Size and temperature dependent foraging capacities and metabolism: consequences for winter starvation mortality in fish

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The foraging related capacities, energy requirements and the ability of individuals to withstand starvation are strongly dependent on body size and temperature. In this study, we estimated size-dependent foraging rates and critical resource density (CRD) in small Arctic char (Salvelinus alpinus) under winter conditions and compared these with previous observations under summer conditions. We investigated if starvation mortality is size-dependent in the laboratory, and we assessed the potential for winter growth and the occurrence and size dependency of winter mortality both in a large scale pond experiment and in natural lakes. The efficiency of foraging on macroinvertebrates increased with size but was lower at 4 than 12°C, still CRD was lower at 4 than 12°C as metabolic rates decreased faster than foraging efficiency with temperature. When starved, small char died before large and at rates which suggest that YOY char need to feed during winter to avoid starvation. Results from both our pond experiment and field study indicate that survival of YOY char over winter is high, despite severe winter conditions, because YOY char are able to feed and grow during winter. In seasonal environments with declining resources, the size scaling and temperature dependency of foraging and metabolic demands may provide conditions which can favour either small or large individuals. This size advantage dichotomy relates to that larger individual’s by having a higher CRD are more likely to start starving, but once resource levels are below CRD for all size classes, small individuals starve to death at a higher rate. Negative size-dependent winter mortality from starvation is suggested to be more pronounced in species that are not adapted to feed at low temperatures and in species feeding on zooplankton, since zooplankton abundance, in contrast to macroinvertebrate abundance, is generally low during winter.


The ability of individuals to find, capture and process food, together with the ability to withstand starvation and individual energy requirements are all strongly dependent on body size (Werner and Gilliam 1984, Persson et al. 1998, Post et al. 1999, Biro et al. 2004, Byström and Andersson 2005). The size dependency of both foraging related capacities and energy requirements has major effects on size related responses to decreasing resource levels, since in general smaller individuals can sustain themselves at lower resource levels than larger individuals (Werner 1994, Persson et al. 1998, Aljetlavi and Leonardsson 2002, Byström and Andersson 2005). This relates to that the size scaling of foraging capacity increases with a lower exponent than that for metabolic

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rate, so that the critical resource density (CRD, i.e. the resource density at which energy intake balances metabolic demands) increases with increasing body size (Persson et al. 2000, Bystro¨m and Andersson 2005). On the other hand, once access to resources becomes so limiting that starvation is initiated, larger individuals can withstand starvation for longer time periods than smaller individuals because of their higher ratio of energy reserves to metabolic rate (Post and Parkinson 2001). In addition, all foraging related capacities, as well as other vital rates in ectotherms, are strongly dependent on temperature, in turn imposing strong constraints on energy acquisition, physiological adaptations and behaviour (Gregory 1982, Schultz and Connor 1999, Garvey et al. 2004, Biro et al. 2005, Larsson et al. 2005).

With declining temperatures, energy costs are reduced and many ectotherms are generally assumed to become dormant, avoiding biotic interactions and rely heavily on accumulated energy reserves (Shul'man 1960, Gregory 1982, Bodie and Semlitsch 2000, Garvey et al. 2004). Temporally variable environments may thus induce periodic constraints in individual resource acquisition and necessitate storage of energy reserves in order to survive periods with strong resource limitation (Shul'man 1960, Gregory 1982, Werner and Gilliam 1984, Post and Parkinson 2001). In temperate regions, starvation mortality during winter has been suggested to be a major cause of mortality in young-of-the year (YOY) fish due to their small size and consequently low ratio of energy stores to metabolic rates (Oliver et al. 1979, Toney and Coble 1979, Byström et al. 1998, Biro et al. 2004). Although there are several studies supporting that smaller individuals experience higher mortality rates than larger individuals over winter, this is not always the case (Copeland and Carlile 1998, Garvey et al. 1998, Fullerton et al. 2000, Pratt and Fox 2002, Connolly and Petersen 2003). In fact, in many cases the causal mechanism for observed size-dependent mortality in natural systems is unknown but is assumed to be due to size-dependent depletion of energy reserves followed by starvation mortality, based on collaborating evidence from experimental studies at small scales (Byström et al. 1998, Post et al. 1998, Curry et al. 2005). In this study we investigate if winter mortality is present and size-dependent in YOY Arctic char (Salvelinus alpinus). The Arctic char is a circumpolar species found in subarctic and Arctic lakes, where ice cover may last for more than 10 months (Svensson and Gullestad 2002, Klemetsen et al. 2003a, 2003b). Char have also been reported to be able to feed under winter conditions with ice cover and low temperatures (Brånnäs and Wiklund 1992, Klemetsen et al. 2003a). Since char are able to feed under winter conditions, we hypothesize that survival over winter in YOY char should follow the allometric rules for the CRD concept, in which small individuals are less likely to starve compared to larger individuals, rather than the allometric rules of starvation, were the ratio of energy reserves to metabolism causes small individuals to starve at faster rates than larger individuals. Hence we expect to find no evidence for negative size selective starvation mortality over winter in char.

