

## Size-dependent resource limitation and foraging-predation risk trade-offs: growth and habitat use in young arctic char

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Variation in growth and habitat use is closely connected to individual responses to habitat specific resource levels and predation risk. In three mountain lakes which differed in the density of young-of-the-year (YOY) arctic char (*Salvelinus alpinus*), we studied the growth, diets and habitat use of YOY char in relation to resource levels. With two model approaches, we further examined the extent to which YOY and 1-yr old char were resource limited and, if so, whether resource limitation was associated with habitat use and small char densities. Benthic prey dominated the diet of YOY char and YOY char habitat use was restricted to the near-shore habitat in all lakes. In all lakes were chironomid densities higher in the near-shore habitat than in the offshore benthic habitat whereas zooplankton densities were higher in the pelagic than in the near-shore habitat. Growth of YOY char in all lakes was close to predicted maximum growth despite large variation in YOY densities between lakes. Model results suggested that density dependent resource limitation in YOY char is unlikely to occur despite restricted near-shore habitat use. In contrast, strong density dependent resource limitation was predicted in 1-yr old char with a restricted habitat use to the near-shore habitat. Correspondingly, field data suggested that the habitat use of 1-yr old char was density dependent as the use of the offshore habitat increased earlier in time and to a larger extent at high densities. As small individuals are vulnerable to predation but constrained by their low food processing capacity relative to their encounter capacity, we suggest that resource limitation in small individuals should be less pronounced and habitat use should mainly depend on predation risk. A trade-off in habitat use between foraging gain and predation risk is therefore expected to be more likely for individuals, large enough to be resource limited but still small enough to be vulnerable to predation.

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Most organisms undergo major changes in size and basic morphology over their ontogeny and high growth rates in early life stages have been suggested to increase individual survival (Werner 1988, Wilbur 1988, Post et al. 1999). In order to sustain high growth rates over ontogeny, resource dependent habitat shifts are common (Mittelbach 1981, Stephens and Krebs 1986, Osenberg et al. 1992). Individual growth rate is also affected by predation risk as individuals may reduce activity

levels or increase their use of less risky habitats to reduce predation risk, which both may incur a cost in terms of reduced growth rates (Sih 1982, Werner and Gilliam 1984, Lima and Dill 1990, Houston et al. 1993, Werner and Anholt 1993).

In the study of the mechanisms behind habitat use and the presence of trade-offs between foraging gain and predation risk, it is essential to know the degree of resource limitation that the individual experiences when

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feeding in different habitats. Resource limitation in organisms basically depends on the individual's ability to gain energy and ambient resource levels. This ability is, in turn, a function of two size-dependent components: the encounter capacity (attack rate) and the capacity to process food (digestion, Lundberg and Persson 1993, Persson et al. 1998). The likelihood for resource limitation has been suggested to increase with body size due to the differences in size-scaling in these two components as the digestion capacity increases faster than the encounter capacity with size (Werner 1994, Persson et al. 2000b). In contrast, predation risk is generally a decreasing function of body size (Calef 1973, Paine 1976, Werner and Gilliam 1984, Persson and Crowder 1997). As these two relationships go in different directions it can be hypothesized that the habitat use in small individuals are more likely to depend on predation risk whereas the habitat use of larger individuals is more likely to depend on foraging gain. Given these relationships, it can also be hypothesized that intermediately sized individuals are the ones that are most likely to experience a trade-off between predation risk and foraging gain as the likelihood for resource limitation increases at the same time as these individuals are still vulnerable from predation.

