Løvik & Kjellberg 1982, Halvorsen et al. 2004), and likely to be translated to many related ecosystems. Stable isotope analyses on selected zooplankton species form the first of such detailed studies in Norway, and the aim of the present study is the following:

1. Analyses of the ratios of stable isotopes of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) in sorted out zooplankton. The selected species are typical filter feeder (*Daphnia galeata*), typical predator cladoceran (*Bythotrephes longimanus*), carnivorous/omnivorous copepod seizer (*Heterocope saliens*) and omnivorous filter-feeder copepod (*Arctodiaptomus laticeps*);
2. These results will be compared with a large compilation of equivalent data from similar species in the food chain and other ecosystems in Europe;
3. The origin of pelagic carbon is analysed and compared with the particularly well studied neighbouring Lake Atnsjø with the same zooplankton community to further understand the importance of allochthonous support to zooplankton production.

Site description – Lake Savalen

Lake Savalen is a subalpine, oligotrophic, dimictic and regulated lake situated in Norway, north Europe (Figure 1). It is located between 703-708 meters above sea level in the central part of Norway with geographical position lat. 62°15'N and long. 10°15'E.

Morphometry, catchment area and regulation history

Lake Savalen (Figure 1) is one of the lakes in Glomma's catchment area (Norway's largest river system) and has been regulated with a surface area after 1976 of 10.9 and 15.2 km^2 at lowest and highest water level, respectively. Lake Savalen was first regulated in 1924 with approximately 0.5 meters, and consequently the small dam in the outlet probably led to a largely reduced population of spawning trout. The regulation in 1976 also involved a transfer of water from the Einunna watercourse via a tunnel. Although the largest registered depth is 62 meters, large parts of Lake Savalen are relatively shallow (Figure 1). The interface between the catchment area, the littoral and the pelagic region in Lake Savalen is therefore considerable, and the west side consist of a large marsh area composed of so-called rich bog structure (Figure 1). The bedrock structure in the catchment area of Lake Savalen is dominated by phyllite, mica shale and amphibolites. Lake Savalen is located within the subalpine vegetation province in central Norway. About 80 percent of the catchment area is below the forest boundary.

Lake Savalen is situated in a region with typical continental climate; the precipitation is low and around 400 mm annually, highest during summer and small during winter. The area is covered with snow from November to the beginning of May. Even if the total precipitation is low in this region, strong spring spates with extensive terrestrial inputs are occasionally observed, such as in the neighbouring Lake Atnsjø during the aberrant year of 1995 (Brabrand 1998).

General limnology, biotic and trophic structure

The subalpine Lake Savalen has a maximum depth of 62 m, mean depth 17 m (Figure 1) and is ice-covered from November to June. The lake was in 2019 vertically increasingly stratified until August with surface and hypolimnion temperature of 14,4 and 5-6°C, respectively (Johnsen et al. 2021), and the surface temperature was close to 15-16°C as in 1977 (Nicholls 1980). The lake water shows low nutrient levels, the present epilimnion pH is about 7.7 and the conductivity about 54 µS cm^{-1} (Table 1). Primary productivity was approximately 22 g C m^{-2} year^{-1} (Nicholls 1980, 1981), which indicates the oligotrophic level of the lake. Secchi depths were 7,2 and 9,6 m in June and August 2019, respectively, and varies depending on the influence of allochthonous matter from the catchment and the littoral region. Leaching from the littoral region, as well as the transfer of water from Einunna watercourse,

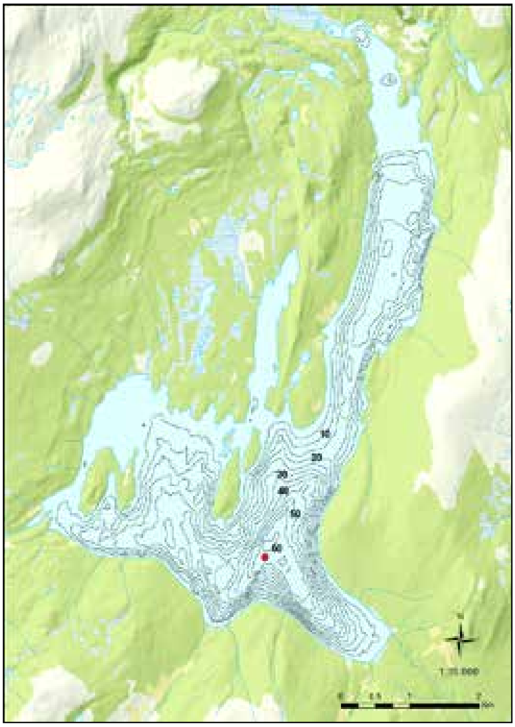

Figure 1. Lake Savalen bathymetry with depth levels in 5 m intervals. The surrounding watershed; Green: vegetation, light blue shaded: marsh areas and white: above forest border. Red dot: sampling point.

Table 1. Water chemical parameters analysed in Lake Savalen, this study and earlier investigations (see references): Alk-alkalinity, Cond-conductivity and Turb-turbidity.

Param./ Year	pH	Alk.	Cond. (25 °C)	Turb.	Colour	Ca^{2+}	NO_3-N	PO_4^{3-}	References
Unit		µekv L^{-1}	µS cm^{-1}	FNU	mgPt L^{-1}	mg L^{-1}	µgN L^{-1}	µgP L^{-1}	
1974	7,45		54,5	0,44	27		20	<2	(Källqvist 1974)
1977	7,57	410	49,9	0,53		8,8	16	2,1	(Nicholls 1980) Epi.
1977	7,08	410	50,0	0,28		9,5	57	2,1	(Nicholls 1980) Hypo.
1992	7,46	403	50,2		10	7,7	38		(Rognerud 1992)
2012	7,6	418		0,51	11	7,8			(Løvik et al. 2013)
2019	7,7		58,9	0,47					This study, Epi.
2019	6,8		59,8	0,54					This study, Hypo.
Average	7,38	410,3	53,8	0,46	16	8,5	33	2	

significantly increased water colour and decreased Secchi depth in the period following the main regulation in 1971 (Nicholls 1980). This effect gradually diminished, and already in 1987 water quality was characterized with a high pH and greatly increased Secchi depth (Rognerud 1992).

Nine lakes in the Glomma watershed were sampled in 1978-1980 (Løvik & Kjellberg 1982). Most lakes were oligotrophic and harboured almost similar zooplankton communities as Lake Savalen, especially lakes situated in the upper part of this watershed, such as Lake Atnsjø. Lake Savalen has a considerable stock of Arctic charr (*Salvelinus alpinus*), but also brown trout (*Salmo trutta*) has increased after Savalen's regulation negatively affecting these species (Borgstrøm 1974, Enerud 1981, Hansen & Stubsjøen 1984). However, both charr and trout populations have been reduced by heavy fishing, which has led to increasing growth for both species. Arctic charr earlier spawned inside the lake, i.e. around Skolholmen in the south-west end. These shallow areas are now excluded as a spawning ground due to the regulated low winter water levels. Such drying out also leads to depletion in the regulation zone, so that benthic-eating fish have reduced access to food items. Both the Arctic charr and brown trout are heavily exploited with ice fishing and bottom seine fishing.