Specifically, we estimated size-dependent foraging rates of small char at 4°C which were subsequently used to estimate CRD at this temperature. These results were then compared with previously derived estimates of CRD obtained at higher temperatures which allowed us to study how CRD scales to both size and temperature. Secondly, in laboratory experiments we investigated if lipid depletion rates and starvation mortality is size-dependent. Third, we conducted a large scale pond experiment during winter to estimate size-dependent growth responses and to investigate whether winter mortality is size-dependent in char. Finally, we investigated if the results from above studies were valid in natural subarctic lakes by measuring size and lipid changes in small char over winter and by estimating survival over winter in YOY char.

**Methods**

**Fish used for foraging, starvation and pond experiments**

In all foraging experiments, in this study and in previously reported (Byström and Andersson 2005) and in the starvation and pond experiment we used off-springs from wild caught parents originating from Lake Torrön (63°49’13”N, 13°06’19”E). For the foraging experiment, char were reared to the desired size in the laboratory or in a commercial rearing station. To create a size range of relatively small char in autumn for the starvation and pond experiment, char were reared in two rearing tanks over summer under a cold water temperature regime (6–9°C temperature range) and fed at six times a day at low ration levels using commercial dry pellets.

**Foraging experiments, attack rate estimates and estimations of CRD**

We used our own previously published data for attack rates and CRD at 12°C, with benthic chironomids as food resource (Byström and Andersson 2005), and performed similar experiments and calculations of CRD for char in the size range of 1.0 to 4.5 g, at a temperature of 4°C. Fish (n = 12) were fed with chironomids for a minimum of two weeks prior to movement to individual aquaria, and thereafter they were trained in the specific experimental procedure for another week. All experiments were performed on single
individuals at a temperature of 4 °C in aquariums with a volume of 30 l. The aquaria were covered with black plastic on three sides and light was provided from above using fluorescent tubes. Before the start of the trial, the fish was put behind a non-transparent plastic sheet, resulting in a smaller holding chamber and a larger performance arena. Thereafter the appropriate density of prey was added. We used frozen chironomids (size, 9.6 ± 2.4 mm, mean ± 1 SE) at densities of 0.3, 0.4, 0.5, 0.6, 0.7, 0.8 dm⁻², which were individually placed in 2.5 × 2.5 cm plastic patches (eight in total) made out of doormats (Astroturf®) which were evenly distributed on the bottom of the aquaria. We measured the time between the attack on the first and third chironomid to avoid saturation effects affecting our estimates. Handling time was measured separately at high chironomid density as the time between an attack and when the char started searching once again. To estimate the attack rates, we fitted the capture rate measurements to a Holling type II functional response function using non-linear regression techniques:

\[ C = \frac{aR}{1 + ahR} \]  

where C is capture rate, a is attack rate, R is resource density, and h is handling time.

We assumed temperature dependency in the allometric scalar constants for the attack rate, metabolic demand and digestion capacity, whereas the allometric (size-scaling) exponents are assumed to be independent of temperature (Jobling et al. 1993). To obtain a size-dependent attack rate for chironomids at 4 °C, we then fitted all individuals attack rates to the equation:

\[ a(w) = bw^\beta \]  

where a(w) is the attack rate of an individual of weight w, b is the allometric scalar and the allometric exponent β is assumed to be 0.3 (Byström and Andersson 2005). To calculate the critical resource density (CRD, i.e. the minimum resource density required for an individual to cover its metabolic costs), we assumed that the intake rate must equal the metabolic demands:

\[ c\left(\frac{a(w)R}{1 + a(w)H(w)R}\right) = m(w) \]  

where R is density of chironomids, a(w) is the attack rate as a function of weight, c is the conversion factor with a value of 0.61 (Claessens et al. 2000), m(w) is the metabolic demand and H(w) is digestion rate as a function of weight. We assume that metabolic rate can be expressed by a power function:

