

# Diel variation in activity and feeding in sympatric brown trout (*Salmo trutta*) and Arctic char (*Salvelinus alpinus*) throughout the ice-free season in a Norwegian lake

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Most animals are active during distinct diel periods. Salmonid fishes may shift from being mostly diurnal to being nocturnal in autumn and winter. As visual foragers, diurnal variation in prey availability and predation risk may drive variation in their activity pattern. In an oligotrophic lake, we studied diel activity and feeding of brown trout (*Salmo trutta*) and Arctic char (*Salvelinus alpinus*) using gill nets in the epibenthic habitat from May through October. Brown trout demonstrate an overall crepuscular activity pattern, whereas Arctic char demonstrate a more complex diel activity pattern. The variation in activity reflected the variation in stomach content in both species, with highest stomach-content mass in individuals sampled during night. Diet overlap of brown trout and Arctic char was high in early spring and reduced thereafter. Our results characterize both brown trout and Arctic char as indiscriminate particulate feeders and neither species had a diel change in their feeding mode.

## Introduction

Scandinavian lakes are usually species-poor when it comes to freshwater fish. Two of the most common species, the salmonids brown trout (*Salmo trutta*) and Arctic char (*Salvelinus alpinus*), are often found in sympatry. Their distribution across Norway may be the result of different competitive mechanisms (Finstad *et al.* 2011). The aggressive and dominant brown trout often seem to exclude the more energy-efficient Arctic char from relatively warm and productive lakes, whereas Arctic char tend to out-

compete brown trout in cold, low-productivity lakes — probably due to contest competition and scramble competition, respectively (Finstad *et al.* 2011). However, based on a long-term study, Persson *et al.* (2013) found no support for the hypothesis that a strong interspecific competition was the main driver of the population dynamics of either species. They suggested that brown trout-Arctic char interactions are mainly predation by brown trout on Arctic char, or intraspecific density-dependent competition in the Arctic char. Their conclusion may, however, depend on environmental conditions.

Both the brown trout and Arctic char have for generations been important for recreation, household and commercial fishing in Norway (Qvenild 2004). Their wide distribution and economic interest have resulted in numerous studies describing how they segregate into different niches. Early studies indicated that brown trout and Arctic char compete for food and space when coexisting (Dahl 1920, Sømme 1933). Later, Nilsson (1965) showed that the diet of each species shifted depending on food availability. The feeding habits were similar when food was in abundant, whereas the two species segregated into different niches when food availability was reduced. Arctic char increased their consumption of zooplankton, while brown trout increased intake of winged insects in late summer (Nilsson 1965). This observation has been supported by later studies, showing that Arctic char feed almost exclusively on zooplankton, whereas brown trout have a more variable diet, consisting of surface insects, zooplankton, aquatic insects and fish (Hegge *et al.* 1989, Langeland *et al.* 1991, Jensen *et al.* 2017). Experimental studies have further shown that Arctic char are more efficient at feeding on zooplankton and brown trout more efficient feeding on macro-zoobenthos (Jansen *et al.* 2002).

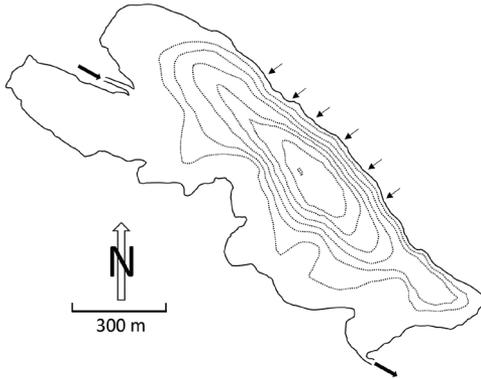
Sympatric populations of brown trout and Arctic char also demonstrate segregation in habitat use. While brown trout mostly use shallow littoral areas, Arctic char use both pelagic and epibenthic areas (Hegge *et al.* 1989, Langeland *et al.* 1991). In epibenthic areas, all size groups of Arctic char chiefly use profundal area, whereas the larger individuals also use shallow pelagic layers. The mechanism behind this is suggested to be a trade-off between food demand and predation risk (Hegge *et al.* 1989, L'Abée-Lund *et al.* 1993). In addition, Arctic char are more efficient feeder than brown trout at lower water temperature, although both species demonstrate variability in optimum temperature for growth efficiency among populations (Larson 2005, Larsson and Berglund 2005, Forseth *et al.* 2009). The difference in vertical distribution between brown trout and Arctic char could therefore be influenced by temperature.

Studies on how the two species segregate in habitat use and feeding has usually been con-

ducted by gillnet sampling and stomach content analyses, where the gill nets have been emptied once (morning) or twice (morning and evening) a day during the ice-free season (May–October). The study by Dervo *et al.* (1991) revealed that Arctic char in Atnsjøen (62°N) feed almost exclusively on zooplankton both day and night, while brown trout had a diurnal shift in diet. Regular gill net sampling routines limiting the ability to investigate fine-scale diel difference in habitat use and diet. Further, classical stomach analysis gives a picture of the relatively recent niche use. Analysis of stable carbon and nitrogen isotopes, on the other hand, has been used to document the long-term niche use of fish. For example, using stable isotope analysis, Eloranta *et al.* (2017) showed that brown trout may substantially restrict the summer-time use of littoral niche by the Arctic char.

The interspecific difference in diet can be explained by differences in their ability to detect food items visually. The physiological adaptations of the retina in brown trout and Arctic char differ. In brown trout the eyes are specialized for detecting prey in front or above, whereas the eye of Arctic char has no specialized features (Ahlbert 1976, Ali *et al.* 1984). In an experimental study, Elliott (2011) showed that feeding ability in Arctic char and brown trout on *Gammarus pulex* was affected both by light intensity and water temperature. Arctic char was superior from dusk to dawn, whereas brown trout was superior during day. No difference in feeding ability was detected at water temperature above 10°C, whereas Arctic char was superior at low (5°C) water temperature.