Material and Methods

The qualitative sampling of zooplankton in 2010 and 2019 was performed with a plankton net (Ø: 25 cm and mesh size 90 µm). In both periods, vertical net hauls were taken from 40 meters (bottom), 20 meters and 10 meters up to the surface, respectively. Copepods were further subdivided to main groups of life stages (nauplii, copepodids and adults). Cladocera were determined to species with or without eggs. A representative number of individuals were counted from the entire sample by removing approximately 1/10 (subsample), giving an estimated number of copepods and cladocerans in the pelagic for the entire sample (Figures 3 and 4).

On 27 August 2019, separate samples of zooplankton net hauls were collected in the open water masses for stable isotope analyses (SIA), collected with the same methods as above. These samples were immediately added distilled water after collection to prevent more food uptake and to release intestinal contents and placed in a cooling bag. On the same day, all samples were stored at -20 °C. Later, some frozen samples were thawed to select the required biomass of individual zooplankton species and "Zooplankton mix" (Figure 5), and then stored again at -20 °C until preparation for SIA. The SIA were conducted using a Flash EA 1112 Series Elemental Analyzer connected to a Thermo Finnigan Delta-Plus Advantage mass spectrometry. Analytical precisions (SD) were ≤0.15 ‰ and ≤0.20 ‰ for $\delta^{13}C$ and $\delta^{15}N$ respectively.

Results and Discussion

Zooplankton species and community structure

The species observed in Lake Savalen were based on 2010 and 2019 samplings (Johnsen et al. 2011, Johnsen et al. 2021) and presented in Table 2 related to taxonomical subdivision and as percentage distribution (Figures 3 and 4). Copepods dominated compared to cladocerans both during June and August 2010 and 2019, and this trend was most noticeable during August both years. However, the differences between the depth layers are even greater than apparent (Figures 3 and 4), as samples from greater depths also contain individuals from the above water layers.

Rotifers

During the last decade rotifer community in Lake Savalen was dominated by *Kellicottia longispina*, *Conochilus unicornis* and *Polyarthra* spp., while *Keratella hiemalis* and *Keratella cochlearis* showed medium appearance. *Collotheca* spp. and *Synchaeta* spp. occurred less abundantly, while *Asplanchna priodonta* was rare (Table 2). The registered rotifers are divided into suspension feeders (*Keratella* spp., *K. longispina*, *Conochilus* spp.), graspers or specialised feeders (*Polyarthra* spp., *Synchaeta* spp., *Ascomorpha* spp., *Collotheca* spp., and carnivorous/-omnivorous species (*A. priodonta*).

Crustaceans

The crustaceans in Lake Savalen during the last decade were dominated by *C. scutifer*, *B. longispina*, *D. galeata* and *A. laticeps. Holopedium gibberum*, *H. saliens* and *Mesocyclops leuckarti* showed medium to low densities, while *Bythotrephes longimanus*, *Sida crystallina and Acanthodiaptomus denticornis* were rare (Table 2). The low densities of *B. longimanus* and *H. saliens* were probably caused by predation from fish, while the typical low-land copepod *M. leuckarti* (Nilssen 1976) was scarce in this subalpine lake.

Cyclops scutifer was the dominant copepod in Lake Savalen (Figure 3), as in the nearby located Lake Atnsjø (Halvorsen et al. 2004). The prevailing life cycle stage of cyclopoid copepods was nauplii of *C. scutifer* in all samples, with the

Table 2. The registered metazoan species observed in the pelagial of Lake Savalen, average based on 2010 and 2019. Relative species abundance within each group of animals is indicated as: XXX = dominating, XX = frequent, X = few specimens and R = rare

Rotifera		**Cladocera:**	
Kellicottia longispina (Kellicott, 1879)	XXX	*Bosmina longispina* Leydig, 1860	XX
Conochilus unicornis Rousselet, 1892	XXX	*Daphnia galeata* G. O. Sars, 1863	XX
Polyarthra spp. Ehrenberg, 1834	XXX	*Holopedium gibberum* Zaddach, 1855	X
Keratella hiemalis (Carlin, 1943)	XX	*Bythotrephes longimanus* Leydig, 1860	R
Keratella cochlearis (Gosse, 1851)	XX	*Sida crystallina* (O. F. Müller, 1776)	R
Collotheca spp. Harring, 1913	X		
Synchaeta spp. Ehrenberg, 1832	X		
Asplanchna priodonta Gosse, 1850	R	**Copepoda:**	
		Arctodiaptomus laticeps (G. O. Sars, 1863)	XX
Fish:		*Acanthodiaptomus denticornis* (Wierzejski, 1887)	R
Salvelinus alpinus (Linnaeus, 1758)	XXX	*Heterocope saliens* (Lilljeborg, 1863)	X
Salmo trutta Linnaeus, 1758	XX	*Cyclops scutifer* G. O. Sars, 1863	XXX
Phoxinus phoxinus (Linnaeus, 1758)	X	*Mesocyclops leuckarti* (Claus, 1857)	X

exception of the upper 20 m in June 2010. On the latter sampling date, and around the same period in 2019, *C. scutifer* had high occurrence of copepodids at all depths and some adults. This was probably because of the yearly life cycle of this species, similar to Lake Atnsjø (cf. Halvorsen et al. 2004). *Mesocyclops leuckarti* had very small numbers and based on this and the large occurrence of especially copepodids of *C. scutifer*, most nauplii in Figure 3 probably belonged to the latter species.