\[ m(w) = m_1w^{m_2} \]  

where \( m_1 \) equals 0.015 (g day⁻¹) at 4 °C and \( m_2 \) equals 0.76 (Elliott 1976, Jobling et al. 1993). Similarly, digestion time is expressed by:

\[ H(w) = \xi_1w^{\xi_2} \]  

where \( \xi_1 \) equals 11.7 (day g⁻¹) at 4 °C and \( \xi_2 \) equals −0.66 (Jobling et al. 1993). Rearranging Eq. 4, the critical resource density (CRD) can be expressed as:

\[ \text{CRD} = \frac{m(w)}{a(w)(c - m(w)H(w))} \]  

**Laboratory starvation experiment**

On the same date as the start of the pond experiment, a random sample of 24 YOY char (size range; 48 mm, 0.68 g to 82 mm, 3.86 g) from the rearing tanks were randomly and individually placed in 2.5 l aquaria (20 × 12 × 11 cm). Based on their length, individuals were then assigned to one of three size classes; small (n = 9) medium (n = 8) or large (n = 7) (average length and weight ± 1 SD, small; 55.7 ± 3.8 mm, 1.17 ± 0.21 g, medium; 63.6 ± 4.2 mm, 1.83 ± 0.35 g, large; 75.0 ± 5.2 mm, 2.84 ± 0.61 g). Aquaria were placed in an indoor water channel (length 3.6 m, width 0.4 m, water depth of 0.09 m) in a cooling room (set to 4 °C) with a 4:16 h day:night light regime, and had a continuous flow of water (4 °C, range 3.8–4.1 °C) from an inlet at one end of the water channel to an outlet at the other end. The aquaria had small holes on each short side and were positioned in the water channel such that water was continuously exchanged as it flowed through the aquaria. Every second day the aquaria were checked for dead fish. Date of death was noted and the length and weight of dead individuals recorded prior to freezing for later analysis of lipid concentrations. The experiment was terminated after 165 days, when length and weight measures of surviving individuals were recorded prior to freezing for later analysis of lipid concentrations. At that time 100% of small-, 62% of the medium- and 43% of the large individuals had died. In order to have enough material to analyse lipid contents, both dead and live char at termination of experiment were included in samples for medium and large size classes of char. Since lipids are the initial energy source for starving young fish (Jobling 1995), the estimated lipid levels in medium and large char, most likely still give a relatively correct estimate of the minimum lipid levels in char prior to death from starvation.

**Pond experiment**

We conducted a large scale pond experiment to estimate size-dependent growth responses and to test whether winter survival of YOY Arctic char is size-dependent. The experiment was carried out in two closely adjacent experimental ponds (32 × 10.8 m) in Umeå, north-central
Sweden. Each pond was divided into eight enclosures (size 4 x 10.8 m, mean water depth 0.90 m) with a reinforced dark green plastic sheet. Both ponds had a narrow vegetation belt of Carex sp. along the shoreline. To each enclosure a set of artificial plastic crates was added, which provided additional structural complexity to the shore line of each enclosure. Each crate set was constructed by using four plastic bottle crates (0.39 x 0.25 x 0.25 m), each attached at the base to a plastic plant crate (0.38 x 0.38 x 0.07 m), and linked together. Each shore side of the enclosures received one crate set which was positioned just below the water surface, covering 1.6 m (45%) of the width of the shore line.

Previous studies on char performance in these ponds have shown that growth rates differ between ponds due to variation in submerged vegetation cover, which in turn affect the available macroinvertebrate resource densities (Andersson et al. 2005, Byström and Andersson 2005, Nilsson 2005). Henceforth, in our analysis we use the terminology low and high productive pond to refer to the pond with low and high availability of resources, respectively.

We used a design with three single YOY char size class treatments with 50 individuals each (corresponding to a density of 1.2 individuals m⁻²) of small; 54.1 ± 6.15 mm, 1.32 ± 0.47 g, medium; 65.6 ± 4.53 mm, 2.34 ± 0.47 g) and 50 large; 76.5 ± 5.26 mm, 3.84 ± 0.90 g (mean ±ISD) YOY char, respectively in each enclosure. We randomly assigned the enclosures within each pond to two replicates of each of the three treatments. On the 21st of October when the enclosures were covered with a thin ice layer, YOY char were introduced into the enclosures via a small hole in the ice at the shore line of each enclosure. The following spring, immediately after the ice had disappeared, the enclosures were sampled with a seine net for surviving char between 31st May and 2nd of June (depending on variation in ice break up time between enclosures). Captured char were directly stored on ice and thereafter frozen for later measurements of length, weight and lipid concentrations.