Most aquatic insects have distinct synchronized diel emergence patterns. In most groups, hatching and emergence occurs at low light intensities at dusk or night (Elliott 1971, Brittain 1982, Jackson 1988) although synchronous emergence also may take place at other time of the day (Brittain 1982). During such periods of emergence, fish may converge on this abundant food source, whereas during the rest of the day and night other food sources may be more available. Therefore, animals can be classified as being either diurnal, nocturnal or crepuscular, since adaptations for activity at one light level tend to reduce efficiency at another (Fraser and Metcalfe 1997).



**Fig 1.** Lake Songsjøen ( $63^{\circ}19'6''\text{N}$ ,  $9^{\circ}40'26''\text{E}$ ) with 5 m depth contours. The inlet and outlet as well as the locations used for gill net sampling are indicated.

In the northern hemisphere, the day length changes considerably throughout the year, and north of  $65^{\circ}44'\text{N}$ , the sun never sets in the summer. In a light context, gillnets emptied once or twice a day will therefore capture under a great variety of light and thus visual acuity conditions during different seasons. A biotelemetry study of the behaviour of Arctic char in Lake Ellasjøen located on Bear Island ( $74^{\circ}23'17''\text{N}$ ), demonstrated diel activity rhythms reflecting the above-surface photoperiod (Hawley *et al.* 2017). During the dark winter period, char activity became arrhythmic and much reduced, even though light levels were sufficient for feeding. When twilight resumed, char activity returned to diel vertical migration.

The populations of brown trout and Arctic char in Lake Songsjøen have been studied intensively. The depth distribution of the two species is correlated with Secchi disc depth (Langeland *et al.* 1991), where the brown trout mainly use littoral areas down to a depth of 1 Secchi disc unit whereas the Arctic char was most abundant in epibenthic areas at depths between 2 and 5 Secchi disc units. This habitat segregation broke down in winter. Arctic char underwent ontogenetic habitat shifts between the epibenthic and pelagic zones as many individuals moved into pelagic waters during summer after reaching a body length of 13–18 cm (L'Abée-Lund *et al.* 1993). This habitat shift indicates that juvenile Arctic char demonstrated a trade-off between food demand and predation risk. An experimental test demon-

strated that Arctic char can facultatively respond to predation risk and adjust the size at which they migrate to the pelagic zone to feed on zooplankton (Langeland and L'Abée-Lund 1998). Brown trout started feeding upon Arctic char at 20 cm length while Arctic char did not show piscivorous behaviour (L'Abée-Lund *et al.* 1992). However, in pond experiments Arctic char became cannibalistic by eating eggs from conspecifics (L'Abée-Lund and Langeland 1989).

Here, we assess if and how sympatric brown trout and Arctic char in the Lake Songsjøen change activity and feeding behaviour on short time scales throughout the ice-free season. Each diel cycle (24 h) was divided into eight sampling periods to keep the solar influx near constant within each period. We quantified their activity level and food choice in three-hour periods during six sampling sessions throughout the ice-free season.

## Methods

### Study Area

The study was carried out in the oligotrophic Lake Songsjøen ( $63^{\circ}19'6''\text{N}$ ,  $9^{\circ}40'26''\text{E}$ ) in central Norway. The lake is situated at 261 m above sea level, has a surface area of 0.7 km<sup>2</sup> and a maximum depth of 32 m. The shoreline in the south-east has a stable depth gradient down to approximately 24 m depth (Fig. 1), and is dominated by stone and rocks. The aquatic vegetation is scarce. The southern and northern area is shallow with dense aquatic vegetation. Brown trout and Arctic char are the only fish species in the lake.

Water temperature and Secchi disc transparency was recorded over the deepest areas during each fishing period. Water temperature was recorded at 1 m intervals down to 8 m in addition to at 10, 15, 20 and 25 m (Table 1). A full circulation in the water column occurred in May. A thermocline developed in June and extended downwards in July. The thermocline was gradually reduced in strength in late summer and was absent in October. The Secchi disc transparency varied between 3.5 m in May and 5.5 m in the other months.

## Sampling

The sampling was conducted with monofilament gill nets (1.5×25 m) along the south-eastern shore. Gill nets are very size selective (Hamley 1975, Hovgård and Lassen 2000). Therefore, we used three mesh sizes (12.5, 16 and 19.5 mm) to achieve representative sampling of fish in the most abundant size classes in Lake Songsjøen (Langeland and L'Abée-Lund 1996). Each gang consisted of three gill nets with identical mesh size.

Three gangs of gill nets were used during the first sampling (June 1990). However, due to low catch, the effort was doubled thereafter. The gangs were set perpendicular to the depth contours from the shoreline to the deepest area of the lake. The distance between the gangs was approximately 150 m. The gangs were moved 50 m after being emptied of fish to secure that no

area was fished with the same mesh size within the same period, and to maintain high catches (Jensen 1977).

Sampling was carried out over seven periods during the ice-free season, but are treated as six distinct periods (Table 2). Period I: 2 May 1991 (called May). Period IIa: 30 May 1991 and period IIb: 7 June 1990 were compiled and called June. Period III: 1 July 1991 (called July I). Period IV: 24 July 1990 (called July II). Period V: 4 September 1990 (called September). Period VI: 8 October 1990 (called October). Sampling was done over two years (1990–1991), but we assume that the underlying mechanisms of interest (seasonality, diurnal variation) are independent of year of sampling.