The calanoid copepod *H. saliens* (adults only) and *A. laticeps* (all stages) generally accounted for a small percentage of the total, with decreasing amounts towards deeper waters (Figure 3). *Arctodiaptomus laticeps* had the largest occurrence of calanoids in June 2010, with almost 50 percent of the total copepods in the upper 10 m of the water column, and with a decreasing trend towards the bottom, to approximately 30 percent. On the other test dates and depths, *A. laticeps* accounted for less than around 10 percent. *Heterocope saliens* was absent in June both years with a small occurrence in August 2010

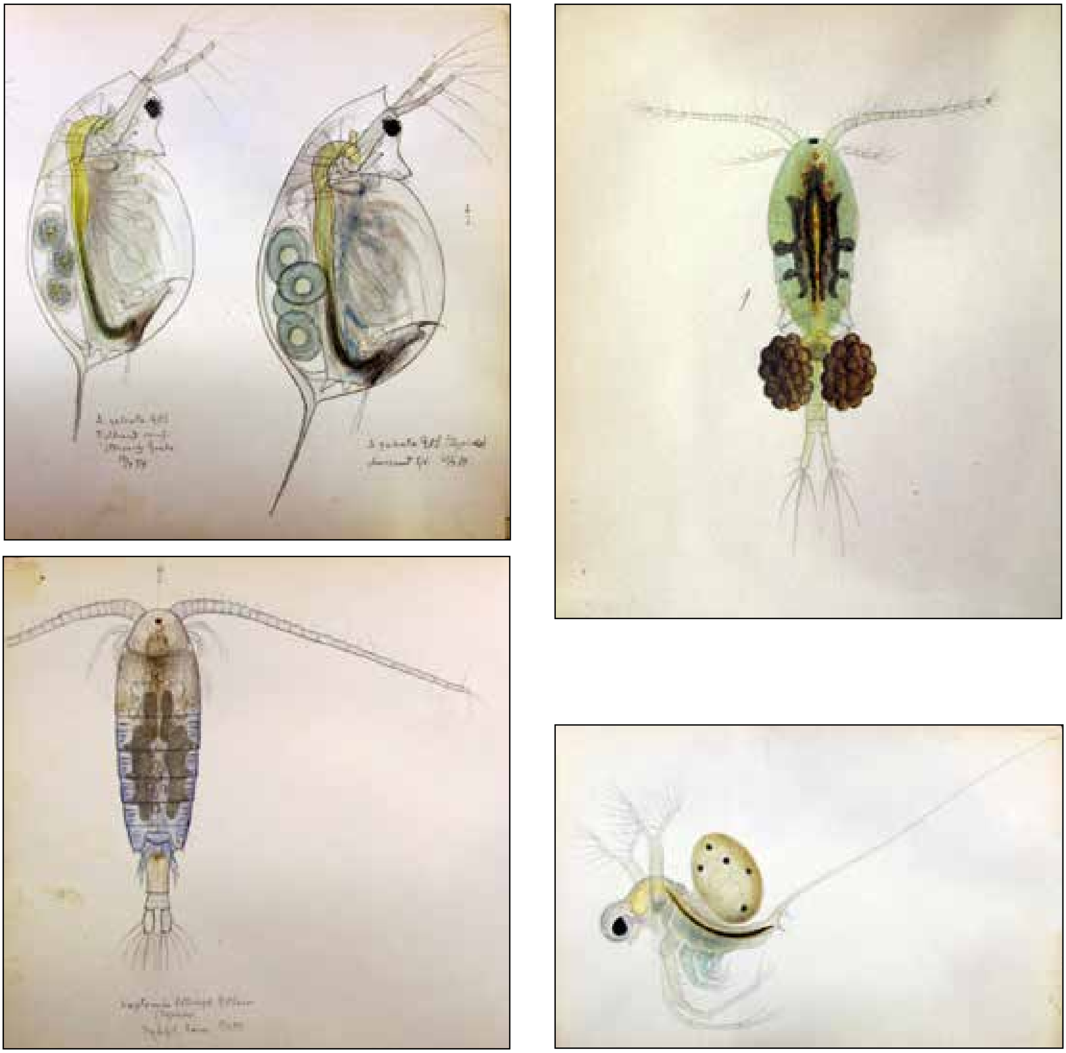

Figure 2. Some registered zooplankton species observed in the pelagial of Lake Savalen; top left Daphnia galeata, top right Cyclops scutifer, bottom left Arctodiaptomus laticeps and bottom right Bythotrephes longimanus (illustrations by Georg Ossian Sars, Manuscript Dept., National Library of Norway, Oslo).

and 2019, about 1-2 and 0.5-1 percent, respectively.

The absolutely dominant cladoceran during June both years was *B. longispina* (Figure 4). *Holopedium gibberum* was an early summer (Figure 4) species (cf. Løvik & Kjellberg 1982), as in Lake Atnsjø (Halvorsen et al. 2004). *Daphnia galeata* was dominant during August the two years (Figure 4). The populations of some crustacean plankton, especially *D. galeata* and *B. longimanus* build up over the summer and in addition became more important food for the Arctic charr over the summer and autumn (Johnsen et al. 2021). However, both the littoral *S. crystallina* and the pelagic *B. longimanus* had very low occurrences in Lake Savalen (Figure 4).

Bosmina longispina dominated in most depths during June 2010 and 2019, with increasing densities towards the bottom; the only exception being the net haul from 10 m in 2010 where *H. gibberum* had its largest occurrence with around 35 percent (Figure 4). In June both years *H. gibberum* appeared with an incidence below 15 percent, but the species was not found in any depth in August either year, probably because of its life cycle (cf. Halvorsen et al. 2004). *Bosmina longispina* had far smaller occurrences in August both years, with the exception of net haul from 40 m in 2019 where it occurred in almost the same amount as *D. galeata*. The latter species dominated totally in August both years with high abundances of females both with and without eggs, with a total of approximately 80-95 percent of the total cladocerans (Figure 4).

The body size of *D. galeata* was large (on average 1.8 mm and 2.3 mm in June and August, respectively) in relation to the substantial amount of Arctic charr in the lake (Johnsen et al. 2021), and the reason for this partly unexpected observation is treated later in this chapter. In August, there were generally far more females with eggs than in June (with a greater amount of juveniles), which contributed to larger individuals in August. The average length of the other zooplankton species in August 2019 was *B. longimanus* 3.4 mm (without spine) and adult calanoid copepods (without setae) as a mixture of both sexes were for *H. saliens* 2.7 mm and *A. laticeps* 1.72 mm.

Zooplankton food spectra and trophic role

The most common pelagic cladocerans in Lake Savalen have slightly different feeding niches: *H. gibberum* filters large particles, *D. galeata* smaller and medium particles, and *B. longispina* medium-sized to a variety of particles (Geller & Mueller 1981, Hessen 1985), while the less common *B. longimanus* is primarily carnivorous (e.g. Monakov 1972).

The copepods (both cyclopoid and calanoid) can change their feeding mode several times in an annual period when developing through the different ontogenetic stages and can exhibit more than one feeding mode annually (e.g. Fryer 1957). *Cyclops scutifer* was the only invertebrate predator occurring in high densities. *Cyclops scutifer* showed spatial and temporal overlap with many other species because it is distributed in the lower water masses during the ice-free period and also found in the plankton throughout the year (cf. Halvorsen et al. 2004). During summer it overlapped with many rotifers, cladocerans and other copepods. *Cyclops scutifer* is essentially omnivorous and can use algal, detritus, and animal food (Monakov 1972, 1976) and is able to survive, grow and reproduce utilising allochthonous material (Taube & Nauwereck 1967). The most important food items for cyclopoid copepods such as *Cyclops* and *Mesocyclops* are rotifers and cladocerans, especially younger stages (Monakov & Sorokin 1959). Usually, smaller-sized cyclopoid species are less carnivorous than larger ones, but the minor species *M. leuckarti* seems to be an exception to this rule by being more carnivorous than expected solely based on its body size (Hopp et al. 1997).