During the experimental period, water temperature was recorded at 4 h interval, using a logger placed close to the bottom of each pond in one of the enclosures. There were no differences in temperature between ponds, with temperature varying from 4.1°C at the start, to 1.9°C in late February and to 4.4°C at ice break at the end of the experiment with an average temperature ±1 SD of 3.1 ± 0.96°C overall.

Mortality of char in one enclosure (size class medium) in the high productive pond was extremely high (96%) compared to the mortality (0–20%) in all other enclosures. This enclosure had the highest densities of submerged vegetation in autumn and as a smell of anaerobic breakdown products was present in spring from that enclosure, we strongly suspect that the oxygen level in that pond was reduced, due to high decomposition of vegetation, to levels below what is needed for char survival. Hence, data from this enclosure was excluded from further analysis.

**Lake study**

Data on YOY char performance in natural systems were obtained from three small subarctic lakes in northern Sweden. The dynamics of allopatric char populations have been intensively studied during the years 2000–2004 in these lakes (Byström et al. 2004, Byström and Andersson 2005, Byström 2006). Two of the lakes, Vuorejaure (4.9 ha, max depth 8.2 m, 712 m a.s.l.) and Ruozutjaure (3.8 ha, max depth 8.5 m, 710 m a.s.l.) are very similar in temperature regimes, chemical characteristics and morphometrics, and situated 2 km from each other. The third, Lake Suorujaure, is larger (16.9 ha, max depth 16 m, 993 m a.s.l.) and positioned 22 km from the other two lakes. Due to its higher altitude, Lake Suorujaure has a cooler temperature regime compared to the other two, and consequently smaller YOY sizes at the end of the first growth season (Byström et al. 2004). For more detailed information on lake surroundings and characteristics, see Karlsson et al. (2001) and Byström et al. (2004).

Densities of YOY char in autumn were high enough in Lake Ruozutjaure (2000) and in Lake Vuorejaure (2003) to enable estimation of both autumn densities of YOY char and the following spring densities of then 1-year old char based on Petersen’s mark–recapture estimates in closed populations. In September, YOY char were captured by electrofishing along the whole shore line of the lake and marked with blue dye injected using a Pan Jet Injector (Hart and Pitcher 1969) and thereafter evenly redistributed along the shoreline. The following day, a second electrofishing was conducted to obtain recaptures for YOY char density estimation. Similar methods were applied to obtain a density estimate of 1-year old char the following spring with the exception that 1-year old char were also captured using additional net traps (mesh size 6 mm). In those two years, size changes in char from autumn to the following spring were also analyzed. For more details on sampling methods see Byström et al. (2004) and Byström and Andersson (2005).

To analyze the general patterns in natural lakes of size-dependent lipid levels and the differences in lipid levels between autumn and spring, samples of YOY char and 1-year old char were obtained for analysis in all three lakes during the study years. Samples were either preserved in alcohol, or if possible deep frozen the same day.
Lipid analysis

To obtain sufficient material (>3 g) to analyze lipid concentrations, we had to pool char into groups of 2–5 depending on the size of the individuals. Sizes used were as homogenous as possible within pooled groups. Individual fish in samples were length measured and the pooled sample of intact fish was weighed and then homogenized. Lipid concentrations were expressed at the individual level as the average char size (length or weight) of the sample, with estimated lipid concentration divided by number of individuals in the sample. For the analysis of body composition of fat we used mid infrared transmission (MIT) spectroscopy technique (Elvingsson and Sjauua 1992). The equipment (Miris AB, Uppsala, Sweden) was calibrated for fish tissue using standard analytical methods for the compounds in question (Kiessling et al. 2004).