Each sampling period started at 12:00 (GST) and continued for 24 h. The gill nets were emptied every third hour and immediately reset, thereby resulting in eight data collections during

**Table 1.** Water temperature (°C) at different depths in Lake Songsjøen in 1990–1991.

| Depth (m) | May | June | July I | July II | September | October |
|-----------|-----|------|--------|---------|-----------|---------|
| 1         | 4.0 | 12.5 | 13.8   | 13.2    | 13.0      | 7.0     |
| 2         | 4.0 | 11.5 | 13.7   | 13.1    | 13.0      | 7.0     |
| 4         | 4.0 | 8.4  | 13.3   | 13.0    | 13.0      | 7.0     |
| 5         | 4.0 | 7.9  | 13.3   | 12.8    | 13.0      | 7.0     |
| 6         | 4.0 | 7.5  | 13.0   | 11.3    | 13.0      | 7.0     |
| 7         | 4.0 | 7.1  | 12.5   | 9.6     | 13.0      | 7.0     |
| 8         | 4.0 | 6.8  | 12.0   | 8.4     | 12.5      | 7.0     |
| 10        | 4.0 | 6.5  | 11.4   | 7.8     | 10.0      | 7.0     |
| 15        | 4.0 | 5.9  | 6.2    | 7.1     | 10.0      | 7.0     |
| 20        | 4.0 | 5.5  | 6.1    | 7.2     | 8.0       | 6.8     |
| 25        | 4.0 | 5.3  | 6.0    | 7.3     | 8.0       | 5.8     |

**Table 2.** Number of sampled brown trout (BT) and Arctic char (AC) and number of stomachs analysed in six periods in Lake Songsjøen 1990–1991. S = small fish (BT: 10–14.5 cm; AC: 10–15 cm), MS = medium sized fish (BT: 14.5–19 cm; AC: 15–20 cm), L = Large fish (BT: > 19 cm; AC: > 20 cm).

| Period    | Sampled |          |     |     |          |    | Stomach Analysed |     |
|-----------|---------|----------|-----|-----|----------|----|------------------|-----|
|           | S       | BT<br>MS | L   | S   | AC<br>MS | L  | BT               | AC  |
| May       | 64      | 84       | 40  | 25  | 45       | 7  | 44               | 42  |
| June      | 192     | 92       | 62  | 81  | 82       | 18 | 69               | 71  |
| July I    | 74      | 40       | 15  | 74  | 110      | 8  | 52               | 71  |
| July II   | 60      | 55       | 15  | 20  | 78       | 17 | 59               | 53  |
| September | 69      | 117      | 20  | 42  | 51       | 12 | 66               | 48  |
| October   | 181     | 80       | 24  | 25  | 30       | 5  | 69               | 26  |
| Total     | 640     | 468      | 176 | 267 | 396      | 67 | 359              | 311 |

a full 24 h period. To reduce potential disturbance, the nets was reset approximately 50 m away from where they were emptied. Thus, any gill net position was re-used after 9 hours and with another mesh size. The time for sunrise and sunset was found in [www.timeanddate.com](http://www.timeanddate.com) for the nearest available position (Orkanger; 9 km from Songsjøen).

A total of 1284 brown trout (hereafter referred as BT) and 730 Arctic char (AC) were captured of which 366 and 315 stomachs, respectively, were analysed (Table 2).

### Treatment of material

We used the number of fish caught within each 3-hour period as a proxy for activity (catch per unit of effort, CPUE). We assumed that our fishing did not affect the population of either species, as number of fish captured and sampled was small relative to the estimated population size (see Langeland and L'Abée-Lund 1996).

The fish were killed by a blow to the head when captured. Total fish length (to the nearest 0.1 cm) was measured with the tail spread in a natural position. The fish were classified into three groups — small (10–14.5 cm for BT and 10–15 cm for AC), medium sized (14.5–19 cm for BT and 15–20 cm for AC), and large (> 19 cm for BT and > 20 cm for AC). We grouped BT and AC differently mainly because the three mesh sizes have different selectivity for the two species (Jensen 1995, Langeland and L'Abée-Lund 1996).

Stomachs were stored in 96% ethanol for later laboratory analyses. Due to the low number of large fish in many sampling periods, we did not include stomach analyses of large fish (BT > 19 cm; AC > 20 cm). Fish stomach contents were identified and counted, and body length (excluding appendages) of intact prey individuals was measured under a stereoscopic microscope. The stomach content was identified into 32 different food items (Table 3). In large samples containing zooplankton, a subsample of a tenth was counted and if possible, thirty individuals were measured. Recognizable fragments of prey were counted as intact specimen of the same taxon. The biomass of the different food items was estimated by dry weight, using regression equations between body length and mass as given by Bottrell *et al.* (1976), Langeland (1982), Hindar *et al.* (1988) and Langeland *et al.* (1991). Based on these estimations of mass, the proportion of each prey taxa within each stomach (excluding undetermined prey groups) were estimated and used for calculating the food resource overlap between BT and AC (Schoener 1968):

$$D = 1 - \frac{1}{2} \sum_{i=1}^n |(p_{xi} - p_{yi})|, \quad (1)$$

where  $p_{xi}$  is the proportion of prey group  $i$  used by species  $x$ ,  $p_{yi}$  proportion of habitat/prey group  $i$  used by species  $y$ , and  $n$  number of habitat/prey categories. The index gives  $D$ -values from 0 to 1, where 0 and 1 indicates no overlap and complete overlap, respectively. The diet similarity is considered to be biologically significant at an index value  $\geq 0.60$  (Wallace 1981). To illustrate sea-