The calanoid predator and omnivorous species, the plankton-littoral *H. saliens*, was very uncommon in the lake because of the lakes' morphometry and fish predation. The other omnivorous calanoid species *A. laticeps* was common in Lake Savalen. Food collection of omnivorous calanoid copepods such as

Arctodiaptomus (and *Acanthodiaptomus*) is very broad and they can both catch single food items and filter the water (Lair & Hilal 1992). Filter feeding calanoids can therefore utilise both algal, bacteria, and animal food – especially ciliates (Lair & Hilal 1992). Many calanoid copepods also have the ability to withstand starvation during longer periods, in contrast to its cladoceran competitors.

Lake Atnsjø (701 m a.s.l.), the neighbouring lake to Lake Savalen and located in the same vegetation region, harbours nearly identical zooplankton species (Løvik & Kjellberg 1982, Dervo et al. 1991, Halvorsen et al. 2004). In contrast to Lake Savalen it has been studied in detail for a very long period of time, from 1985 to 1997 (Hegge et al. 1989, Dervo et al. 1991, Halvorsen et al. 2004), so significant parts of their observations may elucidate the zooplankton ecology of Lake Savalen (cf. Løvik & Kjellberg 1982, and the present study).

Among the crustaceans in Lake Atnsjø *C. scutifer* and *B. longispina* dominated, *H. gibberum*, *Daphnia longispina* and *A. laticeps* were less common, while *B. longimanus*, *Polyphemus pediculus* and *H. saliens* occurred in low numbers. Comparable to Lake Savalen, *C. scutifer* was most important in spring when the overall density of crustaceans was low, and in autumn when the new generation of nauplii was present. The relative abundance of *C. scutifer* in Lake Atnsjø was lowest in July before the new generation of nauplii appeared. *Heterocope saliens* had a one-year life cycle, whereas *C. scutifer* had predominantly a combined one and two year cycle and *A. laticeps* a one year cycle with a possibility of two generations a year (Halvorsen et al. 2004). *Bosmina longispina* dominated the cladoceran zooplankton in Lake Atnsjø (Halvorsen et al. 2004), while *D. longispina* occurred in low numbers, and usually constituted only a small fraction of the crustacean community. *Holopedium gibberum* was a typical summer species, being most common in June and July, as in Lake Savalen. It disappeared quite early in autumn and survived the winter as resting eggs (Halvorsen et al. 2004). The number of zooplankton species found in Lakes Savalen and Atnsjø was similar to what is found in comparable Norwegian lakes (Løvik & Kjellberg 1982), and was also similar to cold oligotrophic lakes in other areas (Patalas 1971). Among the crustaceans, two dominating species of copepods and three species of cladocerans are common over large areas (Patalas 1971).

The basic scientific theory behind the stable isotope ratio of a consumer, carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$), reflects the input of carbon revealing the contributions of different food sources, and nitrogen isotope indicates the trophic role of the organisms (e.g. Post 2002, Layman et al. 2012). However, although often considered a homogeneous compartment, zooplankton is composed of organisms that differ substantially from each other not only in their taxonomy, but also in metabolic rate, body size and ecological roles (e.g. Monakov 1972). Correct identification of species, including zooplankton, is therefore crucial in ecological studies, since all species inhabit definite niches (e.g. Makarewicz & Likens 1975, Lane et al. 1978, Makarewicz & Likens 1978).

The most significant differences were found between the zooplankton species in the $\delta^{15}N$-values (cf. Figure 5), showing their belonging to different trophic levels from more or less carnivorous (*B. longimanus*) to *primarily* herbivorous (*D. galeata*). The highest stable isotope measurements of zooplankton with $\delta^{15}N$-values above 6 ‰ in Lake Savalen (Figure 5) were found in the typical carnivorous cladoceran species *B. longimanus* (e.g. Monakov 1972, Nilssen 1976) with a broad nutrition spectre primarily consuming copepods, cladocerans and rotifers (Grigorovich et al. 1998). *B. longimanus* has been found to have its optimal habitats in central deep-water areas in large lakes in the highlands of the temperate zone (Grigorovich et al. 1998), a description that coincides well with Lake Savalen. The breadth of fish predation on *B. longimanus* is thoroughly summarized by Grigorovich et al. (1998), and specifically from brown trout and Arctic charr which are both found in Lake Savalen are also described from

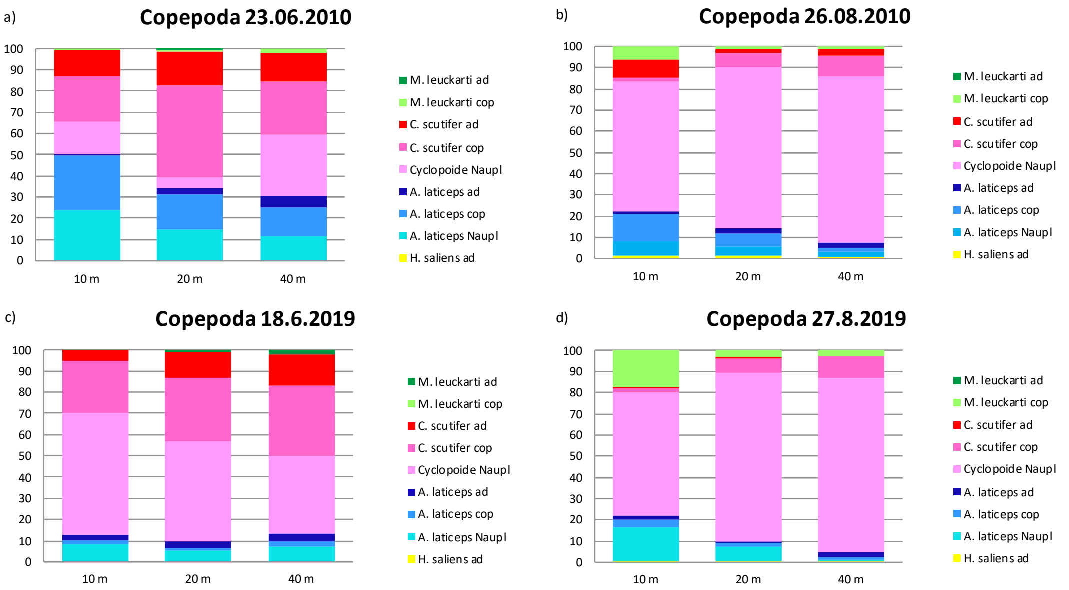

Figure 3. Percentage distribution of copepods (nauplii, copepodids, adults) in samples from 10, 20 and 40 m to surface vertical net hauls in Savalen in 2010 and 2019.