In this study we present field data on growth and habitat use of young-of-the-year (YOY) arctic char (*Salvelinus alpinus*) from three small mountain lakes. In these lakes we found no evidence for any density dependency in growth of YOY arctic char despite large differences in YOY char densities. Based on our arguments above, we hypothesized that this was due to the lack of resource limitation and that the habitat use of YOY char should depend on predation risk only, which in these lakes pertains to the risk of being cannibalized by larger conspecifics. To test this hypothesis we examined whether YOY char were resource limited during their first growth season in these lakes. Specifically, we studied the growth, habitat use and diets of YOY char in relation to the habitat specific resource densities (zooplankton and macroinvertebrates). To analyze the presence of resource limitation in YOY char we used two approaches. First, we used information on temper-

ature dependent growth rates of char to estimate maximum growth under ambient temperature conditions in the lakes. Second, we performed laboratory experiments to estimate the size-dependent foraging rate of small char on zooplankton and benthic chironomids. These estimates were then used in a physiologically structured population model (PSPM, Persson et al. 1998, Claessen et al. 2000) parameterized for char to analyze growth responses and diet of YOY char in relation to lake specific resource levels, YOY char densities and habitat use. Finally, we extended our analysis of resource limitation and habitat use with the PSPM approach, to include 1-yr old char and compared model predictions with field data from the lakes on the habitat use of 1-yr old char.

## Material and methods

### Lake descriptions

The study was carried out in the years 2000 and 2001 in three small oligotrophic mountain lakes, Lakes Vuorejaure, Ruozutjaure and Suorujaure situated in northern Sweden (Table 1). Arctic char is the only fish species present in these lakes. Maximum depth varies between 8–16 m and the lakes have similar morphometrics. Furthermore, the near-shore habitat of each lake is very similar in their stone and boulder composition, complexity and area suggesting that differences in density (and performance) of small char are not dependent on lake specific near-shore habitat differences or differences catchability of YOY char. The lakes surroundings are characterized by low to high alpine vegetation and there are no inlets to the lakes and only a small outlet stream from each lake. The outlet streams are too small and steep to allow immigration of fish from downstream lakes. For more detailed information on lake surroundings and characteristics, see Karlsson et al. (2001). The ice break is around middle to late June and the ice cover normally forms in middle to late September. In year 2000, Lakes Vuorejaure and Ruozutjaure had very similar temperature regimes and seasonal de-

Table 1. Locations and physical and chemical characteristics of the study lakes. Chemical data were obtained from Karlsson et al. (2001).

	Lake Vuorejaure	Lake Ruozutjaure	Lake Suorujaure
Location	68°11'38"N 19°36'40"E	68°12'22"N 19°34'15"E	68°16'48"N 19°06'00"E
Surface area (ha)	4.9	3.8	16.9
Circumference (km)	0.95	0.83	1.90
Altitude (m)	712	710	993
Maximum depth (m)	8.2	8.5	15.8
Mean summer temperature in 2000 (°C)	9.4	9.4	6.1
pH	6.9	6.4	6.7
Total P (µg/l)	7.9	7.9	5.5
Total N (µg/l)	207	113	142

velopments whereas Lake Suorujaure had a general lower temperature regime (Table 1).

### General sampling, year 2000

#### *YOY char*

In the summer of 2000, YOY arctic char were sampled on three occasions (July, August and September) by electrofishing along the shoreline of the lakes. On each sampling occasion, the whole lake circumference was sampled once. In order to increase sample size additional electrofishing along the shoreline was also carried out. In addition to electrofishing samplings, minnow traps (in pairs of two, mesh-size 5 mm) were set at 10 littoral and 5 pelagic and 5 benthic stations at each sampling occasion. Traps were set at 1:00 to 5:00 p.m. and raised the following day at 9:00–11:00 a.m. at least once during each sampling period. Minnow traps were only able to catch YOY char in the lakes during the September samplings due to the small sizes of YOY char in July and August. In September, captures of YOY char were high enough to allow for density estimates based on mark and recapture techniques in one lake, Lake Ruozutjaure. YOY char were marked with blue dye injected with a pan jet injector (Hart and Pitcher 1969) and thereafter evenly redistributed along the shoreline of the lake. The following day, a subsequent sampling was performed to obtain recaptures for YOY char density estimation.