Calculations of maximum growth rate, treatment of data and statistical analysis

A Ratkowsky growth model (Larsson et al. 2005) incorporating the temperature dependency of maximum growth rate was used to estimate maximum YOY char size at the end of the pond experiment. We used initial size of the three size classes of YOY char as start size in the model and integrated the estimated temperature dependent daily maximum growth rates to obtain the maximum size of YOY at the end of the experiment. Temperature data were obtained on a daily basis from the temperature logger positioned at the bottom of one enclosure in each pond. For details on parameter values in the model and calculations see Bystrøm et al. (2004) and Larsson et al. (2005). Proportion of maximum growth rate was calculated as the ratio between observed specific growth rates (Eq. 8) in the ponds and predicted maximum specific growth rate from the growth model:

$$\text{Specific growth rate} = \frac{\ln(w_2) - \ln(w_1)}{t}$$  
(8)

where $w_1$ is start weight, $w_2$ is final weight and $t$ number of days equal to 221.

Since char body weight loss when starved exceeded initial lipid mass at the start of the experiment by almost two orders of magnitude (see results from starvation experiment) we related estimated lipid mass to char length, rather than calculate ratios of lipid to body mass. Differences between initial lipid mass and final lipid mass following the experimental treatments where then analyzed using analysis of covariance (ANCOVA), with char length as covariate. Dependent variables from the pond experiment were transformed to meet the distribution and homogeneity assumptions of univariate ANO-

Results

Foraging capacity and critical resource demands

Attack rates on benthic chironomids increased with char size at 4°C (non-linear regression, $r^2 = 0.36$, $P < 0.01$, Fig. 1a). In comparison, the constant $b$ at 4°C was approximately half of that the constant $b$ at 12°C, $b_4 = 0.58 \pm 0.11$ (±95% CL) and $b_{12} = 1.1 \pm 0.12$ (Bystrøm and Andersson 2005). Critical resource density (CRD) increased with char size at 4°C (Fig. 1b). Although attack rates were lower at 4°C than 12°C, CRD was lower at 4°C than 12°C due to the relatively larger decrease in metabolic demands with increasing temperature (Fig. 1).

Fig. 1. (a) The size-dependency of the attack rate of Arctic char feeding on benthic macrovertebrates (chironomids) at 4°C (filled line) and at 12°C (dotted line, from Bystrøm and Andersson 2005). Hatched lines represent the 95% CL of the estimated relationship at 12°C. (b) Corresponding critical resource density (CRD) at 4°C (filled line) and 12°C (dotted line) respectively.
Starvation experiment

Average survival time increased with char size (Table 1) (one-way ANOVA $F_{2.21} = 3.45$, $P = 0.05$). Large char lost more weight than small char (one-way ANOVA $F_{2.21} = 8.80$, $P = 0.002$) whereas there was no statistical difference between differently sized char in final lipid mass (one-way ANOVA $F_{2.3} = 0.39$, $P = 0.73$) (Table 1, Fig. 3).

Pond experiment

Survival (average ± 1 SD) over the winter for the three size classes of char (small; $84 ± 8\%$, medium; $98 ± 3\%$ and large; $87 ± 10\%$, data pooled for ponds), was high and independent of both size and pond (two-way ANOVA, size $F_{2.5} = 2.41, P = 0.18$; pond $F_{1.5} = 0.002, P = 0.97$; size × pond $F_{2.5} = 0.28, P = 0.77$). Char increased in weight over the winter, but the weight increase was generally higher in the high productive than in the low productive pond (two-way ANOVA, size $F_{2.5} = 255.3, P < 0.001$; pond $F_{1.5} = 188.2, P < 0.001$; size × pond $F_{2.5} = 19.7, P = 0.004$, Fig. 2). Growth rate was size-dependent, and small char grew at maximum rate in the high productive pond and in general smaller char grew closer to maximum rate than larger individuals (two-way ANOVA, size $F_{2.5} = 39.5, P = 0.001$; pond $F_{1.5} = 150.6, P < 0.001$; size × pond $F_{2.5} = 8.85, P = 0.02$, Fig. 2). As indicated by the significant interaction term, these patterns were stronger in the high than in the low productive pond.

Lipid levels at the end of the experiment were higher in the high productive than in the low productive pond (ANCOVA, pond as factor and length as covariate, pond; $F_{1.41} = 28.0, P < 0.001$, length; $F_{1.41} = 0.001$, Fig. 3). There was no statistical difference between start and end levels of lipids in the high productive pond whereas in the low productive pond lipid levels were lower at the end than at the start of the experiment (ANCOVA, start and end (time) as factor and length as covariate: high productive pond, time; $F_{1.29} = 0.007, P = 0.932$, length; $F_{1.29} = 1.14, P = 0.30$, low productive pond, time; $F_{1.33} = 84.3, P < 0.001$, length; $F_{1.33} = 30.1, P < 0.001$, Fig. 3). Lipid levels were dependent on body length at the start of the experiment, but at the end of the experiment this was true only in the low productive pond (Fig. 3).