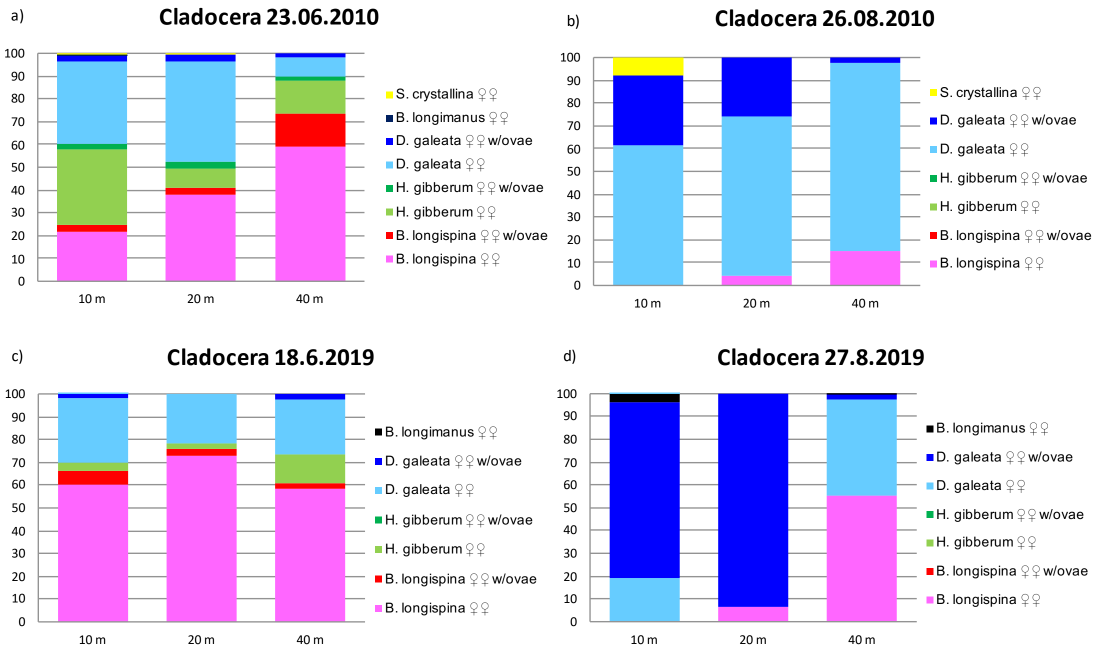

Figure 4. Percentage distribution of cladocerans (female with/without ovae) in samples from 10, 20 and 40 m to surface vertical net hauls in Savalen in 2010 and 2019.

i.e. Northern Sweden (Nilsson & Pejler 1973). Since a lot of *B. longimanus* was found in stomach samples, primarily from charr (Johnsen et al. 2021), it shows that the population has good growth and production. However, since there is very little of the species in all pelagic samplings, this indicates that the predation pressure on the species was significant.

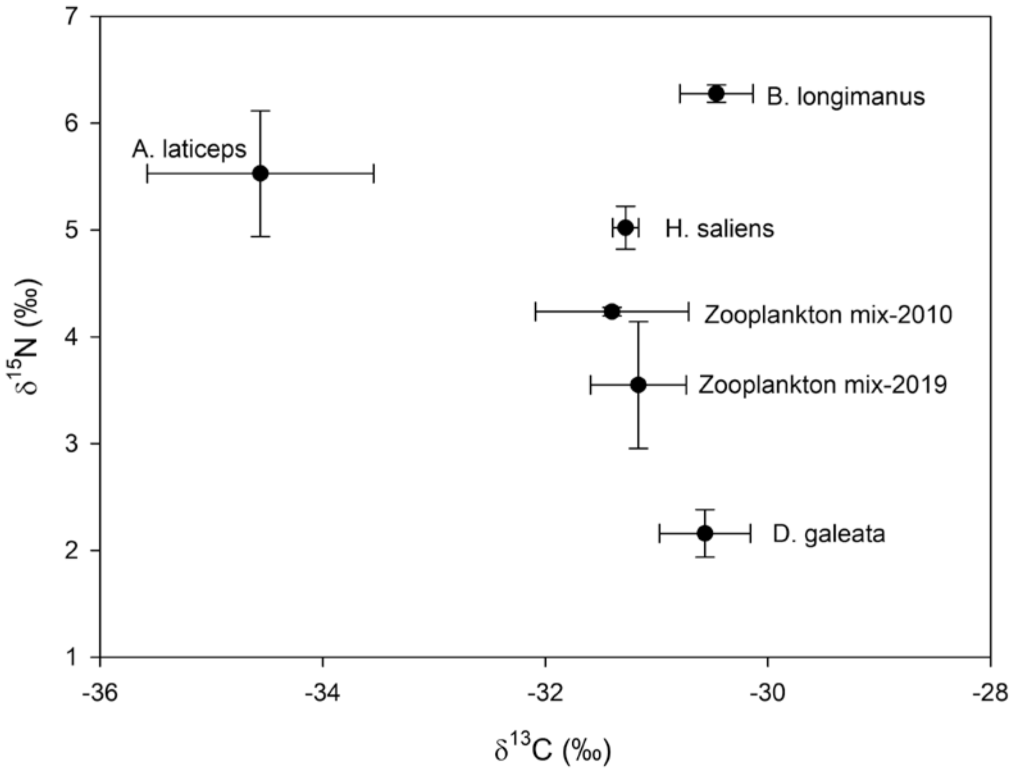

Figure 5. Stable isotopes $\delta^{15}N$ *and* $\delta^{13}C$ *as* $^{0}/_{00}$ *in the zooplankton of Lake Savalen (species names in Table 2). "Zooplankton mix" are based on vertical plankton net hauls.*

Arctodiaptomus laticeps and *H. saliens* also have clear carnivorous markings with $\delta^{15}N$ values between 5 and 6 ‰. This is measured only on adult individuals of these species, so the average for all their life stages will be somewhat lower as the degree of omnivorous nutrition increases downwards in these stages from copepods to their nauplii. *Arctodiaptomus laticeps* is a macro-filtrator while *H. saliens* is an omnivore and seizer (Monakov 1972), and both can thereby filter single-celled animals just like algae and thereby come out with somewhat unexpectedly high $\delta^{15}N$ values. Somewhat higher $\delta^{15}N$ values are expected at these more carnivorous adult stages of these species than their smaller copepods, but other studies have also shown that calanoid copepods feed on more animal food as omnivores than previously suggested (Lair & Hilal 1992).