**Table 3.** Grouping of food items identified in stomachs of brown trout and Arctic char in Songsjøen 1990–1991.

| Group                | Food items  |
|----------------------|---|
| Zooplankton          | <i>Bosmina longispina</i> , <i>Daphnia spp.</i> , <i>Holopedium gibberum</i> , <i>Diaptomus spp.</i> , <i>Cyclops scutifer</i> , <i>Leptodora kindtii</i> , <i>Heterocope spp.</i> , <i>Bythotrephes longimanus</i> , <i>Polyphemus pediculus</i> |
| Littoral crustacea   | <i>Eurycerus lammelatus</i> , <i>Sida crystallina</i> , <i>Gammarus lacustris</i>   |
| Zoobenthos           | Ephemeroptera, Tricoptera, Plecoptera, Coleoptera, Zygoptera, Ceratopogonidae, Gastropoda, Hirudinea, Pisidium, Hydracarina, undetermined   |
| Chironomids          | Chironomidae (larvae)   |
| Aquatic insect pupae | Chironomidae, Nematocera  |
| Surface insects      | Coleoptera, Formicidae, Nematocera, Arachnids, undetermined   |
| Fish                 | Arctic char egg   |

sonal variation in food choice between species, the 32 food items were grouped into seven distinct groups (zooplankton, littoral crustacea, zoobenthos, surface insects, chironomids, aquatic insect pupae, fish eggs; Table 3).

It should be commented that the stomach content at capture should be analysed with care, as many factors impact on digestibility and gut passage time (Amundsen and Sánchez-Hernández 2019). First, the feeding behaviour, food intake and digestive processes is substantially affected by temperature (Volkoff and Rønnestad 2020). These processes are reduced at cooler water temperature. Digestive processes decrease at temperature below the optimal range (Amin et al. 2016). Thus, stomach content should reflect food intake close to the time of capture when the water temperature is high, but will to a higher degree describe food intake over a longer time period when temperature is low. We are not aware of any quantitative estimates of how large this difference might be. Moreover, when the fish perform vertical migrations, food intake in one depth stratum will be considered as intake at the depth when caught. We are not able to adjust for these factors in the present sampling procedure. However, as we mainly compare species and size classes sampled at the same time intervals, we consider these issues of minor importance.

In order to test for variation in catch per unit of effort (CPUE) between species and among seasons and diurnal periods (night, day, dusk/dawn), we used generalized linear models with a Poisson error distribution and a log-link function. In this model, we also included an interaction between season and period. Size group and sample depths were not included in the model done due to lim-

ited statistical power, and potential trends are therefore only described qualitatively.

To test for variation in overall feeding activity in the two species, we summed the mass of all food items per individual and used that as a measure of feeding intensity. To test for how feeding intensity varied with light intensity, we collated the various 3-h sampling periods into three different light-intensity classes: night, day, dusk/dawn. We used a general linear model approach, using individual food mass (ln-transformed) as response variable, fish mass as co-variate (ln-transformed), and species, season (6 months) and light intensity classes (periods; 3 classes) as factors. In particular, we wanted to test for species differences among seasons and light intensity classes (periods) and therefor included the two-way interactions species  $\times$  season and species  $\times$  period.

All statistical analyses were performed in the program JMP Pro v16.1.0 (SAS 2021).

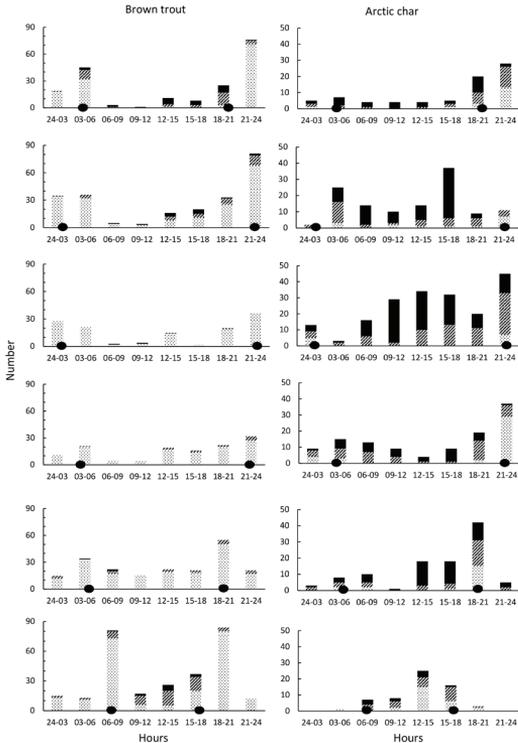
## Results

### Activity

We use the catch per unit of effort (CPUE; number of fish captured per 3-h period) as a measure of activity. Overall, CPUE was higher for the brown trout (BT) than the Arctic char (AC) (average; BT:  $24.4 \pm 7.5$  (SD), AC:  $14.0 \pm 5.7$ ). Overall, there was large variation in CPUE between species, and among seasons and periods during the diurnal cycle (Figs. 2 and 3; Table 4). We describe the overall variability in CPUE more qualitatively below.

**Table 4.** Effect test summary from a generalized linear model testing for variation in catch per unit of effort for brown trout and Arctic char caught in Lake Songsjøen during the ice-free season in 1990–1991. The model uses a Poisson error distribution and a log-link. The factors tested are species (BT and AC), season (May–October, 6 levels) and periods during the diurnal cycle (8 periods).