Captured YOY char were length measured to nearest mm and weighed to nearest 0.1g in the field and thereafter returned to the lakes apart for a random sub-sample of individuals ( $n = 10$  if possible) from each sampling occasion, which was preserved in alcohol for later diet analysis. The stomach contents were identified to order, family or species in the laboratory, and the length of 10 prey of each group (all individuals if less than 10 were found in a stomach) were measured. Lengths were transformed to dry weights using length-weight relationships given in Dumont et al. (1975) and Bottrell et al. (1976, zooplankton) or using our own length-weight relationships (macroinvertebrates, see Persson et al. 1996). Macroinvertebrates were classified into two groups, chironomids and predator-sensitive macroinvertebrates (PSM) which included the taxa Ephemeroptera, Trichoptera and Coleoptera which are relatively sensitive to fish predation (Persson et al. 1996). To determine the habitat use of YOY char in more detail, a diving survey in September was performed in Lake Ruozutjaure. The whole shoreline was sampled which covered the stony near-shore area and the first two meters outside the stony area of soft bottom habitat. Furthermore, 4 transects (10 m long) diagonal from the shoreline covering the benthic habitat outside the shoreline and two transects across the lake covering the pelagic were surveyed.

#### *Char $\geq 1$ -yr old*

Char  $\geq 1$ -yr old were sampled in July, August and September with fyke nets (mesh-size 15 mm), Ella traps (mesh-size 10 mm), minnow traps (mesh-size 5 mm) and electrofishing. On each sampling occasion, one fyke net was set at 5 littoral stations and 10 Ella traps and 20 minnow traps (in pairs of two) were set at 10 littoral stations. Ella traps and minnow traps (in pairs of two) were also set at 5 deep stations and 5 pelagic stations. Littoral, pelagic and benthic stations were sampled for at least one day/night per lake. In Lake Suorujaure, the pelagic was not sampled with minnow traps. In each of the 3 lakes, the traps were set at 1:00–5:00 p.m. and raised at 9:00–11:00 a.m. the following day. In July all captured char  $\geq 1$  yr were marked with blue dye injected with a pan jet injector in order to obtain population estimates based on mark and recapture techniques. All captured char were length measured to nearest mm and weighed to nearest 0.1g in the field and thereafter released back in lakes, evenly distributed in the offshore habitat. In addition to trap samplings, pelagic and benthic survey gill nets with twelve 3-m sections, each with different mesh-sizes (5, 6.25, 8, 10, 12.5, 15.5, 19.5, 24, 29, 35, 43, and 55 mm), were set in each lake in September 2000. One net was set in each of the pelagic, benthic and littoral habitats in Lake Ruozutjaure and Vuorejaure and two nets were set in each habitat in Lake Suorujaure. Nets were set in the morning and raised the following day. The captured fish were deep-frozen and later measured (to nearest mm) and weighed to nearest g. Size-distributions of char in the lakes are based on the captures from the multi-mesh survey gillnet samples.

#### *Lake resource levels*

Zooplankton was sampled 5–6 times during June–September in the summer of 2000. Samples were taken at 3 pelagic stations and 3 littoral stations in each lake. Pelagic samples were taken by pulling a 100- $\mu$ m mesh net ( $\varnothing 25$  cm) vertically at an approximate speed of 0.5 m/s from 4 m depth to the surface. Littoral samples were taken with a net (mesh-size 100  $\mu$ m,  $\varnothing 25$  cm) drawn 12 m parallel to the shore at an approximate speed of 0.5 m/s. Zooplankton samples were preserved with Lugol's solution. Animals were classified by species, counted, and the lengths of 15 individuals (all, if fewer were found) of each species from each sample were measured in an inverted microscope. Lengths were transformed to dry mass using regressions relating body length to dry weight (Dumont et al. 1975, Bottrell et al. 1976).

Macroinvertebrates were sampled with an Ekman dredge during August in the summer of 2000. Samples were taken at 3 offshore stations and 3 near-shore littoral stations in Lake Ruozutjaure and Vuorejaure and 5 stations for each habitat for Lake Suorujaure. Near-shore littoral samples were taken immediately

outside the stony shore area and offshore samples were taken in the pelagic area of the lakes. Samples were conserved in alcohol, stained with rose bengal in laboratory and classified to family, counted, and the lengths of all individuals of each group from each sample were measured. Lengths were transformed to dry biomass by using regressions relating body length to dry weights using our own length-weight relationships (Persson et al. 1996).