With $\delta^{15}N$ values just above 2 ‰, it is suggested that the primary food choice of the unselective filtrator *D. galeata* is autochthonous algae, bacteria and small amounts of protists. We also assume that *B. longispina* has similar $\delta^{15}N$ level to *D. galeata* since vertical net hauls ('Zooplankton mix') in August 2010 and 2019 were so closely situated (Figure 5), and since these two species make up the bulk of the zooplankton together with cyclopoid nauplii. Fish predation on zooplankton was mainly restricted to large-sized cladocerans, such as *B. longimanus*, and to a lesser extent *D. galeata*, *B. longispina* and other zooplankton (Borgstrøm 1974, Johnsen et al. 2011, Johnsen et al. 2021). Fish at higher trophic levels often target the predatory zooplankton species due to their larger size and conspicuous nature, e.g. Arctic charr (*Salvelinus alpinus*) select *B. longimanus* from the plankton of many lakes during the summer, despite the very low contribution this zooplankter makes to community biomass.

The registered amounts of zooplankton in Lake Savalen can be interpreted in relation to the size and nutrition of the fish populations (cf. Johnsen et al. 2021). Only in August 2010 and 2019 was zooplankton found in the brown trout's diet, where *B. longimanus* accounted for close to 20 percent in both years, *B. longispina* accounted for only 0.1 and 1.8 percent, respectively. Overall, brown trout exerted low predation pressure on the zooplankton compared to Arctic charr, and especially on populations in the pelagic area that are dominated by charr. Of the charr's share of the diet caught at the top of the pelagic in June 2019, *B. longispina* accounted for 36.7 percent, and close to zero throughout 2010. In June 2019, *B. longimanus* and *D. galeata* accounted for only 10.8 and 4.2 percent of the diet, respectively, while in August 2019 *D. galeata* accounted for a very small share in contrast to 2010. In August 2019, *B. longimanus* accounted for as much as 82.3 percent in charr taken between 15-21 m depth and about 20 percent in the charr sampled in the deep profundal.

For small charr, the $\delta^{15}N$ signature showed that they had taken most of their nutrients from the zooplankton, and the stomach analyzes showed that these were mostly *D. galeata* and *B. longimanus* (Johnsen et al. 2021). Larger charr had a higher $\delta^{15}N$ signature, suggesting that the plankton predator *B. longimanus* were very important in the diet. Changes in the trout and charr diet from 2010 to 2019 are confirmed by $\delta^{13}C$ and $\delta^{15}N$ values (Johnsen et al. 2021). High $\delta^{13}C$ value shows a diet consisting mainly of benthic animals or fish from the littoral zone, while low $\delta^{13}C$ value shows a diet dominated by pelagic zooplankton, benthic animals from deep water (profundal) and/or small plankton-eating fish (Johnsen et al. 2021).

Zooplankton in food webs – trophic structure and terrestrial influences

Table 3 shows data for $\delta^{13}C$ and $\delta^{15}N$ from a number of localities, species and to different seasons. As demonstrated in the table, the stable isotopes both within $\delta^{13}C$ and $\delta^{15}N$ differ considerably between different lake ecosystems, but some logical patterns persist, and these data will be compared with species and functional groups of zooplankton in Lake Savalen. The isotope ratio of a consumer concludes that the ratio of the stable carbon ($\delta^{13}C$) isotope reflects the input of carbon displaying the contributions from different food sources (allochtonous and autochtonous), whereas the nitrogen isotope $\delta^{15}N$ define or indicates the trophic role of the organisms.

The highest stable isotope measurements of zooplankton with $\delta^{15}N$-values usually above 6 ‰ were generally measured within the pure predatory cladocerans *Bythotrephes* and *Leptodora* (Table 3). The omnivorous copepods both within calanoides and cyclopoids usually have clear carnivorous markings with $\delta^{15}N$ values between 5 and 6 ‰. However, it should be noted that the cyclopoid copepods may have as high $\delta^{15}N$ values as the predatory cladocerans, whereas calanoid copepods usually have lower values (Table 3). The pure filter-feeders (*Daphnia*, *Bosmina*, *Holopedium*) confirm their place as the first consumers, with $\delta^{15}N$ values just above 2 ‰. When $\delta^{15}N$ values of this functional group are higher (consult Table 3), it implies that these unselective filtrators also consumes protists, which are often animals. The aggregation samples ('Zooplankton mix') are often mainly composed by filtrators which characterize their frequent lower $\delta^{15}N$ values.

In contrast to the trophic parameter $\delta^{15}N$, carbon ($\delta^{13}C$) isotopes vary widely, which is naturally taken into account the variation in ecosystems, seasons and species (Table 3). The omnivorous *A. laticeps* in Lake Savalen is characteristic by consuming substantial amounts of autochthonous material in this lake, while most of the other omnivorous copepods (both calanoids and cyclopoids) use carbon that is substantially derived from the littoral zone or the watershed (Table 3). Further, in Lake Savalen, the carbon ($\delta^{13}C$) isotopes are situated close together (for *Daphnia* and *Bythotrephes*), which indicate that they form part of the same food chain.

In a detailed study Piscia et al. (2018) found that carbon and nitrogen isotopic signatures differed among five north Italian lakes, reflecting depth, morphometry and trophic status of the lakes (Table 3). These observations implicate that zooplankton taxa specific trophic roles differ among lakes and in time (Piscia et al. 2018), and consequently showed seasonal changes of the stable isotopes as expected (Grey et al. 2000, Visconti & Manca 2011, Leoni 2017, Piscia et al. 2018, Visconti et al. 2018, Piscia et al. 2019). Furthermore, Cole et al. (2011) found that zooplankton (*Holopedium*, *Daphnia* and a diatomid species) were comprised of 20-40 percent of organic material of terrestrial origin. Calanoid copepods are found to consume small zooplankton, heterotrophic protists such as ciliates, phytoplankton and detritus (e.g. Lair & Hilal 1992, Cole et al. 2011).

The determination of the actual food-web structure based on visual observation is difficult and is shown to vary greatly between lakes. Kling et al. (1992) found by studying δ^{15}N-values that e.g. the omnivorous copepod *Heterocope septentrionalis* often was functioning as an herbivore when the other calanoid *Diaptomus pribilofensis* was absent, rather than expected as a predator or partly omnivorous species (Monakov 1972, Kling et al. 1992). So, based on isotope δ^{15}N analyses more detailed and exact food-web structure may be revealed, as well as 'potential' vs. 'realized' trophic structure in the planktonic community (Kling et al. 1992). Finally, *D. pribilofensis* was also found to be more herbivorous than omnivorous than traditionally expected (Kling et al. 1992). The actual zooplankton food-web structure varies greatly between lakes, even in lakes which are relatively similar and containing almost the same species strengthen the idea that studying δ^{15}N-values will add new dimension to food-web structure understanding (Pimm et al. 1991, Kling et al. 1992).