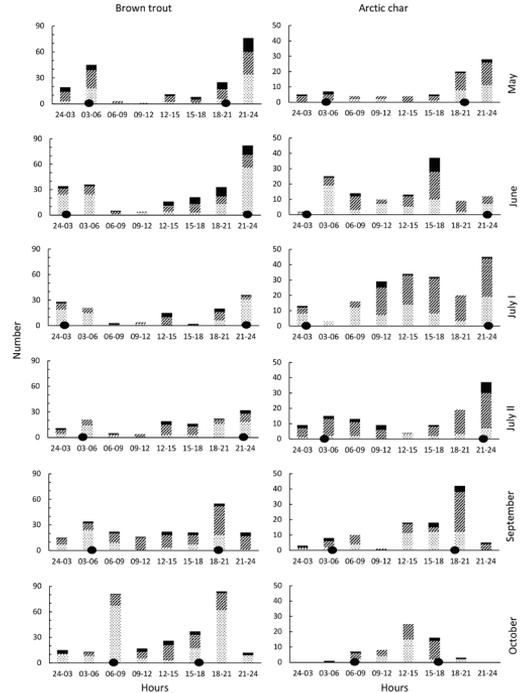
| Source                                | df | $\chi^2$ | <i>p</i> |
|---------------------------------------|----|----------|----------|
| <i>Species</i>                        | 1  | 85.2     | < 0.001  |
| <i>Season</i>                         | 5  | 47.4     | < 0.001  |
| <i>Period</i>                         | 7  | 183.6    | < 0.001  |
| <i>Species</i> $\times$ <i>Season</i> | 5  | 182.1    | < 0.001  |
| <i>Species</i> $\times$ <i>Period</i> | 7  | 118.3    | < 0.001  |
| <i>Season</i> $\times$ <i>Period</i>  | 35 | 463.8    | < 0.001  |



**Fig 2.** The gill net catch of brown trout (left panel) and Arctic char (right panel) at three depth intervals (dotted columns: 0–8 m; hatched columns: 8–16 m; solid columns: 16–24 m) in Lake Songsjøen during six months from 1990–1991. Time for sunrise and sunset is marked by circles.

The overall gill net catches showed that BT chiefly (82%) was caught in littoral areas down to 8 m depth and less in the 8–16 m (13%) and 16–24 m (5%) depth intervals. BT activity as measured CPUE differed considerably within and between seasons (months) (Fig. 2). Highest activity was in the periods close to dusk and dawn. However, this modal pattern was less pronounced in July, and September when water temperature reached the highest values (Table 1). In these three months, BT used the profundal areas (16–24 m) in a restricted manner compared with the other months, as number caught was 5 and 53, respectively. The diurnal variation in activity was especially pronounced for small BT, reduced in medium sized BT and not apparent in large BT (Fig. 3). BT was caught in all 3 h samplings throughout the study.

The overall gill net catches of AC contrasted that of BT. AC was chiefly (81%) caught in the

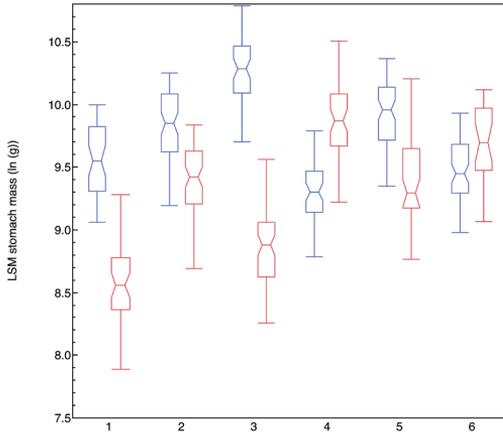


**Fig 3.** The gill net catch of three length groups of brown trout (left panel) and Arctic char (right panel) in Lake Songsjøen during six months from 1990–1991. Dotted columns: small fish (BT: 10–14.5 cm; AC: 10–15 cm); hatched columns: medium sized fish (BT: 14.5–19 cm; AC: 15–20 cm); solid columns: large fish (BT: > 19 cm; AC: > 20 cm). Time for sunrise and sunset is marked by circles.

8–24 m depth interval; 0–8 m (19.2%), 8–16 m (35.2%) and 16–24 m (45.6%). Although there was considerable difference in activity within and between seasons, AC showed less stringent pattern than BT (Fig. 2). In May, July and September, the highest AC activity corresponded with sunset. This was due to increased AC activity in the littoral areas in May, July II and September and in the 8–16 m depth interval in July. AC activity was overall higher in July than in the other months. In contrast to BT, no AC was captured during the dark hours in October. Both small- and medium-sized AC contributed to the increased diurnal activity (Fig. 3).

## Diet

The analysis of the total individual stomach content (as mass) demonstrated considerable variation

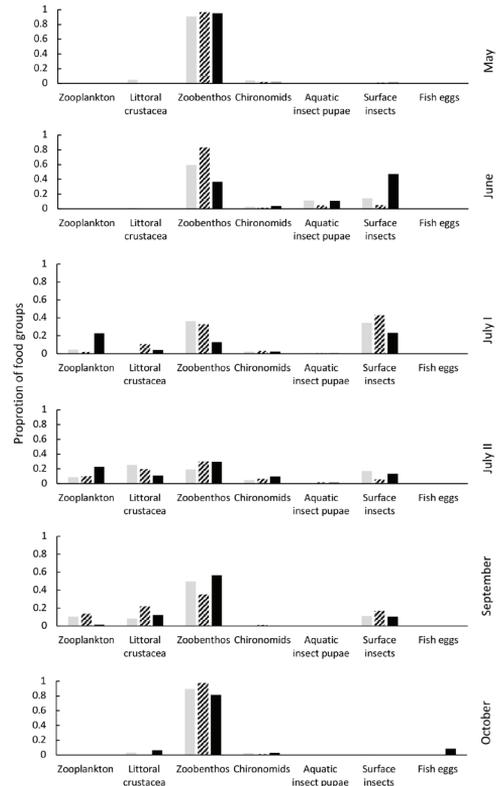


**Fig 4.** Notched box plot showing the Least Squares Mean estimates of seasonal variation in stomach mass ( $g$ ;  $\ln$ -transformed) for brown trout (blue colour) and Arctic char (red colour) caught in Songsjøen 1990–1991 (1 = May, 2 = June, 3 = July I, 4 = July II, 5 = September, 6 = October). For details see Table 4.

in both species during the season (Table 5). During the ice-free season the mass of the stomach content tended to increase over time in AC, whereas the stomach content mass in BT was highest during spring and summer and lower from late July to October (Fig. 4). The seasonal trend differed significantly between the species (Table 5B). There were also significant differences in total stomach mass among the diel time periods, with stomach mass being heavier during the night than during dusk and dawn for both species (Table 5A).