### Additional sampling, year 2001

In the following year (2001) a new set of Ella traps was used with a mesh-size of 5 mm and set on three sampling occasions as in year 2000 (July, August and September). At each sampling occasion 10 Ella traps were set at 10 near-shore littoral stations, 10 stations approximately 8–10 m out from the shore line and 10 benthic deep stations. In this paper, we restrict our analysis to the temporal and spatial patterns of habitat use in 1-yr old char and use only catches in the near-shore and offshore deep stations from Lakes Vuorejaure and Ruozutjaure. Density estimates in the spring of 2001 further showed that the density of 1-yr old char in Lake Ruozutjaure was similar as the estimated autumn density of YOY char (P. Byström, unpubl.). This fact suggests that mortality over winter was negligible and that the differences in 1-yr old densities between lakes in 2001 were similar to those for YOY char in year 2000.

### Foraging experiments and attack rate estimates

YOY char roe was collected from Lake Torrön (63°49'13"N, 13°6'19"E), artificially fertilized and hatched in a commercial rearing station. After hatching, we moved the fry to our experimental facilities where they were placed in flow-through aquariums. When the fry started exogenous feeding they were fed frozen copepods and were placed in 30 l aquariums. Each aquarium was divided into two chambers with a non-transparent plastic sheet and with one individual placed in each chamber. Altogether we used 10 individuals for the capture rate estimates. During the holding period, water temperature was 12°C and char were fed with live zooplankton collected from ponds and frozen chironomids. The fish were fed two times a day, once zooplankton and once chironomids. We performed capture rate estimates three times during the holding period (wet weights;  $0.21 \pm 0.003$ ,  $0.63 \pm 0.008$ , and  $1.26 \pm 0.03$  g, mean  $\pm$  1 SE). Before each round of trials, the char were allowed to train on the specific prey and experimental procedures for five days. From the same lake, we also used 1-yr old char for capture rate estimates of larger size classes of char, size range

2.2–6.6 g for zooplankton and 1.8–7.8 g for chironomids. These char were collected from a commercial rearing station and placed in holding ponds with natural prey for 55 days before trials. Thereafter they were individually placed in separate aquaria (30 l) with all sides except the front covered with black plastic. Training on experimental procedures and different prey types was the same as for the YOY char experiments.

For the YOY char experiments, a temporarily 2 l holding chamber was created for each of the two fry at opposite sides of the aquarium using two non-transparent plastic sheets. Thereafter the plastic sheet, which sub-divided the aquarium into two halves and separated the individuals between experimental periods, was removed resulting in a 26 l performance arena. The back and the sides of the aquaria were covered with dark grey plastic. For 1-yr old char experiments, the single individual was placed behind a non-transparent plastic sheet forming one holding chamber (4 l) and a performance arena (26 l). For all trials, an 11 W fluorescent tube was placed 50 cm above the bottom and temperature was held at 12°C. For the capture rate estimates on *Daphnia* ( $1.2 \pm 0.04$  mm, mean  $\pm$  1 SE), we added the desired number of zooplankton in a 0.5 l beaker (corresponding to the experimental chamber densities 1, 1.5, 2, 3, 4, 6, 8, 16,  $24 \text{ l}^{-1}$  for YOY char and 1, 2, 4, 6, 8,  $16 \text{ l}^{-1}$  for 1-yr old char). The selected *Daphnia* density was then poured from above into the performance arena. When all zooplankton were evenly distributed, we removed one of the plastic sheets and the char were allowed to start foraging. The trial started when the char attacked the first prey and we measured the time until the fifth prey had been consumed. After this, the char was once again placed behind the plastic sheet, the consumed prey was replaced, and the same measurements were repeated with the other individual in that aquarium. For 1-yr old char, the trial was ended when the individual had consumed 5 zooplankton. For the capture rate estimates on chironomids ( $9.6 \pm 2.4$  mm, mean  $\pm$  1 SE), we used frozen chironomids (experimental chamber densities 0.3, 0.4, 0.5, 0.6, 0.7,  $0.8 \text{ dm}^{-2}$ , same densities for both age classes) placed in  $2.5 \times 2.5$  cm plastic patches made out of doormats evenly distributed on the bottom (Astroturf®). Due to the risk of predator saturation as chironomids are a much larger prey than zooplankton, we measured the time between the attack on the first and third chironomid. For chironomids, we measured the handling time as the time between a successful 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:

