

# The effects of winter ice cover on the trophic ecology of whitefish (*Coregonus lavaretus* L.) in subarctic lakes

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**Abstract** – Lakes in Arctic and subarctic regions display extreme levels of seasonal variation in light, temperature and ice cover. Comparatively little is known regarding the effects of such seasonal variation on the diet and resource use of fish species inhabiting these systems. Variation in the diet of European whitefish *Coregonus lavaretus* (L.) during periods of ice cover in this region is often regarded as ‘common knowledge’; however, this aspect of the species’ ecology has not been examined empirically. Here, we outline the differences in invertebrate community structure, fish activity, and resource use of monomorphic whitefish populations between summer (August–September) and winter (February–March) in three subarctic lakes in Finnish Lapland. Benthic macroinvertebrate densities did not exhibit measurable differences between summer and winter. Zooplankton diversity and abundance, and activity levels of all fish species (measured as catch per unit effort) were lower in winter. The summer diet of *C. lavaretus* was typical of a generalist utilising a variety of prey sources. In winter, its dietary niche was significantly reduced, and the diet was dominated by chironomid larvae in all study sites. Pelagic productivity decreases during winter, and fish species inhabiting these systems are therefore restricted to feeding on benthic prey. Sampling time has strong effect on our understanding of resource utilisation by whitefish in subarctic lakes and should be taken into account in future studies of these systems.

**Key words:** diet; subarctic lakes; summer ecology; winter ecology; zooplankton

## Introduction

Freshwater ecosystems in Arctic and subarctic regions exhibit extreme seasonal climatic variation. During the summer, midnight sun provides continuous foraging opportunities for visually feeding whitefish; in the winter, 24-h polar darkness and thick ice and snow cover create cold and dark conditions, representing a challenging environment to poikilothermic fish (Warwick et al. 2008). Such climatic variation alters resource availability within these systems, as pelagic productivity is largely limited to the ‘ice-free’ summer period (Rautio et al. 2000; Forsström et al. 2005). However, few authors have empirically assessed the implications of such variation on fishes

residing in these systems. Such studies in subarctic Europe are largely limited to investigations of Arctic charr, *Salvelinus alpinus* (L.) (Klemetsen et al. 2003; Svenning et al. 2007). Logistical difficulties associated with sampling under ice have precluded many investigators from examining the role of seasonal variation on the trophic ecology of fish species in such extreme habitats (but see Amundsen & Knudsen 2009). Here, we examine and contrast the trophic ecology of the European whitefish [*Coregonus lavaretus* (L.)] under subarctic summer and winter conditions.

*C. lavaretus* is widely distributed across northern Europe, and is the dominant salmonid species in many subarctic lakes of northern Fennoscandia. However,

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information regarding the diet of *C. lavaretus* in this region is overwhelmingly dependent on data collected during the ice-free summer period (Kahilainen & Østbye 2006; Kahilainen et al. 2011). As the species inhabits lakes that are naturally ice-covered for up to 6–7 months per year, it is likely that our understanding of the diet of these populations, and their role in the ecosystem, is biased towards their trophic activity in summer months. Potential differences between winter and summer diet may have profound effects on food consumption estimates, resource competition and ecological divergence of whitefish, while also affecting the species response to climate change in the region (Graham & Harrod 2009).

Temperate poikilothermic fishes are less active during the cold winter period than in summer (Heggenes et al. 1993), and most fishes cease growing during winter period in Arctic and subarctic lakes (Magnuson et al. 1979; Edsall 1999). Consequently, their metabolic demands for food decrease (Mookerji et al. 1998; Fiogbe & Kestemont 2003). In conjunction with a reduced pelagic invertebrate fauna, this results in many fish species reducing their feeding rates and feeding predominantly on benthic prey during the ice-covered winter period (Tolonen 1998). Although such seasonal variation in the diet of *S. alpinus* (Langeland et al. 1991; L'Abée-Lund et al. 1993) and brown trout, *Salmo trutta* (L.), is well established (Amundsen & Knudsen 2009), information regarding the winter diet of *C. lavaretus* in seasonally ice-covered subarctic lakes is limited.

In subarctic Lake Kilpisjärvi (hereafter truncated to L. Kilpis etc.), *C. lavaretus* has a diverse summer diet including equal amounts of pelagic and benthic prey (Kahilainen et al. 2007; Harrod et al. 2010). In winter, Tolonen (1998) reported reduced feeding activity and a diet dominated by chironomid larvae and copepods. In L. Mjøsa, in southern Norway, benthic crustaceans dominate the year-round diet of most *C. lavaretus*, while some individuals shift to feeding on zooplankton in late summer (Næsje et al. 1991). While such investigations provide some information regarding the effects of winter ice cover on the trophic ecology of the species, a dedicated investigation is required to fully elucidate the issue.

In the absence of such detailed studies, our understanding of seasonal variation in the diet of *C. lavaretus* comes either from analysis of southern European populations in lakes that do not exhibit winter ice cover or from inferences garnered from studies of other salmonids. For example, an increase in the proportion of chironomid larvae consumed during winter months has been observed in Alpine *C. lavaretus* populations (Gerdeaux et al. 2002; Janjua & Gerdeaux 2011). Studies of seasonal variation in the diet of *S. alpinus* are more frequent and

typically highlight a shift from a generalist diet in summer to one dominated by chironomid larvae (Amundsen et al. 2008; Eloranta et al. 2010) and a reduced feeding rate in winter (Klemetsen et al. 2003). However, the winter conditions in ice-covered subarctic and Arctic lakes differ considerably from those of ice-free systems in southern latitudes (Warwick et al. 2008). Consequently, further study is required to accurately determine the winter ecology of *C. lavaretus* in Arctic and subarctic systems.

This study is, to the best of our knowledge, the first to make a detailed examination of comparisons between summer and winter diet of monomorphic *C. lavaretus* in multiple ice-covered subarctic lakes. We examined pelagic and benthic invertebrate prey availability, activity level (catch per unit effort was used as a proxy for fish activity) and diet of *C. lavaretus* in three subarctic lakes during 'ice-free' summer conditions and 'ice-covered' winter conditions. The study was based on two principal hypotheses. Firstly, pelagic prey, insect pupae, adults and zooplankton availability would decrease during periods of winter ice cover, resulting in a trophic shift by *C. lavaretus* from a generalist diet in summer to one dominated by benthic prey in winter. Secondly, *C. lavaretus* would be less active during winter periods and therefore be less susceptible to capture by gill nets and display reduced stomach fullness.