The diet of small and medium sized fish showed great similarities within both BT and AC, as the Schoener index exceeded 0.67 in all 12 comparisons (Table 6). Thus, we treated small- and medium-sized fish as one homogenous group when comparing the diet composition of BT and AC.

The diet of BT and AC did not differ from day to night as the Schoener index were high ( $> 0.6$ ) in 10 out of 12 periods (Table 6). The index was lower in June for BT (0.57) as the number of food items increased (*Cyclops* sp., *Gammarus lacustris*, *Pisidium* sp., Hirudinea, Nematocera). The index was relatively low for AC in September (0.41) as the intake of *Bosmina longispina* increased by night, and as *Polyphemus pediculus* and *Heterocoep* sp. were eaten at daytime but not during night.



**Fig 5.** Proportion of different groups of food items (see Table 3 for information) of small and medium sized brown trout (10–19 cm) caught in Songsjøen 1990–1991. Light columns: day; hatched columns: dusk/dawn; 6 dark columns: night.

The diet overlap between BT and AC was in general low (Table 6). The low overlap index demonstrate that BT and AC fed on different food items throughout the study period (Figs. 5 and 6). The index was higher ( $> 0.53$ ) in May, before the spring bloom, than in the other periods ( $< 0.51$ ) when AC fed almost exclusively upon zooplankton. However, in September aquatic insect pupae made up a significant part of the food of AC, but not BT. In this period aquatic insect pupae made up a higher proportion in the diet during day than at dusk/dawn and night.

## Discussion

The present study on the short-term variation in activity and feeding in brown trout and Arctic char during 24 h cycles from May to October

**Table 5.** Parameter estimates (A) and Anova summary (B) from the general linear model testing for variation in total stomach content mass (ln-transformed) for individual brown trout and Arctic char caught in Lake Songsjøen during the ice-free season in 1990–1991. Individual total mass (g; ln-transformed) was used as co-variate, and season (May–October) and period during the 24-h cycle (day, night, dusk/dawn) was used as factors. October, brown trout and dusk/dawn are set as the intercept in the model.

## A) Parameter estimates

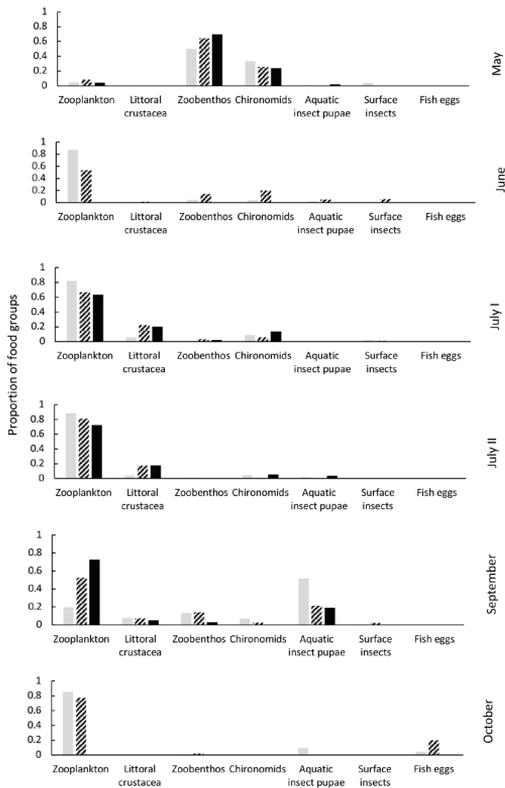
| Parameter                | Estimate ± se | t-ratio | p       |
|--------------------------|---------------|---------|---------|
| <i>Intercept</i>         | 7.90 ± 0.38   | 20.69   | < 0.001 |
| <i>Fish mass (g; ln)</i> | 0.50 ± 0.11   | 4.35    | < 0.001 |
| <i>May</i>               | -0.50 ± 0.13  | -3.57   | < 0.001 |
| <i>June</i>              | 0.11 ± 0.11   | 1.04    | 0.297   |
| <i>July I</i>            | 0.06 ± 0.11   | 0.53    | 0.591   |
| <i>July II</i>           | 0.07 ± 0.11   | 0.65    | 0.514   |
| <i>September</i>         | 0.13 ± 0.12   | 1.11    | 0.269   |
| <i>Arctic char (AC)</i>  | 0.21 ± 0.06   | 3.28    | 0.001   |
| <i>May × AC</i>          | 0.27 ± 0.17   | 2.16    | 0.032   |
| <i>June × AC</i>         | -0.01 ± 0.11  | 0.08    | 0.939   |
| <i>July I × AC</i>       | 0.52 ± 0.11   | 4.70    | < 0.001 |
| <i>July II × AC</i>      | -0.49 ± 0.11  | 4.34    | < 0.001 |
| <i>September × AC</i>    | 0.01 ± 0.12   | 0.12    | 0.901   |
| <i>Day</i>               | 0.04 ± 0.08   | 0.46    | 0.645   |
| <i>Night</i>             | 0.23 ± 0.10   | 2.21    | 0.028   |
| <i>AC × Day</i>          | -0.02 ± 0.08  | 0.23    | 0.817   |
| <i>AC × Night</i>        | -0.07 ± 0.10  | 0.66    | 0.507   |