$$C = \frac{aR}{1 + ahR} \quad (1)$$

where  $C$  is capture rate,  $a$  is attack rate,  $R$  is resource density, and  $h$  is handling time. For zooplankton prey, both  $a$  and  $h$  were estimated from the capture rate measurements (Eq. 1). For chironomid prey the experimentally estimated handling times were used and hence, only the attack rate was estimated from Eq. (1).

## Model approaches

### Maximum growth rate

A Ratkowsky growth model (Forseth et al. 2001) re-parameterized for arctic char which incorporates the temperature dependency of maximum growth rates was used to estimate maximum YOY char size in the lakes in August and September: Eq. 2 and 3.

$$W_t = \{W_0^b + \Omega bt/100\}^{1/b} \quad (2)$$

$$\Omega = d(T - T_L)\{1 - \exp(g(T - T_U))\} \quad (3)$$

Parameter values of growth capacities were obtained from Berglund et al. (2002) and were calculated as mean values for six stocks of arctic char from Sweden. Where  $W_t$  is the weight at day  $t$ ,  $W_0$  is the weight at day 0 and  $\Omega$  is the temperature dependent standardized maximum growth rate of a 1g char. The parameter  $b$  (0.3) is the power transformation of mass to produce linear growth and parameters  $d$  (0.40) and  $g$  (0.37) are growth capacity related constants.  $T$  is water temperature and  $T_L$  (1.95) and  $T_U$  (21.4) are the lower and the upper critical temperature for growth (Forseth et al. 2001, Berglund et al. 2002).

Temperature was measured in the lakes on five to six occasions, between late June and early September (Table 1) and we used linear changes between sampling dates to obtain daily temperatures over the growth season. We used the YOY char sizes in the lakes from the first sampling date as start size in the growth model and calculated the predicted daily maximum growth rates to obtain the maximum size of YOY char in the lakes at the second sampling date (August). The YOY char size distribution in August in the lakes was then used as new entries into the model to obtain the maximum size of YOY char at the last sampling date in September.

### The physiologically structured model

Individual growth rates and the degree of resource limitation were also estimated through simulations with a physiologically structured population model (PSPM) which, based on individual foraging capacities, can yield estimates of individual consumption rates and growth rates while taking into account consumer densities and the dynamic feedback of consumption on resource densities (De Roos and Persson 2001). The present model was based on previous models derived

for fish (Persson et al. 1998, Claessen et al. 2000). In our model, weight ( $w$ ) represents the individual state that influences the individual's performance and demands. We assumed that the capture rate ( $c$ ) of an individual follows a Holling type II functional response described by:

$$c(w, R_m, R_z) = \frac{a_m(w)R_m + a_z(w)R_z}{1 + h(w)(a_m R_m + a_z R_z)} \quad (4)$$

where  $a_m(w)$  and  $a_z(w)$  are attack rates for macroinvertebrates and zooplankton,  $R_m$  and  $R_z$  are the macroinvertebrate and zooplankton densities, and  $h(w)$  is handling time. We further assumed that individuals spent 12 h per day of feeding and that prey of both types were searched for simultaneously and that prey specific encounter rates ( $a_i(w)R_i$ ) determine the consumption rates of each prey.

In the studied size interval of YOY char, the attack rate can be described by a power function for each prey (see results foraging experiments):

$$a_i(w) = \beta_i w^{\alpha_i} \quad (5)$$

where  $\alpha_i$  and  $\beta_i$  are prey specific positive constants (Table 2). The handling time of an individual was assumed to be equal to the digestion time described by a power function with both prey digested at the same rate:

$$h(w) = \xi_1 w^{\xi_2} \quad (6)$$

where  $\xi_1$  and  $\xi_2$  are constants (Claessen et al. 2000, Table 2).