Lake study

There was no evidence for a decrease in cohort densities over winter when comparing autumn estimates of YOY with estimates of one-year-old the following spring (Fig. 4) and size of char increased by approximately 20 mm from autumn to the next spring (t-test of size difference, Lake Vuorejäure, $t = 26.2, P < 0.001$, Lake Vuorejäure, $t = 27.0, P < 0.001$, Fig. 4). There was no difference in lipid mass between spring and autumn in small char (ANCOVA, with autumn and spring (season) as grouping variable and length as covariate, season; $F_{1.27} = 0.24, P = 0.88$, length; $F_{1.27} = 26.9, P < 0.001$) and both spring and autumn lipid biomass were higher than that of experimentally starved char (Fig. 5).

Discussion

Temperature-dependent foraging capacities, CRD and winter starvation mortality

Survival of YOY char was high over the winter in both our pond experiment and in the lake study, and results from the pond study also suggested that it was independent of size. However, the results from our laboratory starvation study also showed that char may indeed starve to death over winter if they are not able to feed, and that small char if not feeding, are more likely to starve to death than larger individuals.

Our estimates of temperature dependent foraging efficiency in char suggested that small char are able to feed at low temperatures, although foraging capacity decreased with decreasing temperature. However, since metabolic demands decreased to a greater extent from 12°C to 4°C than did foraging capacity, the estimated critical resource density (CRD) decreased with decreasing temperature. Thus, char can meet their metabolic demands at lower resource levels at low temperatures than at high temperatures, and because CRD also increased with char size, smaller individuals can sustain

<table>
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<th>Survival (days) ± 1SD</th>
<th>Small</th>
<th>Medium</th>
<th>Large</th>
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</thead>
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<tr>
<td>Weight start (g) ± 1SD</td>
<td>1.23 ± 0.21</td>
<td>1.83 ± 0.35</td>
<td>2.84 ± 0.61</td>
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<tr>
<td>Weight end (g) ± 1SD</td>
<td>0.83 ± 0.13</td>
<td>1.26 ± 0.39</td>
<td>1.93 ± 0.65</td>
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<tr>
<td>Lipids start (g) ± 1SD</td>
<td>0.049 ± 0.011</td>
<td>0.077 ± 0.002</td>
<td>0.14 ± 0.013</td>
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<tr>
<td>Lipids end (g) ± 1SD</td>
<td>0.009 ± 0.005</td>
<td>0.012 ± 0.008</td>
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<tr>
<td>Lipid loss (g)</td>
<td>0.04</td>
<td>0.065</td>
<td>0.127</td>
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themselves at lower resource levels than larger individuals. Hence, so long as char are able to feed, small individual are less likely to starve than larger individuals. This agrees with findings of Brännäs and Wiklund (1993), who demonstrated that char can grow at low temperatures under cultivation conditions. Char also have capacity to feed when light levels are low (Ali et al. 1984), and adult char are known to feed in natural systems under ice cover in winter (Klemetsen et al. 2003a). Correspondingly, the results from our large-scale pond experiment and our lake study showed that YOY char were able to grow (and hence feed) under natural winter conditions with ice and snow cover. The growth responses under winter in our pond experiment were also in line with the CRD concept or its analogue, the maximum growth resource density $G_{m\text{RD}}$ (Byström and Andersson 2005), since smaller char had higher growth rates in relation to maximum growth rate than larger individuals.

Because small char starve to death during winter if unable to feed, the critical factor for their survival over winter is availability of resources during this period. Since even small char mainly feed on benthic invertebrates (Byström et al. 2004), variation in zooplankton abundance as an energy source during winter should be of minor importance compared to variation in benthic invertebrate abundance. Benthic invertebrate abundance is also generally higher during winter than in summer in many northern lakes, because new cohorts of invertebrates hatch in autumn and grow over winter (Nyman 1973, Welch 1976, Brittain 1978, Lillehammer 1978). Correspondingly, in our study lakes there was no evidence of lipid loss over winter and growth was instead substantial over winter in YOY char. A study of larger adult char has also showed that estimated daily energy intake is similar to metabolic rates in winter, suggesting that even large char can meet their metabolic demands during winter conditions (Klemetsen et al. 2003a). Hence, it seems unlikely that small char will experience resource level below CRD during winter.
Thus our results from our pond experiment and study lakes, firstly suggest that over winter survival is generally high in YOY Arctic char. Secondly, our results suggest that negative size-dependent starvation mortality is not an important mortality factor over winter for small char, in turn related to a) adequate availability of macroinvertebrate resources during winter, b) the ability of char to feed during winter and c) the low CRD for small char together with the increase in CRD with char size.