## B) Anova table summary

| Source                  | df | Sum of squares | F-ratio | p       |
|-------------------------|----|----------------|---------|---------|
| <i>In body mass</i>     | 1  | 32.04          | 18.88   | < 0.001 |
| <i>Season</i>           | 5  | 22.22          | 2.62    | 0.023   |
| <i>Species</i>          | 1  | 18.22          | 10.74   | < 0.001 |
| <i>Season × Species</i> | 5  | 72.45          | 8.54    | < 0.001 |
| <i>Period</i>           | 2  | 17.50          | 5.15    | 0.006   |
| <i>Species × Period</i> | 2  | 1.94           | 0.57    | 0.565   |

**Table 6.** Food overlap, estimated as the Schoener index, for brown trout (BT) and Arctic char (AC) during six periods in Songsjøen 1990–1991. S = small fish (BT: 10–14.5 cm; AC: 10–15 cm); MS = medium sized fish (BT: 14.5–19 cm; AC: 15–20 cm); D = day; N = night; DD = dusk/dawn. \*D versus DD.

| Period           | S vs MS |      | D vs N |       | BT vs AC |      | N    |
|------------------|---------|------|--------|-------|----------|------|------|
|                  | BT      | AC   | BT     | AC    | D        | DD   |      |
| <i>May</i>       | 0.92    | 0.81 | 0.78   | 0.75  | 0.53     | 0.56 | 0.63 |
| <i>June</i>      | 0.78    | 0.89 | 0.57   | 0.64* | 0.11     | 0.13 |      |
| <i>July I</i>    | 0.78    | 0.73 | 0.71   | 0.78  | 0.10     | 0.08 | 0.10 |
| <i>July II</i>   | 0.67    | 0.70 | 0.65   | 0.78  | 0.25     | 0.34 | 0.51 |
| <i>September</i> | 0.71    | 0.73 | 0.76   | 0.41  | 0.31     | 0.37 | 0.12 |
| <i>October</i>   | 0.90    | 0.93 | 0.77   | 0.82* | 0.01     | 0.03 |      |



**Fig 6.** Proportion of different groups of food items (see Table 3 for information) of small and medium sized Arctic char (10–20 cm) caught in Songsjøen 1990–1991. Light columns: day; hatched columns: dusk/dawn; dark columns: night.

revealed great variation in diel activity throughout the ice-free season. Brown trout had mainly crepuscular activity in contrast to the diurnal and crepuscular activity of Arctic char. In both species, the increase in activity appeared chiefly in the littoral areas. Only small brown trout demonstrated a considerable diel variation in activity. The stomach content was higher in fish caught during night time than fish caught during diurnal and crepuscular phases.

The overall depth stratification and habitat use of brown trout and Arctic char resemble what have been reported repeatedly earlier (Nilsson 1965, Hindar and Jonsson 1982, Hegge *et al.* 1989, Langeland *et al.* 1991, Eloranta *et al.* 2013). However, some more complexity was evident when the 24 h diurnal cycle is split into 3 h periods (this study), or even into 1 h periods

(Hamley *et al.* 2017). We found that both species increased their littoral activity at sunset and that this increase was most evident in small-sized brown trout and small and medium sized Arctic char. Similar behaviour in both species indicate a similar response to common environmental factors.

Most animals can be classified as being either diurnal, nocturnal or crepuscular, since adaptations for activity at one light level tend to reduce efficiency at another (Fraser and Metcalfe 1997). Such diel habitat shifts have been explained to be due to a trade-off between predation risk and foraging profitability. This variation has been shown in threespine stickleback (*Gasterosteus aculeatus*, Milinski and Heller 1978), bluegill sunfish (*Lepomis macrochirus*, Werner and Hall 1988), perch (*Perca fluviatilis*, Eklöv and Persson 1996, Jacobsen and Berg 1998), roach (*Rutilus rutilus*, Eklöv and Persson 1996), Arctic char (L'Abée-Lund *et al.* 1993), and Atlantic salmon (*Salmo salar*, Fraser and Metcalfe 1997). Our study demonstrated that small brown trout but not Arctic char clearly showed crepuscular activity. The difference between the two species is probably a result of an anti-predator behaviour in the Arctic char. It seems that sympatric brown trout, regardless of size, use shallow areas — whereas Arctic char are more confined to deep epibenthic and pelagic areas (Nilsson 1965, Hindar and Jonsson 1982, Hegge *et al.* 1989, Langeland *et al.* 1991). The brown trout in Songsjøen, but not Arctic char, is known to predate juvenile Arctic char (L'Abée-Lund *et al.* 1992). In addition, different visual adaptation may affect their feeding ability (Elliott 2011). High crepuscular activity was not reflected in higher stomach content compared with diurnal or nocturnal catches. Instead, the largest total mass of the stomach content was found in fish caught during night. One reasonable explanation for this is that the digestive processes is too slow compared with our 3 h sampling procedure. The vertical migration of small and medium sized Arctic char add more complexity to the interpretation of the diel variation in stomach content as the water temperature especially in July was much higher in the littoral than at depth of 15 m. Thus, food items eaten at larger depth will remain in the stomach for a longer time, and

appear to be eaten in the littoral where the fish were caught. We are not able to adjust for this in our study.

The different diel activity levels in brown trout and Arctic char may also be explained by the behaviour of their main prey types. Brown trout relies chiefly upon aquatic insects which have distinct synchronized diel emergence patterns at low light intensities at dusk or night (Elliott 1971, Brittain 1982, Jackson 1988). In contrast, Arctic char converge on zooplankton, which often have distinct vertical migrations being in the upper water layers at night (Bandara *et al.* 2021). Despite these vertical diel migrations, Arctic char demonstrated high diurnal and crepuscular activity in June and July when a bloom of zooplankton usually appears. Before and after the bloom, in May and October, respectively, the activity was crepuscular. In May, zoobenthos constituted a major part of the diet, and in October zooplankton was the main food item.