The consumed prey was used for metabolic demands and growth according to:

$$c(w)k = E_m(w) + E_g(w) \quad (7)$$

where  $c(w)$  is capture rate from Eq. 4,  $k$  is the conversion factor (assimilation efficiency – specific dynamic action) (Claessen et al. 2000, Table 2),  $E_m(w)$  is the metabolic demands and  $E_g(w)$  is the net mass intake that is allocated to growth.

Based on Persson et al. (1998) and Claessen et al. (2000), we assumed that the metabolic demands was described by a power function:

$$E_m = m_1 w^{m_2} \quad (8)$$

where  $m_1$  and  $m_2$  are constants (Table 2).

The dynamics of the two resources was described as the sum of semi-chemostat resource growth dynamics and predation pressure:

Table 2. Definitions of parameters used in the physiologically structured population model (PSPM).

Symbol	Value	Unit	Description	Reference/comment
V	3.0 E+6	L	Nearshore volume	Estimated from lake
L <sub>D</sub>	1.0	m	Average depth in nearshore	Estimated from lake
<b>Resources</b>				
R <sub>m</sub>		g m <sup>-2</sup>	Macroinvertebrate density	
r <sub>m</sub>	0.05	m <sup>2</sup> day <sup>-1</sup>	Macroinvertebrate production, inflow rate	Nyman 1973, Larsson et al. 1978
K <sub>m</sub>	3.0	g m <sup>-2</sup>	Macroinvertebrate carrying capacity	Estimated from lake
R <sub>z</sub>		g L <sup>-1</sup>	Zooplankton density	
r <sub>z</sub>	0.05	L day <sup>-1</sup>	Zooplankton production, inflow rate	Claessen et al. 2000
K <sub>z</sub>	1.0 E-4	g L <sup>-1</sup>	Zooplankton carrying capacity	Estimated from lake
<b>Consumer</b>				
β <sub>m</sub>	57.9	m <sup>2</sup> (g <sup>zm</sup> day <sup>-1</sup> )	Macroinvertebrate attack rate scalar	Experiment, this study
α <sub>m</sub>	0.31	–	Macroinvertebrate attack rate exponent	Experiment, this study
β <sub>z</sub>	6.3 E+3	L (g <sup>zz</sup> day) <sup>-1</sup>	Zooplankton attack rate scalar	Experiment, this study
α <sub>z</sub>	0.50	–	Zooplankton attack rate exponent	Experiment, this study
ξ <sub>1</sub>	5.3	day g <sup>-(1+ξ<sub>2</sub>)</sup>	Handling time scalar	Jobling et al. 1993
ξ <sub>2</sub>	-0.66	–	Handling time exponent	Jobling et al. 1993
m <sub>1</sub>	0.076	g <sup>(1-m<sub>2</sub>)</sup> day <sup>-1</sup>	Metabolic scalar	Jobling et al. 1993
m <sub>2</sub>	0.63	–	Metabolic exponent	Jobling et al. 1993
k	0.61	–	Intake conversion efficiency	Claessen et al. 2000
			Assimilation efficiency–Specific dynamic action	Persson et al. 1998
N	Varied		Number of char	

$$\frac{dR_z}{dt} = r_z(K_z - R_z) - \left( \frac{a_z(w)R_z}{1 + h(w)(a_m(w)R_m + a_z(w)R_z)} \right) N/V$$

$$\frac{dR_m}{dt} = r_m(K_m - R_m) - \left( \frac{a_m(w)R_m}{1 + h(w)(a_m(w)R_m + a_z(w)R_z)} \right) N/L_s \quad (9)$$

where  $r_z$  and  $r_m$  are the inflow rates,  $K_z$  and  $K_m$  are the carrying capacities and  $R_z$  and  $R_m$  are the densities for each prey.  $N$  is the number of char individuals,  $V$  is the water volume and  $L_s$  is the benthic surface. As we intended to analyze the density dependence in resource limitation for small char under restricted habitat use to the near-shore habitat, we used a benthic surface area with macroinvertebrates and a water volume with zooplankton that correspond to the near-shore morphometrics of a lake. For macroinvertebrates,  $K_m$  was set to be equal to estimated near-shore density of macroinvertebrates. As  $K_z$  for zooplankton we used the average ambient density measured in the pelagic habitat, which under the assumption of semi-chemostat zooplankton dynamics are assumed to represent both near-shore production and inflow of pelagic zooplankton to the near-shore habitat (Lövgrén and Persson 2002). The environment in the model was characterized by a near-shore water volume ( $V$ ) with a benthic surface ( $L_s$ ):