## Materials and methods

### Field study

The study was conducted in three subarctic lakes, L. Kilpis, L. Kuohkima and L. Siilas, at the head waters of the Tornio–Muonio watercourse, in northern Fennoscandia (Table 1, Fig. 1). All lakes are oligotrophic and are typically ice-covered between November and June. The monomorphic, large sparsely rakered (LSR) morph of *C. lavaretus* is the dominant species in all of the study lakes (Kahilainen et al. 2007; Harrod et al. 2010). Other species in all these lakes are *S. trutta*, grayling (*Thymallus thymallus* L.), pike (*Esox lucius* L.), burbot (*Lota lota* L.), alpine bullhead (*Cottus poecilopus* Heckel) and minnow (*Phoxinus phoxinus* L.); *S. alpinus* is also present in L. Kilpis. Each lake was surveyed on one occasion in late summer August–September (ice-free) and in winter February–March (ice-covered) (Table 1). Day and night were of approximately equal length (12 h Light – 12 h Dark) during both sampling periods. Depth of ice and snow cover (cm) was recorded during winter sampling. Water temperature was recorded at 1 m intervals from 1 to 10 m from the lake surface to a maximum depth of 20 m at each winter sampling event. Light compensation depth, i.e., the depth at which light intensity

Table 1. Abiotic characteristics of the three study lakes during summer and winter sampling periods. Distinct measurements are provided for the depth of ice and snow covering each lake in winter.

	L. Kilpis		L. Kuohkima		L. Siilas	
Latitude (°N)	69°03'		69°03'		69°04'	
Longitude (°E)	20°49'		20°33'		20°45'	
Surface area (km <sup>2</sup> )	37		0.3		1	
Mean depth (m)	19.4		2.6		5.2	
Max depth (m)	57		9		15	
Survey time	September 2005	March 2011	August 2010	March 2011	September 2007	March 2011
Secchi depth(m)	10	–	4.5	–	8	–
pH	7.1	–	–	–	6.9	–
Tot P(mg·l <sup>-1</sup> )	0.4	–	–	–	0.4	–
Tot N(mg·l <sup>-1</sup> )	12	–	–	–	7.4	–
Compensation depth (m)	10	2	8	2	15	3
Ice depth (cm)	–	70	–	50	–	60
Snow depth (cm)	–	20	–	20	–	25
Mean water temp. °C (0–10 m)	9.9*	0.7	–	2.9	–	1.1

\*L. Kilpis summer water temperatures were obtained in 2002.

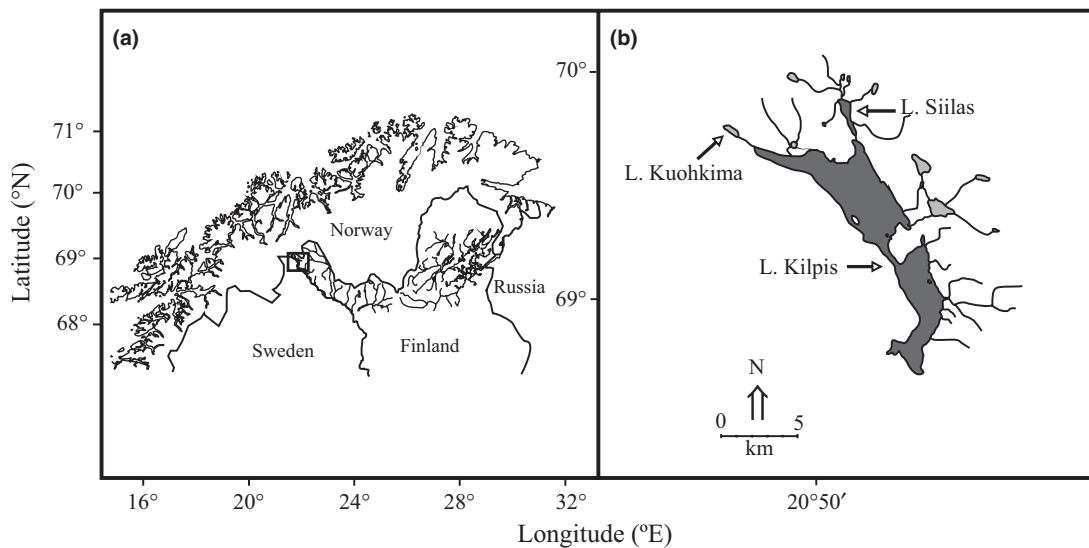


Fig. 1. Map of northern Fennoscandia (a), highlighting location of the three study lakes in northwestern Finland (b).

equals 1% of surface light, was determined in both winter and summer.

Zooplankton density was recorded by hauling a zooplankton net (25 cm diameter, 50  $\mu$ m mesh size) vertically through the water column. Three replicate hauls were taken from the deepest point in each lake (20 m in L. Kilpis), zooplankton were subsequently identified to family level, and density (individuals·l<sup>-1</sup>) was determined at each site. Nauplius larvae of copepods were excluded from subsequent analyses, due to their absence in *C. lavaretus* diet after the 1st months of life (Kahilainen et al. 2005). Benthic macroinvertebrates were collected using an Ekman grab (sampling area of 272 cm<sup>2</sup>). Ekman grabs are limited to sampling soft sediment, and consequently, results may be biased against invertebrates occupying hard or rocky substrate, as such, our estimation of benthic invertebrate community structure was limited

to such soft sediment. Three replicates were taken in the littoral zone (< 2 m depth) and at the deepest point (20 m in L. Kilpis) in each lake to calculate comparable densities of invertebrate groups in both littoral and profundal habitats. Individuals were identified from order to species level, and density (number of individuals·m<sup>-2</sup>) was recorded at each sampling event (Kahilainen et al. 2003).