The degree of carnivory for e.g. *B. longimanus* and *L. kindtii* based on δ^{15}N-values may vary between lakes. In Lake Iseo, Leoni (2017) found twice higher δ^{15}N-values. In the latter study it was also found double δ^{15}N-values for the filtrator *D. longispina*, indicating a considerable higher intake of animal protists than found in the similar species *D. galeata* in Lake Savalen. Zooplankton is normally considered on the lowest animal trophical level as also stated by our findings of δ^{15}N-values. Our 'Zooplankton mix' (Figure 5) gave total δ^{15}N-values of approximately 4‰, which is an average of other surveys (Cabana & Rasmussen 1994).

The level of δ^{13}C-isotopic signatures for all zooplankton species found in Lake Savalen during autumn 2019 were very close to -32.0‰ (±1.86 SD). This is an indication of the importance of autochthonous pelagic food during this autumn in this lake, similar to findings in the Italian Lake Iseo (Leoni 2017). This may have its origin primarily from algae, bacteria and/or small animals produced in the lake. However, the overall carbon isotope signatures in Lake Savalen indicate that terrestrial influence is considerable also in Lake Savalen (Johnsen et al. 2021). This confirms that the investigated zooplankton species consume primarily its carbon both from autochthonous and allochthonous food materials, which may have its origin from algae, bacteria and/or small animals produced in the lake and the littoral zone (Johnsen et al. 2021); consult the findings related to the major spring flood in Lake Atnsjø in 1995, see below.

Also concerning the case of eventual influence of allochthonous organic matter (with the proxy of δ^{13}C-isotopic signature), it is instructive to consider the long-term studies in the closely located Lake Atnsjø. The zooplankton in Lake Atnsjø was claimed to depend to a great extent on allochthonous material as the food resource, as the production of phytoplankton probably did not sustain the production of zooplankton (Dervo 1988). The phytoplankton biomass in Lake Atnsjø was very low, normally less than 0.40 $mm^3\ L^{-1}$ (≈0.40 $mg\ C\ L^{-1}$) (Dervo 1988). In Lake Atnsjø the mean food concentration constituted by algae in the epilimnion is usually lower, but near the surface it may be as high as 0.17 $mg\ C\ L^{-1}$ (Dervo 1988).

Even if the annual precipitation is low in the region where Lakes Savalen and Atnsjø is situated, some years may exhibit extreme spring

Table 3. Data for $\delta^{13}C$ and $\delta^{15}N$ given as promille (${}^{0}/_{00}$) from this study and a number of localities, species and to different seasons (not all published) from literature. With the same author and different localities some lake names are given.

Species/groups	Season collected	$\delta^{13}C$	$\delta^{15}N$	Author
Bythotrepes longimanus	Autumn	-30,46	6,28	This study
Bythotrepes longimanus	Summer	-27,6	10,14	(Leoni 2017)
Bythotrepes longimanus	Autumn	-30,9	11,3	(Leoni 2017)
Bythotrepes longimanus	Summer (L. Mergozzo)	-24,6	3,4	(Piscia et al. 2018)
Bythotrepes longimanus	Autumn	-24,2	7,7	(Visconti et al. 2018)
Bythotrepes longimanus	(Loch Ness)	-27,9		(Grey & Jones 1999)
Leptodora kindtii	Spring	-33,32	5,76	(Leoni 2017)
Leptodora kindtii	Summer	-27,0	9,09	(Leoni 2017)
Leptodora kindtii	Autumn	-32,0	11,3	(Leoni 2017)
Leptodora kindtii	Autumn	-24,1	6,0	(Visconti et al. 2018)
Leptodora kindtii	(Loch Ness)	-27,7		(Grey & Jones 1999)
Daphnia galeata	Autumn	-30,56	2,16	This study
Daphnia galeata	(Loch Ness)	-30,2		(Grey & Jones 1999)
Daphnia longispina	Autumn	-27,7	0,6	(Sandlund et al. 2013)
*Daphnia spp.**	Spring	-33,95	5,76	(Leoni 2017)
*Daphnia spp.**	Summer	-28,51	3,6	(Leoni 2017)
*Daphnia spp.**	Autumn	-31,81	5,9	(Leoni 2017)
Daphnia sp. (cucullata?)	Summer (Comab)	-28,51	3,6	(Piscia et al. 2018)
Daphnia longispina galeata	Autumn	-26,2	3,5	(Visconti et al. 2018)
Daphnia rosea and D. pulex	(L. Paul)	-33,8	1,0	(Cole et al. 2011)
Eubosmina longicornis	Spring	-34,6	3,34	(Leoni 2017)
Eubosmina longicornis	Summer	-28,51	3,6	(Leoni 2017)
Eubosmina longicornis	Autumn	-31,81	5,9	(Leoni 2017)
Holopedium gibberum	(L. Paul)	-32,8	3,1	(Cole et al. 2011)
Holopedium gibberum	(L. Crampton)	-31,8	0,7	(Cole et al. 2011)
Heterocope saliens	Autumn	-31,28	5,02	This study
Heterocope septentrionalis	Autumn (L. Itigak)	-26,5	6,1	(Kling et al. 1992)
Heterocope septentrionalis	Autumn (Lake N-1)	-33,4	8,1	(Kling et al. 1992)
Arctodiaptomus laticeps	Autumn	-34,56	5,53	This study
Eudiaptomus gracilis	(Loch Ness)	-29,2		(Grey & Jones 1999)
Diaptomus pribilofensis	Autumn (L. Itigak)	-26,4	5,9	(Kling et al. 1992)
Diaptomus pribilofensis	Autumn (Lake N-1)	-33,7	6,3	(Kling et al. 1992)
Copidodiaptomus steueri	Spring	-33,4	7,7	(Leoni 2017)
Cyclops spp.**	Summer	-33,8	10.04	(Leoni 2017)
Cyclops spp.	Summer (L. Mergozzo)	-28,4	7,4	(Piscia et al. 2018)
Cyclops abyssorum	(Loch Ness)	-28,8		(Grey & Jones 1999)
Plankton net haul 2010	Autumn	-30,2	4,23	This study
Plankton net haul 2019	Autumn	-31,16	3,55	This study
Plankton net haul	Autumn (L. Skasen)	-29,1	2,0	(Sandlund et al. 2013)
Plankton net haul	Autumn (L. Maggiore)	-28,8	5,0	(Piscia et al. 2019)
Plankton net haul	(L. Ness)	-28,7		(Grey & Jones 1999)
Plankton net haul	Autumn (L. Ness)	-28,1	9,3	(Grey et al. 2001)
Plankton net haul	1998 (n = 25)	-29,4	5,1	(Francis et al. 2011)
Plankton net haul	2008 (n = 21)	-31,4	5,3	(Francis et al. 2011)