$$V = L_s \times L_D \quad (10)$$

where  $L_D$  is the average depth in the near-shore habitat (Table 2). In all simulations, we run the model with one cohort of a single size. Model runs thus, do not include the consumption of resources by other size classes of char. However, since larger char population densities were similar between lakes, their relative effect on resource levels will be similar in all lakes. Furthermore, we used ambient resource levels as estimates of carrying capacities, which yield conservative measures of resource carrying capacities. The model was parameterized by using Lake Ruozutjaure morphometrics and resource densities. Initial values of resource densities were set to half the carrying capacity. We used initial densities of YOY char of  $0.5 \times$ ,  $1 \times$  and  $2 \times$  of the estimated density in Lake Ruozutjaure and assumed no background mortality. For 1-yr old char we used  $0.1 \times$  and  $1 \times$  of the estimated 1-yr old density in Lake Ruozutjaure. A constant temperature of 12°C was assumed and individual char parameters were obtained from our laboratory experiments on foraging capacities for small char and from literature data (Table 2). All simulations were done in the Escalator Boxcar Train (EBT) software (De Roos 1988).

## Results

### Resources

No difference was found in the total pelagic zooplankton biomass between lakes although the seasonal development differed (Repeated measures ANOVA, lake  $F_{2,6} = 3.8$ ,  $P = 0.09$ , lake  $\times$  time  $F_{5,10} = 4.19$ ,  $P = 0.001$ , Fig. 1). Calanoid and cyclopoid copepods and *Bosmina*