Fish were sampled using gill net series: each series consisted of eight nets and 30  $\times$  1.8 m panels with knot-to-knot mesh sizes of 12, 15, 20, 25, 30, 35 and 45 mm. Benthic nets were set in littoral and profundal zones of each lake, and pelagic habitats were not sampled due to the infeasibility of setting floating nets during periods of ice cover. In winter, a large hole was cut through the ice, and a rope was subsequently passed under the ice with the aid of sliding board and retrieved through a separate hole, 120 m

from the origin. The process was then repeated in the opposite direction, and ropes were used to extend the gill net series under the ice. Netting effort differed between winter and summer sampling. During summer sampling, nets were set overnight. In winter, catch rate is often lower than in summer, while setting nets is considerably more time-consuming and labour-intensive, hence fewer net series were set, and fishing time was extended to 48 or 72 h.

All fish captured were identified to species level in the field. Catch per unit effort (CPUE:  $n \text{ fish} \cdot \text{net} \cdot \text{h}^{-1}$ ) was determined for each sampling event. Total length (cm) and wet mass (g) were recorded for each fish. Fish were subsequently frozen ( $-20 \text{ }^{\circ}\text{C}$ ) on site. Stomachs were dissected from fish in the laboratory. Stomach fullness was estimated using the points method on a scale of 0–10 (0 – empty, 10 – extended full stomach), food items were identified to family level, and the relative proportion of each to stomach fullness was calculated (Hynes 1950). Stomach content data were combined into key prey groups for subsequent analysis: chironomid larvae, chironomid pupae, trichopteran larvae, Mollusca (Sphaeriidae, Lymnaeidae & Valvatidae), aquatic insects (Megaloptera, Dytiscidae & Plecoptera), terrestrial insects, benthic zooplankton (small benthic crustaceans, i.e., Ostracoda, Cladocera; *Euryercus* sp. and Copepoda; *Megacyclops* sp.), pelagic zooplankton (Cladocera; *Bosmina* sp., *Daphnia* sp., *Bythotrepe longimanus* & Copepoda; Calanoida, Cyclopoida) and other (fish roe, Hydracarina, Tabanidae, *Gammarus lacustris* & Nostoc).

#### Statistical analysis

Variation in invertebrate and fish community structure and fish stomach content was examined using PERMANOVA, a nonparametric probability-based analogue of analysis of variance between two or more groups based on a distance measure (Anderson 2001; McArdle & Anderson 2001). In each case, a Bray–Curtis similarity matrix was created from square-root transformed abundance data. A two-factor PERMANOVA was performed on the zooplankton, fish community structure and fish stomach content similarity matrices, to test the effect of ‘lake’ (three levels, random) and ‘season’ (two levels, summer/winter, fixed) on variation within the data. A three-factor PERMANOVA was performed on the benthic macroinvertebrate density similarity matrix incorporating an additional factor, ‘depth’ (two levels, littoral/profundal, fixed). Factors ‘depth’ and ‘season’ were both nested within ‘lake’ in all analyses. When significant variation was observed between samples, percentage similarity analysis (SIMPER) was used to determine which prey items

contributed most to the difference (Clarke 1993). Variation in stomach content was subsequently visualised using principal coordinate analysis (PCO). PERMANOVA, SIMPER and PCO analyses were carried out using the PRIMER statistical software (PRIMER 6, Clarke & Gorley 2006).

Due to the use of separate netting strategies, Spearman rank correlation was employed to test for an association between netting time and number of *C. lavaretus* captured in both the summer and winter samples independently.

The dietary niche of each species was calculated using a standardised Levins’ index (Levins 1968). As the value of Levins’ index increases proportionally with sample size, niche width was calculated based on the diet of a randomly selected subsample of individuals ( $N = 78$ ). Total dietary niche width (TNW) was subsequently subdivided into between-individual components (BIC) and within-individual components (WIC), and the level of individual specialisation (WIC/TNW) was calculated using the Indspec software package (Bolnick et al. 2002, 2003). Seasonal variation in stomach fullness was determined using a Wilcoxon test. The proportion of empty stomachs was calculated for both seasonal samples, and seasonal variation was tested using a chi-square test.

#### Results

Winter ice depth was relatively consistent between lakes, measuring between 50 and 70 cm in each system. Ice cover had a profound effect on light levels within each lake. In summer, light compensation depth was 10 m in L. Kilpis, 15 m in L. Siilas and 8 m in L. Kuohkima (Table 1). Conversely, the compensation depth was  $\leq 3$  m in any lake during periods of ice cover.

Benthic macroinvertebrate communities in soft sediment were dominated by chironomid larvae and Oligochaeta. No significant variation in macroinvertebrate community structure was observed between lakes (*Pseudo*  $F_{1,3} = 0.94$ ,  $P = 0.49$ ) or season (*Pseudo*  $F_{1,3} = 1.3$ ,  $P = 0.32$ ). However, profundal and littoral communities were significantly different (*Pseudo*  $F_{1,3} = 12.3$ ,  $P < 0.01$ ), with lower densities of invertebrates recorded from the profundal samples in each lake (Table S1, Fig. 2).

Zooplankton densities displayed significant seasonal variation (*Pseudo*  $F_{1,3} = 121.1$ ,  $P < 0.01$ ), with reduced mean densities recorded during the winter sample in each lake (Table S2). Zooplankton community structure also displayed seasonal variation, cladocerans (*Bosmina* sp., *Daphnia* sp. & *Holopedium* sp.) were effectively absent from the winter sample, single individuals were recorded from L. Siilas