* Daphnia *spp.;* Daphnia longispina-galeata-cucullata *complex.* ** Cyclops *spp.;* Mesocyclops leuckarti, Thermocyclops dybowskii *and* Cyclops abyssorum *(early developmental stages of copepods were not included).*

floods where large amounts of allochthonous material enter the lake ecosystem. This happened in Lake Atnsjø in spring 1995 and was studied in detail afterwards (Brabrand 1998) where the input of allochthonous material overruled all other environmental factors. A short, but very high water flow, where large floodplains were flooded, occurred at the end of May and beginning of June this year, and a large amount of organic and inorganic material was transported into the lake. This large input of allochthonous material, together with a parallel increase in production of phytoplankton and bacteria, resulted in a pronounced increase in zooplankton abundance and production in 1995. Compared with the years before, the density of zooplankton increased nearly three times, and the biomass was nearly doubled. The increase was most pronounced in rotifers, smaller in cladocerans and least in copepods (Halvorsen et al. 2004). The density response of the different zooplankton groups is in accordance with what can be expected knowing the particular life history strategies of these contrasting aquatic animal groups (Allan 1976). The rapidly developing small-clutch rotifers surpass the more slowly developing large-clutch cladocerans in r_{max}. Copepods, with their extended life cycles (cf. Halvorsen et al. 2004) react slower and hence, ranking of three major taxa of freshwater zooplankton with respect to opportunism is: rotifers > cladocerans > copepods (Allan 1976). The flood in 1995 had a restricted long-term influence on lake productivity, however, and already in 1996 and 1997 the standing biomass was only slightly higher than before the flood (Halvorsen et al. 2004).

Zooplankton and fish species community in Lake Savalen and nearby, similar lakes

The structure of the zooplankton community in regular northern lakes is generally heavily influenced by fish (e.g. Nilsson & Pejler 1973). In both Lakes Savalen and Atnsjø three species of fish occur, Arctic charr (*Salvelinus alpinus*), brown trout (*Salmo trutta*) and European minnow (*Phoxinus phoxinus*), where charr especially consumes zooplankton (Dervo et al. 1991, Johnsen et al. 2021). The population of Arctic charr in both lakes was several times higher than the population of brown trout, and the predation on zooplankton considered to be quite high (Saksgård & Hesthagen 2004, Johnsen et al. 2011, Johnsen et al. 2021). Especially larger specimens of cladocerans and copepods, such as *D. longispina*, *D. galeata*, *B. longimanus* and *Heterocope* spp. were eaten, and the low densities of these species suggested to be caused by considerable predation pressure from fish (Dervo 1988, Saksgård & Hesthagen 2004). As populations of crustacean plankton, especially large water flea species such as *B. longimanus* and species within the genus *Daphnia*, build up over the summer, they become more important food for the charr over the summer and autumn (Johnsen et al. 2021). *Bosmina longispina* was in addition an important food item in Lake Atnsjø, especially specimens larger than 0.8 mm (Dervo 1988, Saksgård & Hesthagen 2004). Since *B. longispina* showed an increasing share in Lake Savalen since 2010, and periodically also made up a large proportion of the fish's diet, this may indicate a significant predation pressure from fish. This impression can be reinforced with records of the hyaline species *H. gibberum* and *D. galeata* in significant amounts which may indicate a considerable predation pressure from fish (Nilsson & Pejler 1973), analogous to Lake Savalen. *D. galeata* is among the most hyaline species in this genus and can withstand high predation pressure from fish (Nilsson & Pejler 1973). *C. scutifer*, the most common species, was little affected by fish predation due to its size, behaviour and habitat choice in deep waters during both day and night (Dervo 1988).

As reported earlier, the body size of *D. galeata* was large in relation to the substantial amount of Arctic charr in the lake, and as such suggested a relatively moderate fish predation compared to other lakes, as also suggested by Løvik et al. (2013). Lakes with low predation pressure from fish are often dominated by large *Daphnia*, and *H. saliens* (often at low pH) and *B. longimanus* are relatively common (Nilsson & Pejler 1973). At higher predation pressures in the pelagic zone, *B. longimanus* can be severely grazed (Klemetsen 1967, Grigorovich et al. 1998). Consequently, the data from the above mentioned zooplankton and the fish's nutrition in northern lakes can therefore indicate the entire state from a small to medium-sized Arctic charr stock in Lake Savalen.

The solution to the discrepancy between body-size of the important prey species *D. galeata* and Arctic charr in Lake Savalen probably lies in the competition between Arctic charr and brown trout, which can be considered great in such lakes (cf. Huitfeldt-Kaas 1912, Langeland et al. 1991, Forseth et al. 2003). Since Arctic charr probably are more adapted to finding zooplankton in the dark than trout (L'Abée-Lund et al. 1993, Klemetsen et al. 2003), it is expected that the density of charr would be greatest near the surface, which is not the case in Lake Savalen (Johnsen et al. 2021). The shift to the pelagic habitat for feeding on plankton and surface insects found by many authors was discussed by L'Abée-Lund et al. (1993). They concluded that there is a trade-off between food demand and predator presence in Arctic charr and that the habitat distribution depends on food availability and predation risk, especially from brown trout. In any case, measurements indicate that the charr is pressed into the depths of large trout (Johnsen et al. 2021), and this may explain why the more epilimnetic and hyaline species *D. galeata* may possess such a large body and population size as in Lake Savalen.

Conclusion

The zooplankton taxa in Lake Savalen displayed distinct trophic differences in the $\delta^{15}N$ values. *Daphnia galeata* occupied generally the first consumer level. In contrast, *Arctodiaptomus laticeps*, *Heterocope saliens* and especially *Bythotrephes longimanus* were clear carnivorous zooplankton and occupied roughly the second consumer level, with $\delta^{15}N$ values varying between 4.7–6.3. The $\delta^{13}C$ values (-30 – -34 $^{0}/_{00}$) indicated that all zooplankton taxa in Lake Savalen were mainly pelagic and derived a considerable part of their carbon during autumn from autochonous primary production, but probably also partly from littoral carbon. However, the extreme flood in May/June 1995 demonstrated in a convincing way the importance of allochthonous material for the zooplankton community in the neighbouring Lake Atnsjø, and more generally for similar subalpine lakes with extensive watershed and littoral regions with wetlands. Our results add to the recent analysis of the importance of omnivory in planktonic food webs in lakes (Sprules & Bowerman 1988) and highlight that theories in trophic and species based ecology combined with using stable isotopes can efficiently and in some cases uniquely determine the strength of trophic interactions and thus trace the flow of energy through ecosystems.

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