General patterns of size-dependent winter mortality

It has been argued that winter mortality in fish generally should be negatively size-dependent, since smaller individuals have a smaller ratio of reversible mass (e.g. stored lipids) to metabolic rate than larger individuals, and also a minimum size threshold has been postulated (Post and Evans 1989, Madenjian et al. 1996, Bystrom et al. 1998, Post et al. 1998, Pratt and Fox 2002, Biro et al. 2004). However, as in this study, contradictory results are present, reporting similar and/or low mortality rates among differently sized individuals and even significant growth and increased energy reserves over winter (Copeland and Carline 1998, Pratt and Fox 2002, Connolly and Petersen 2003). The results from this study potentially provide mechanistic explanations for these contradictory results, both across species and systems. Based on our results, a negative relationship between winter starvation mortality and size can only be expected under conditions when all individuals, independent of their size, starve. These conditions in turn are only met when individuals are unable to feed due to temperature related physiological constraints (i.e. CRD approaches infinity), or when resource levels are below CRD for all size classes of individuals. Strong evidence for size-dependent winter mortality are found in large and small mouth bass (Micropterus salmoides and M. dolomieui), especially in high latitude systems, and roach (Rutilus rutilus) (Oliver et al. 1979, Miranda and Hubard 1994, Kirjasniemi and Valtonen 1997b, Post et al. 1998, Fullerton et al 2000, Curry et al. 2005). These species are argued to be more warm water adapted, and to have low ability to feed during winter conditions (Adams et al. 1982, Lessmark 1983, Shuter and Post 1990, Fullerton et al. 2000). In contrast, we do not expect to find strong evidence of negative size selective winter mortality in species that are able to feed under winter conditions, because small individuals have lower CRD than larger individuals and hence are less likely to starve. However, winter mortality may still be present in species that are able to feed under winter conditions if winter resource levels are low, but could be either negatively-, positively- or non- size-dependent based on the complex interactions between foraging rate, metabolism and stored energy reserves. Correspondingly, fish such as walleye (Sander vitreus) and pike perch (Sander luciopeca), which have been shown to be able to feed during winter, also show large variation between systems in size-dependent winter mortality (Toneys and Coble 1979, Madenjian et al. 1996, Kirjasniemi and Valtonen 1997a, Copeland and Carline 1998, Pratt and Fox 2002). Nevertheless, strong evidence for negative size-dependent winter mortality has been found in lake living rainbow trout (Oncorhynchus mykiss), which have experimentally been shown to have the capacity to feed during winter (Connolly and Petersen 2003, Biro et al. 2004). However, small YOY rainbow trout mainly feed on pelagic cladocerans in lakes (Biro et al. 2003), and as zooplankton recourses in general decreases to very low levels during winter (Kalff 2002, Steinhart and Wurtsbaugh 2003), the preferred prey for trout is likely at levels below their CRD. Interestingly, similar patterns of strong negative size-dependent winter mortality have been documented for both yellow perch and Eurasian perch (Perca flavescens and P. fluviatilis) which both are able to feed at low temperatures but mainly feed on zooplankton as young (Lessmark 1983, Post and Evans 1989, Kuras 1990, Byström et al. 1998). Based on results from the above studies, we could thus also expect that negative size-dependent winter mortality would be more common and pronounced in species that mainly feed on zooplankton as young compared to species that feed mainly on macroinvertebrates, as an effect of the opposite seasonal pattern of relative abundance between these two resources.

In conclusion, in seasonal environments with periods of strong resource limitation (e.g winter conditions in temperate regions), temperature dependency and the size scaling of foraging rates and metabolic demands may provide conditions favouring either small or large
individuals. This size advantage dichotomy arises because larger individuals having a higher CRD are most likely to begin starving first, but once resource levels are below the CRD for all size classes, small individuals starve to death at a higher rate. The size advantage dichotomy based on the CRD concept provides a useful conceptual framework for the understanding of winter mortality dependent recruitment variation in fish across species and systems in temperate climates.

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