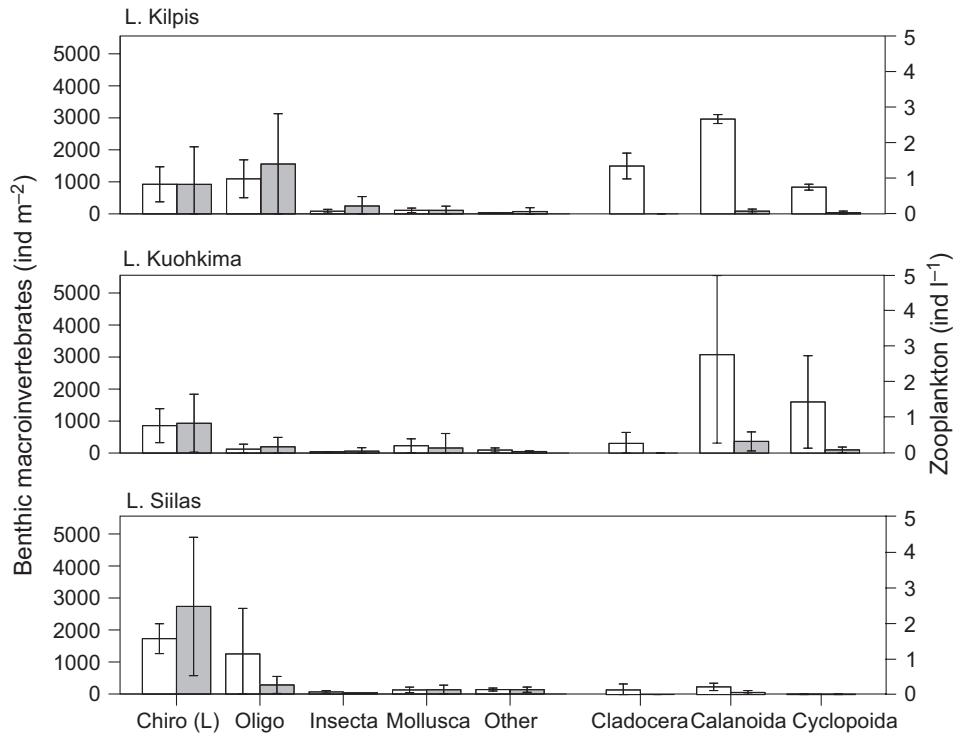


Fig. 2. Seasonal variation in benthic and pelagic invertebrates. Mean ( $\pm$  SD) summer and winter densities of chironomid larvae [Chiro (L)], oligochaeta (Oligo), aquatic insects (Insecta; Megaloptera, Dytiscidae & Plecoptera), Mollusca and other benthic macroinvertebrates (Other; *Gammarus lacustris*, Hydracarina, Hirudinea, Tabanidae, Turbellaria & Trichoptera larvae) are displayed alongside pelagic zooplankton ie Cladocera (*Bosmina* sp., *Daphnia* sp. & *Holopedium gibberum*) Calanoida and Cyclopoida. Summer and winter samples are displayed as white and grey bars respectively, note separate axes for benthic macroinvertebrate and zooplankton densities.

Table 2. Fishing intensity and mean catch per unit effort ( $\text{Ind}\cdot\text{h}^{-1}$ ) of all fish species recorded during summer and winter sampling events, and standard deviations are presented in parentheses.

Season	L. Kilpis		L. Kuohkima		L. Siilas	
	Summer	Winter	Summer	Winter	Summer	Winter
Number of nets	12	4	4	3	8	5
Netting hours	168	291	47	91	93	173
<i>Coregonus lavaretus</i>	2.4 (2.12)	0.56 (0.15)	4.05 (1.69)	0.75 (0.23)	1.57 (0.98)	0.46 (0.28)
<i>Esox lucius</i>	–	–	0.24 (0.08)	0.04 (0.03)	0.08 (0.13)	–
<i>Lota lota</i>	0.03 (0.07)	0.03 (0.02)	–	0.01 (0.01)	0.06 (0.06)	0.03 (0.03)
<i>Salvelinus alpinus</i>	0.07 (0.08)	0.03 (0.03)	–	–	–	–
<i>Cottus poecilopus</i>	0.01 (0.02)	–	–	–	0.01 (0.03)	–
<i>Salvelinus trutta</i>	–	–	–	–	–	0.06 (0.06)
<i>Thymallus thymallus</i>	–	–	0.04 (0.05)	–	0.01 (0.03)	–
Total	2.53 (2.27)	0.63 (0.18)	4.33 (1.59)	0.79 (0.22)	1.73 (0.88)	0.55 (0.27)

and L. Kilpis, while the copepod community was dominated by calanoids in winter (Table S2, Fig. 2).

Fish community structure did not vary significantly between lakes (*Pseudo*  $F_{1,2} = 0.98$ ,  $P = 0.49$ ), and *C. lavaretus* dominated each system (Table 2). Gill raker counts indicated that *C. lavaretus* populations in each lakes consisted solely of the large sparsely rakered (LSR) morph (Table 3). Significantly lower numbers of *C. lavaretus* were captured during winter sampling in each lake (*Pseudo*  $F_{1,3} = 6.3$ ,  $P < 0.01$ , Fig. 3). Soak time, the period of fishing time between

setting to retrieving a net, did not correlate with the number of *C. lavaretus* caught in either the summer ( $r_s = 0.09$ ,  $P = 0.67$ ) or the winter ( $r_s = -0.19$ ,  $P = 0.55$ ) samples.

Diet of *C. lavaretus* varied between lakes in both summer (*Pseudo*  $F_{1,2} = 36.6$ ,  $P < 0.01$ ) and winter samples (*Pseudo*  $F_{1,2} = 4.1$ ,  $P < 0.01$ ). A highly significant dietary shift between winter and summer samples (*Pseudo*  $F_{1,1} = 206.7$ ,  $P < 0.01$ ; Fig. 4) was evident in each lake (Table 3). In addition, a significant interaction between season and lake was evident

Table 3. Mean proportional stomach content values for *Coregonus lavaretus* captured during summer and winter sampling events, and standard deviations are provided in parentheses. Number of fish analysed (n), mean gill raker count (GR), range of gill raker counts in brackets, stomach fullness (SF), P values of pairwise PERMANOVA tests (P), % empty stomachs (% ES), Levins' niche width and specialisation (WIC/TNW) values are displayed. Abbreviations for the different prey categories are chironomid larvae (Chiro L), chironomid pupae (Chiro P), trichopteran larvae (Tric L), molluscs (Moll), aquatic insects (Ins A), terrestrial insects (Ins T), benthic zooplankton (ZPL B), pelagic zooplankton (ZPL P) and other prey items (Other). The most important prey category in summer and winter is highlighted in bold.