The main predator in this system is large-sized brown trout, although we cannot rule out predation by mammals (e.g. mink (*Mustela vison*)) or birds. Brown trout is a visual predator and therefore most likely a diurnal predator. Thus, our result lends support to the explanation that activity is flexible and structured by both predation risk and food availability. However, in their study of an allopatric Arctic char, Hamley *et al.* (2017) showed that photoperiod had a major impact on the activity rhythms. In late winter and spring, Arctic char activity ensued as diel vertical migration, and ceased during the polar day with a sharp increase in arrhythmic fish activity occurring at ice-break. This arrhythmic behaviour continued through June to late July. However, diel rhythms of activity were observed for much of the year in Ellasjøen, where Arctic char recorded the greatest activity during dawn, dusk and daylight (Hamley *et al.* 2017). Our results of diel activity in a sympatric Arctic char population, coincide to a large extent with that of the Ellasjøen Arctic char. Similar activity pattern in allopatric and sympatric Arctic char, at least during summer, may lend support to a hypothesis that daily and seasonal activity pattern is a product of distinct cycles for feeding, growth and reproduction (Hamley *et al.* 2017), and not a result of interspecific competition. The pres-

ence of interspecific competition in brown trout-Arctic char systems has been debated (Persson *et al.* 2013). In their long-term study of brown trout and Arctic charr in Lake Takvatn (northern Norway), Persson *et al.* (2013) showed that the population dynamics of Arctic char and brown trout mostly is based on interspecific predation (brown trout eat Arctic char) and intraspecific density dependence in Arctic char and not interspecific competition.

The diet overlap of brown trout and Arctic char was low in all periods except May, before the plankton boom. In general, the diet of brown trout and Arctic char in Songsjøen was in accordance to what has been found in previous studies of the two species in sympatry (Nilsson 1965, Nilsson and Pejler 1973, Svärdsen 1976, Dervo *et al.* 1991, Forseth *et al.* 2003, Eloranta *et al.* 2013). Brown trout is described as a food generalist and Arctic char as an efficient zooplankton predator. In allopatric populations, Arctic char use littoral areas to a larger extent and eat food items similar to that of brown trout (Nilsson 1965, Langeland *et al.* 1991), and zooplankton may be important food items also for brown trout (Klemetsen 1967). In experimentally enclosures, sympatric brown trout and Arctic char showed distinct niche segregation, and Arctic charr did not expand their niche in allopatry, indicating that the two species compete to a limited degree for the same resources (Forseth *et al.* 2003).

Few studies have been carried out to elucidate the variation in activity in brown trout and Arctic char at a finer temporal scale (see Hamley *et al.* 2017 for Arctic char). Dervo *et al.* (1991) studied diel food selection in pelagic Arctic char and brown trout in Lake Atnsjø, SE Norway, from July-September. The 24 h cycle were divided into four equal periods, and they found that Arctic char feed almost exclusively on zooplankton both day and night, while brown trout had a diurnal shift in diet. For brown trout, zooplankton made up a considerable part of the diet in the daytime, while at night the diet consisted mainly of surface insect and chironomid pupae. Our study contradicted the results of Dervo *et al.* (1991), as we did not find a diel shift in the diet, neither in Arctic char nor brown trout. One reasonable explanation could be different biomass of fish. The biomass of both brown

trout and Arctic char was higher in our lake than in lake Atnsjøen. Based on monthly epibenthic catches during night (CPUE / 12 h × 100 m<sup>2</sup>), the CPUE in our lake varied between 30.7–74.2 for brown trout and 3.6–34.2 for Arctic char, and in Atnsjøen 14.6–27.7 for brown trout and 2.3–20.8 for Arctic char (Hegge *et al.* 1989). This indicates that the food interaction between brown trout and Arctic char was higher in Songsjøen. The feeding on zooplankton of the large Arctic char population in Songsjøen, makes zooplankton a food item of minor importance for brown trout. In contrast, zooplankton was an important food item for brown trout in Atnsjøen from July through September (Derivo *et al.* 1991).

In our study, the level of activity reflects spatial distribution of foraging fish. Spatial distribution of foraging animals is strongly influenced by the abundance of potential predators as well as by food availability. In field enclosures, Jacobsen and Berg (1998) showed a significant diel variation in habitat use by 0+ perch under predation risk by using open water habitat at night and migrating into the macrophytes in the morning. Metcalfe *et al.* (1999) showed by using passive integrated transponder tags that winter diel activity patterns in juvenile Atlantic salmon was dependent on food availability and that a change in food density led to a parallel change in time spent in the refuge.

## Conclusions

We have documented that the activity of brown trout and Arctic char is dynamic and largely connected to the solar phase. Brown trout demonstrate an overall crepuscular activity pattern. Arctic char, on the other hand, demonstrate a more complex diel activity pattern. The activity pattern is predominately crepuscular in May, July II and September, and predominately diurnal in June, July I and October. The diel variation in activity was reflected in variation in stomach content in both species, but with highest values in night catches. The diet overlap of brown trout and Arctic char was high before the spring bloom, and was reduced when Arctic char fed almost exclusively upon zooplankton after the bloom and brown trout continued feeding on

other organisms than zooplankton. Our results characterize both brown trout and Arctic char as indiscriminate particulate feeders and that neither species had a diel change in their feeding mode.

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*Data Availability:* The data that support the findings of this study are available from the corresponding author upon reasonable request.

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