Lake	Season	N	GR count	SF	Chiro (L)	Chiro (P)	Tric (L)	Moll	Ins (A)	Ins (T)	ZPL (B)	ZPL (P)	Other	P	% ES	Levins	WIC/TNW
L. Kilpis	Summer	150	24 (1.8) [20-29]	3.3	0.10 (0.02)	0.01 (0.2)	0.22 (0.1)	<b>0.37 (0.42)</b>	-	0.10 (0.29)	0.20 (0.38)	0.15 (0.15)	-	< 0.01	21	0.35	0.19
	Winter	154	24.3 (1.8) [19-29]	2.5	<b>0.71 (0.39)</b>	-	0.02 (0.15)	0.11 (0.23)	-	-	0.03 (0.11)	0.11 (0.31)	0.04 (0.22)		40	0.09	0.27
L. Kuohkima	Summer	119	25.9 (2.1) [20-31]	3.7	0.09 (0.18)	0.11 (0.25)	0.05 (0.19)	0.15 (0.24)	0.02 (0.13)	0.04 (0.17)	<b>0.43 (0.4)</b>	0.11 (0.14)	-	< 0.01	8	0.49	0.26
	Winter	78	25.6 (1.9) [20-29]	4.0	<b>0.73 (0.33)</b>	-	-	0.19 (0.3)	0.02 (0.13)	-	0.02 (0.04)	0.03 (0.32)	0.01 (0.07)		13	0.07	0.44
L. Siilas	Summer	104	24.8 (2.2) [20-30]	3.6	0.02 (0.14)	<b>0.47 (0.47)</b>	0.02 (0.13)	0.08 (0.23)	-	0.24 (0.41)	0.04 (0.16)	0.14 (0.12)	-	< 0.01	8	0.32	0.13
	Winter	78	25.1 (1.9) [19-30]	3.2	<b>0.82 (0.28)</b>	-	0.02 (0.08)	0.08 (0.18)	0.02 (0.12)	-	0.02 (0.12)	0.02 (0.24)	0.01 (0.06)		15	0.04	0.35

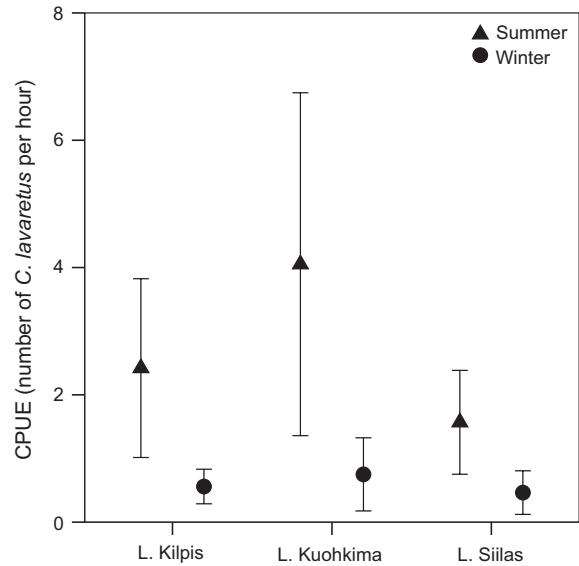


Fig. 3. Seasonal variation in *Coregonus lavaretus* catch per unit effort recorded between summer and winter sampling events. Error bars represent 95% confidence limits.

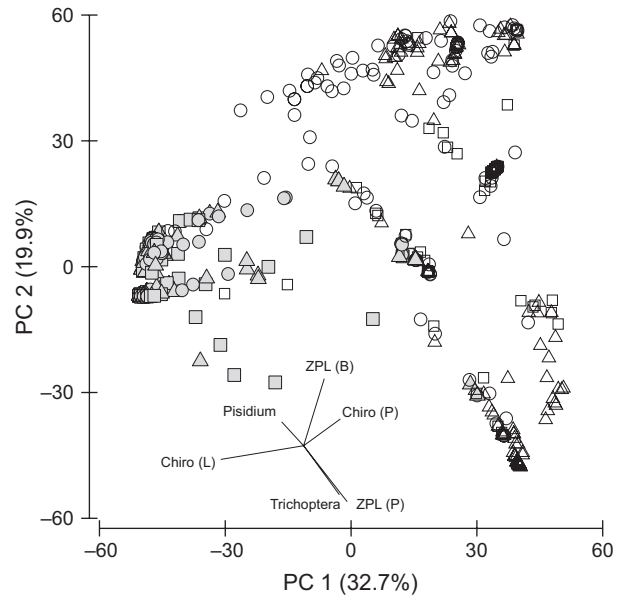


Fig. 4. PCO of *Coregonus lavaretus* stomach content data. Triangles, circles and squares represent L. Kilpis, L. Kuohkima and L. Siilas, respectively. Summer samples are displayed as unfilled markers, winter samples are displayed in grey. The influence of key prey groups; *Pisidium* sp., benthic zooplankton (ZPL B), chironomid pupae (Chiro P), pelagic zooplankton (ZPL P), Trichoptera larvae & chironomid larvae (Chiro L) on the location of individual data-points is highlighted by multiple correlation vectors.

in the diet of *C. lavaretus* ( $Pseudo F_{1,2} = 19.1$ ,  $P < 0.01$ ).

In each lake, the winter diet of *C. lavaretus* was dominated (>75%) by chironomid larvae (Table 3, Fig. 5). In L. Kilpis, variation in chironomid abundance accounted for 35% of the variation between winter and summer diet. In addition, pelagic zooplankton (21%), benthic zooplankton (12%) and

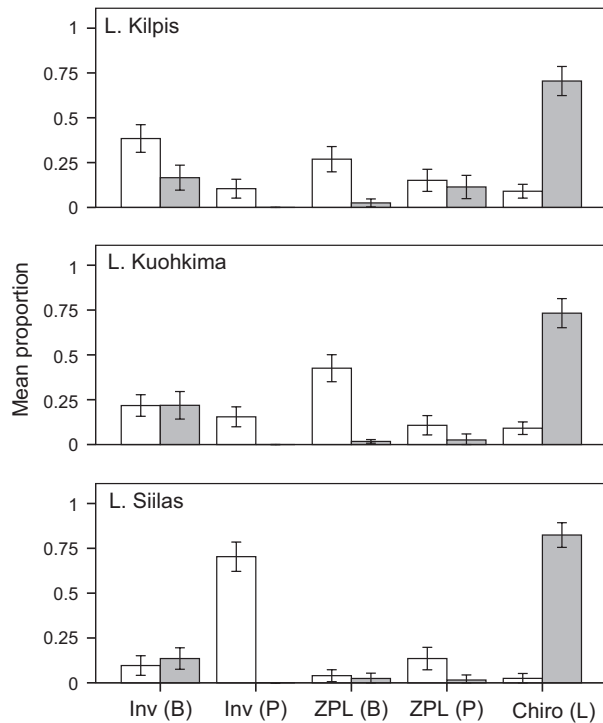


Fig. 5. Seasonal variation in the mean proportions of key prey groups in the stomach contents of *Coregonus lavaretus*. Prey groups are reduced to benthic macroinvertebrates, Inv (B), pelagic macroinvertebrates, Inv (P), benthic zooplankton, ZPL (B), pelagic zooplankton, ZPL (P), and chironomid larvae, Chiro (L), for illustrative purposes. White and grey bars denote summer and winter samples respectively. Error bars indicate 95% confidence intervals.

trichopteran larvae (12%) were all more abundant in the summer sample. Similarly in L. Kuohkima, chironomid larvae and benthic zooplankton were the main drivers of variation (42% and 22%, respectively). In L. Siilas, the relative consumption of chironomid larvae accounted for 41% of the difference between seasons, while chironomid pupae (24%) and terrestrial insects (13%) were more frequently consumed in summer.

The predominance of chironomid larvae in the winter diet led to a marked decrease in niche width during the ice-covered period. In each lake, Levins' index values during the summer were almost one order of magnitude higher than those recorded in winter (Table 3). The increased niche width in summer was associated with an increased level of individual dietary specialisation (Table 3). A reduction in stomach fullness during winter was evident in L. Kilpis ( $W_{1,302} = 1385.5$ ,  $P < 0.01$ ) and marginally significant in L. Siilas ( $W_{1,180} = 4668$ ,  $P = 0.08$ ); however, no seasonal variation was evident in L. Kuohkima ( $W_{1,195} = 4280.5$ ,  $P = 0.35$ ). Empty stomachs were more frequent in the winter sample than in the summer sample when measured across all lakes ( $\chi^2 = 20.2$ , d.f. = 1,  $P < 0.01$ ).

## Discussion

The first hypothesis, concerning seasonal variation in the diet of *C. lavaretus*, was supported by the results. We found that zooplankton abundance was notably lower under ice due to the absence of cladocerans and a reduced amount of copepods. In contrast, no seasonal variation was observed in the relative abundance of benthic macroinvertebrates from soft sediment. This seasonal variation in prey availability was reflected in the diet of *C. lavaretus*. In all lakes, whitefish shifted from a generalist diet in summer to a highly uniform benthivorous winter diet almost exclusively dominated by chironomid larvae and molluscs. Conclusions regarding the second hypothesis are less concrete. CPUE levels were dramatically reduced during the winter sampling, and the proportion of empty stomachs was approximately twice as high as summer levels. However, stomach fullness was significantly lower in winter only in L. Kilpis, the coldest of the study systems.

Summer and winter represented highly divergent foraging conditions within the study lakes. Although L. Kilpis is a considerably larger waterbody, the three study lakes represented ideal replicate systems as *C. lavaretus* numerically dominated the fish community in each system, and *C. lavaretus* gill raker counts were almost identical between lakes. Similarly, the zooplankton and benthic macroinvertebrate communities were statistically indistinguishable between lakes. While zooplankton was less abundant in L. Siilas than the other systems, there was no significant difference in community structure or density between lakes.

Zooplankton in these systems display high seasonal variation in abundance and community structure, with the highest densities and greatest diversity typically observed during the autumn (Rautio et al. 2000). The summer samples we obtained reflected this, displaying a diverse zooplankton community containing numerous cladoceran and copepod species. Winter samples displayed a significant decrease in abundance of zooplankton, as the cladoceran population had entirely collapsed and the copepod community was dominated by calanoids. Benthic macroinvertebrate communities displayed no such seasonal variation. Both summer and winter samples in each lake were dominated by chironomid larvae, *Oligochaeta* and, to a lesser degree, molluscs. The variation between littoral and profundal locations has been recorded in numerous previous investigations and relates to reduced density and biomass in deeper water (Kahilainen et al. 2003; Lampert & Sommer 2007). It is somewhat surprising that no reduction in benthic macroinvertebrate density was recorded between summer and winter when phototrophic production is reduced. In a similar investigation conducted on Arctic L. Linnevatn in Spitsber-

gen, the highest abundance of chironomids was recorded in mid-winter, with a reduction during spring and summer, suggesting that selective predation by *S. alpinus* reduces the abundance (Svenning et al. 2007). As whitefish feed exclusively on benthic invertebrates during the winter months, a similar effect of top-down control may have been expected. However, there is no evidence of such an effect in these lakes, potentially due to the reduced feeding rates of whitefish during the winter period (Tolonen 1998). An alternative explanation for high densities of chironomid larvae in winter refers to ice cover, as all individuals are in larval stages during winter, while the summer population may be reduced following emergence. The current investigation was limited to two sampling events, potentially hiding additional temporal fluctuations in invertebrate community structure. Further investigations, currently underway, will further explore seasonal variation in invertebrate biomass in L. Kilpis.

Given the disparity between the abundance of zooplankton and benthic macroinvertebrates during the winter period, it is not surprising that *C. lavaretus* diet differed between seasons. In line with previously published data concerning summer diet of monomorphic LSR whitefish (Kahilainen et al. 2007; Harrod et al. 2010), the diet observed in the August–September samples was typical of a generalist. No single prey group was dominant in the diet in any lake, and stomach contents indicated that individuals utilised both pelagic and benthic resources. In addition, increased dietary niche width and an associated increase in levels of individual specialisation were observed in the summer sample in each lake. Hence, while some *C. lavaretus* changed their diet to utilise a greater variety of prey types, others maintained a predominantly benthic diet, driving an increase in dietary specialisation, mirroring the findings from L. Mjøsa. (Næsje et al. 1991). The variation in soak time of nets between summer and winter samples is a potential confounding factor in this regard. During winter, fish were in nets for up to 72 h. Variation in digestion and evacuation rates of soft- and hard-bodied prey may have altered the proportions of each in the stomach of *C. lavaretus* during this period. However, digestion rates are often regulated by ambient water temperature (Bernreuther et al. 2009) and, as such, were much reduced in winter. Additionally, soft-bodied chironomid larvae were the most commonly recorded prey item in winter samples, and stomach fullness did not vary between seasons in two of the three sites. Consequently, our estimations of seasonal variation in the studied populations are unlikely to be unduly influenced by the variations in soak period employed.

Despite similarities in prey availability, summer diet differed between systems. In L. Siilas, chirono-

mid pupae were the most commonly exploited resource, while benthic zooplankton and molluscs were more commonly consumed in L. Kuohkima and L. Kilpis, respectively. Stomach contents only represent a snapshot of diet of individual prior to capture. It is therefore likely that this variation in whitefish diet reflects temporal variation in prey availability. Conversely, the winter diet of *C. lavaretus* in all lakes was dominated by chironomid larvae and *Pisidium* sp. Here, the species fed as a specialist in all systems, switching to an exclusive diet of sedentary benthic macroinvertebrates.

The divergence between measurements of CPUE and stomach fullness provides an insight into the seasonal variation in feeding activity of *C. lavaretus*. Although CPUE is not a direct measure of fish activity, it is highly unlikely that the decrease in CPUE represented a decrease in the number of fish in each lake as there were no reported fish kills during the study period. Alternatively, whitefish may have occupied the pelagic zone at an increased rate in winter, avoiding the benthic nets; however, the switch in diet from pelagic to benthic prey indicates that this is unlikely. During the summer period, *C. lavaretus* feed on a variety of pelagic and other motile prey. Feeding on such prey items involves an active, mobile predation strategy - as fish spend an extended period searching and actively pursuing prey, their probability of encountering stationary gill nets increases. During the winter period, stomach fullness did not decrease in L. Kuohkima and L. Siilas, although *C. lavaretus* fed on different prey types. A diet dominated by sedentary or slow-moving prey, for example, chironomid larvae and bivalves, does not require the same level of activity by the fish. Hence, although they maintained similar stomach fullness levels during the two periods, *C. lavaretus* were less likely to encounter survey nets during winter, leading to reduced CPUE values. However, the evidence in this regard is not conclusive. Empty stomachs were recorded twice as frequently in winter as in summer. Similar findings were reported by Klemetsen et al. (2003) in a study of winter feeding in *S. alpinus* in northern Norway, indicating that both species may feed with reduced regularity during winter months. Furthermore, as rates of digestion and excretion are linked to ambient temperature (Bernreuther et al. 2009), it is possible that the levels of stomach fullness observed during the winter are a result of prey not being digested rapidly rather than a consequence of infrequent feeding by whitefish.

Seasonal variation in the foraging activity of *C. lavaretus* will play a role in the response of the species to future predicted climate change, that is, short winter periods and reduced ice cover (Lappalainen & Lehtonen 1997). In this scenario, fish will maintain elevated feeding rates for a longer period, potentially increasing



predation pressure on invertebrate communities. Furthermore, as ambient water temperature increases, additional fish species will migrate north (Graham & Harrod 2009). The study lakes are located above the current latitudinal limits of benthic specialists such as ruffe, *Gymnocephalus cernuus* (L.), and generalists such as perch *Perca fluviatilis* (L.) within the Tornio–Muonio watercourse. Both species forage predominantly on the benthos, and while in summer, generalist *C. lavaretus* may utilise a pelagic resource to avoid resource competition, during winter, pelagic resources will not be available, potentially increasing resource competition between resident and invading species. Further investigation incorporating a wider variety of study sites and species assemblages will be required to fully uncover the implications of such extreme seasonal variation on these processes.

In effect, these lakes represent a ‘best case’ scenario to establish the differences between summer and winter diet of *C. lavaretus* in subarctic systems. It is the dominant species in each of the study lakes, and potential benthic competitors were either absent or only present in small numbers in the study lakes. As such, *C. lavaretus* effectively forages in the absence of strong interspecific competition. Allied with this, its generalist morphology allows it to exploit a variety of prey items, when available, and specialise on specific resources when prey availability is reduced. As yet, how these species interact in challenging winter conditions remains unknown and will form the basis for future research in this area.

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## References

- Amundsen, P.-A. & Knudsen, R. 2009. Winter ecology of Arctic charr (*Salvelinus alpinus*) and brown trout (*Salmo trutta*) in a subarctic lake, Norway. *Aquatic Ecology* 43: 765–775.
- Amundsen, P.-A., Knudsen, R. & Klemetsen, A. 2008. Seasonal and ontogenetic variations in resource use by two sympatric Arctic charr morphs. *Environmental Biology of Fishes* 83: 45–55.
- Anderson, M.J. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26: 32–46.
- Bernreuther, M., Temming, A. & Herrmann, J.P. 2009. Effect of temperature on the gastric evacuation in sprat *Sprattus sprattus*. *Journal of Fish Biology* 75: 1525–1541.
- Bøhn, T. & Amundsen, P.-A. 2001. The competitive edge of an invading specialist. *Ecology* 82: 2150–2163.
- Bolnick, D.I., Yang, L.H., Fordyce, J.A., Davis, J.M. & Svanback, R. 2002. Measuring individual-level resource specialization. *Ecology* 83: 2936–2941.
- Bolnick, D.I., Svanback, R., Fordyce, J.A., Yang, L.H., Davis, J.M., Hulsey, C.D. & Forister, M.L. 2003. The ecology of individuals: incidence and implications of individual specialization. *American Naturalist* 161: 1–28.
- Clarke, K.R. 1993. Non-parametric multivariate analysis of changes in community structure. *Australian Journal of Ecology* 18: 117–143.
- Clarke, K.R. & Gorley, R.N. 2006. PRIMER v6: user manual. Plymouth: PRIMER-E.
- Edsall, T.A. 1999. The growth-temperature relation of juvenile lake whitefish. *Transactions of the American Fisheries Society* 128: 962–964.
- Eloranta, A.P., Kahilainen, K.K. & Jones, R.I. 2010. Seasonal and ontogenetic shifts in the diet of Arctic charr *Salvelinus alpinus* in a subarctic lake. *Journal of Fish Biology* 77: 80–97.
- Fiogbe, E.D. & Kestemont, P. 2003. Optimum daily ration for Eurasian perch *Perca fluviatilis* L. reared at its optimum growing temperature. *Aquaculture* 216: 243–252.
- Forsström, L., Sorvari, S., Korhola, A. & Rautio, M. 2005. Seasonality of phytoplankton in subarctic Lake Saanajärvi in NW Finnish Lapland. *Polar Biology* 28: 846–861.
- Gerdeaux, D., Bergeret, S., Fortin, J. & Baronnet, T. 2002. Diet and seasonal patterns of food composition of *Coregonus lavaretus* in Lake Annecy: comparison with the diet of the other species of the fish community. In: Todd, T. & Fleischer, G., eds. *Advances in limnology 57: biology and management of coregonid fishes - 1999. ergebnisse der limnologie*. Stuttgart: E Schweizerbart'sche Verlagsbuchhandlung, pp. 199–207.
- Graham, C.T. & Harrod, C. 2009. Implications of climate change for the fishes of the British Isles. *Journal of Fish Biology* 74: 1143–1205.
- Harrod, C., Mallela, J. & Kahilainen, K.K. 2010. Phenotype-environment correlations in a putative whitefish adaptive radiation. *Journal of Animal Ecology* 79: 1057–1068.
- Heggenes, J., Krog, O.M.W., Lindas, O.R., Dokk, J.G. & Bremnes, T. 1993. Homeostatic behavioral responses in a changing environment - brown trout (*Salmo trutta*) become nocturnal during winter. *Journal of Animal Ecology* 62: 295–308.
- Hynes, H.B.N. 1950. The food of freshwater sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*), with a review of methods used in studies of the food of fishes. *Journal of Animal Ecology* 19: 36–58.
- Janjua, M.Y. & Gerdeaux, D. 2011. Evaluation of food web and fish dietary niches in oligotrophic Lake Annecy by gut content and stable isotope analysis. *Lake and Reservoir Management* 27: 115–127.
- Kahilainen, K. & Østbye, K. 2006. Morphological differentiation and resource polymorphism in three sympatric whitefish *Coregonus lavaretus* (L.) forms in a subarctic lake. *Journal of Fish Biology* 68: 63–79.
- Kahilainen, K., Lehtonen, H. & Könönen, K. 2003. Consequence of habitat segregation to growth rate of two sparsely

- rakered whitefish (*Coregonus lavaretus* (L.)) forms in a sub-arctic lake. *Ecology of Freshwater Fish* 12: 275–285.
- Kahilainen, K., Alajärvi, E. & Lehtonen, H. 2005. Planktivory and diet-overlap of densely rakered whitefish (*Coregonus lavaretus* (L.)) in a subarctic lake. *Ecology of Freshwater Fish* 14: 50–58.
- Kahilainen, K.K., Malinen, T., Tuomaala, A., Alajärvi, E., Tolonen, A. & Lehtonen, H. 2007. Empirical evaluation of phenotype–environment correlation and trait utility with allopatric and sympatric whitefish, *Coregonus lavaretus* (L.), populations in subarctic lakes. *Biological Journal of the Linnean Society* 92: 561–572.
- Kahilainen, K.K., Siwertsson, A., Gjelland, K.Ø., Knudsen, R., Bøhn, T. & Amundsen, P.-A. 2011. The role of gill raker number variability in adaptive radiation of coregonid fish. *Evolutionary Ecology* 25: 573–588.
- Klemetsen, A., Knudsen, R., Staldvik, F.J. & Amundsen, P.-A. 2003. Habitat, diet and food assimilation of Arctic charr under the winter ice in two subarctic lakes. *Journal of Fish Biology* 62: 1082–1098.
- L'Abée-Lund, J.H., Langeland, A., Jonsson, B. & Ugedal, O. 1993. Spatial segregation by age and size in arctic charr - a trade off between feeding possibility and risk of predation. *Journal of Animal Ecology* 62: 160–168.
- Lampert, W. & Sommer, U. 2007. *Limnoecology: the ecology of lakes and streams*. Oxford: Oxford University Press.
- Langeland, A., L'Abée-Lund, J.H., Jonsson, B. & Jonsson, N. 1991. Resource partitioning and niche shift in Arctic charr *Salvelinus alpinus* and brown trout *Salmo trutta*. *Journal of Animal Ecology* 60: 895–912.
- Lappalainen, J. & Lehtonen, H. 1997. Temperature habitats for freshwater fishes in a warming climate. *Boreal Environment Research* 2: 69–84.
- Levins, R. 1968. *Evolution in changing environments: some theoretical explorations*. Princeton, NJ.: Princeton University Press.
- Magnuson, J.J., Crowder, L.B. & Medvick, P.A. 1979. Temperature as an ecological resource. *American Zoologist* 19: 331–343.
- McArdle, B.H. & Anderson, M.J. 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology* 82: 290–297.
- Mookerji, N., Heller, C., Meng, H.J., Bürgi, H.R. & Müller, R. 1998. Diel and seasonal patterns of food intake and prey selection by *Coregonus* sp. in re-oligotrophicated Lake Lucerne, Switzerland. *Journal of Fish Biology* 52: 443–457.
- Næsje, T.F., Jonsson, B., Sandlund, O.T. & Kjellberg, G. 1991. Habitat switch and niche overlap in coregonid fishes - effects of zooplankton abundance. *Canadian Journal of Fisheries and Aquatic Sciences* 48: 2307–2315.
- Rautio, M., Sorvari, S. & Korhola, A. 2000. Diatom and crustacean zooplankton communities, their seasonal variability and representation in the sediments of subarctic Lake Saanajärvi. *Journal of Limnology* 59(Suppl. 1): 81–96.
- Svenning, M.A., Klemetsen, A. & Olsen, T. 2007. Habitat and food choice of Arctic charr in Linnevatn on Spitsbergen, Svalbard: the first year-round investigation in a High Arctic lake. *Ecology of Freshwater Fish* 16: 70–77.
- Tolonen, A. 1998. Application of a bioenergetics model for analysis of growth and food consumption of subarctic whitefish *Coregonus lavaretus* (L.) in Lake Kilpisjärvi, Finnish Lapland. *Hydrobiologia* 390: 153–169.
- Warwick, V.F., MacIntyre, S., Spigel, R.H. & Laurion, I. 2008. The physical limnology of high-latitude lakes. In: Warwick, V.F. & Laybourn-Parry, J., eds. *Polar lakes and Rivers*. New York: Oxford University Press, pp. 65–81.

### Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Table S1.** Mean density (Ind·m<sup>-2</sup>) of benthic invertebrate groups recorded during summer and winter sampling events, standard deviations are presented in parentheses.

**Table S2.** Density (Ind·l<sup>-1</sup>) of pelagic zooplankton recorded during summer and winter sampling events, standard deviations are presented in parentheses.