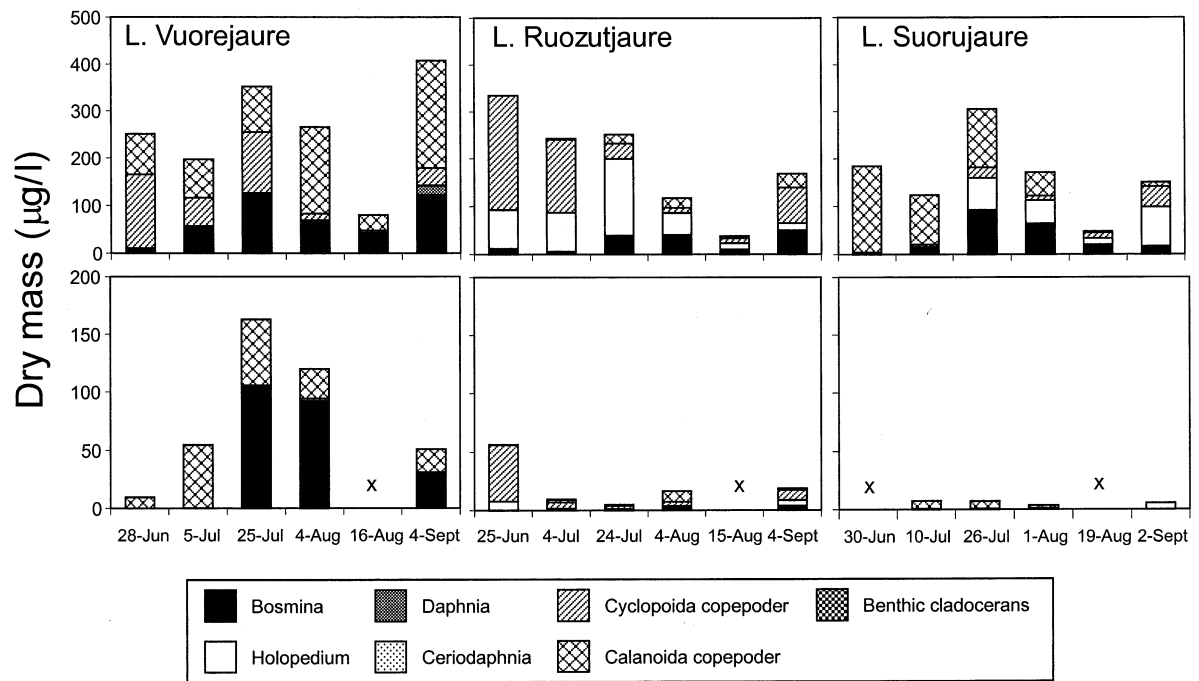


Fig. 1. Seasonal development of zooplankton biomass in the three lakes in the pelagic (top) and near-shore (bottom) habitats. X indicates no sampling.

were the dominant species in the pelagic of Lake Vuorejaure. The large cladoceran *Holopedium* was present in both Lake Ruozutjaure and Suorujaure. Cyclopoid copepods were the dominant copepod in Lake Ruozutjaure, whereas calanoid copepods were the dominant copepod in Lake Suorujaure. Near-shore zooplankton biomass was lower than pelagic zooplankton biomass especially in Lake Ruozutjaure and Suorujaure (no statistical test was performed due to missing values, Fig. 1). *Bosmina* was the dominant species in the littoral of Lake Vuorejaure and the species present in the pelagic habitat were generally also present in the near-shore habitat.

The dominant macroinvertebrates were chironomids and only a few individuals of other taxa were found, mainly large benthic cladocerans (*Eurycerus* sp) in near-shore samples. The biomass of chironomids was generally higher in the near-shore benthic habitat compared to the offshore benthic habitat although not significant in Lake Suorujaure (t-tests, Lake Vuorejaure;  $t = 3.2$ ,  $df. = 4$ ,  $P = 0.034$ , Lake Ruozutjaure;  $t = 3.1$ ,  $df. = 4$ ,  $P = 0.036$ , Lake Suorujaure;  $t = 0.86$ ,  $df. = 8$ ,  $P = 0.41$ , Fig. 2).

#### Densities of $\geq 1$ -yr old char and char population size-structure

The densities of char  $\geq 1+$  and the size structure of

the char populations were similar between lakes, although a small fraction of the population in Lake Suorujaure consisted of larger individuals ( $> 30$  cm) not present in the two other lakes (Table 3, Fig. 3). This similarity between lakes suggests that any differences in YOY char diets, growth and habitat use between lakes is unlikely due to lake specific densities of larger char, at least not between Lakes Vuorejaure and Ruozutjaure.

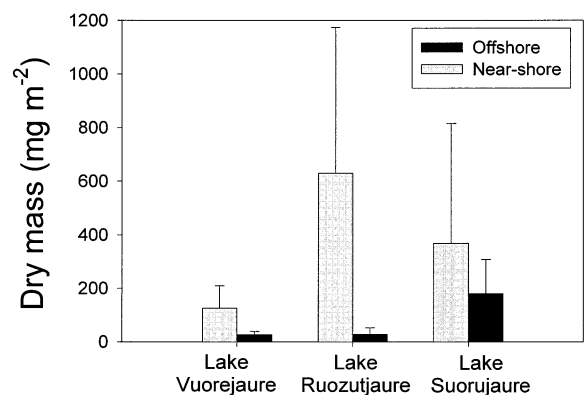


Fig. 2. Biomass of chironomids in the near-shore and offshore benthic habitats in the study lakes in August.

Table 3. Densities ( $\text{ha}^{-1} \pm 95\% \text{ CL}$ ) of 1-yr old and  $\geq 2$ -yr old arctic char in the three study lakes, based on mark-recapture methods.

	Vuorejaure		Ruozutjaure		Suorujaure	
	1-yr	2 $\geq$ yr	1-yr	2 $\geq$ yr	1-yr	2 $\geq$ yr
Density ( $\text{ha}^{-1}$ )	81	380	124	457	109	573
95% CL	34–237	252–622	37–700	278–888	33–615	361–955

### YOY char densities, habitat use, diets and growth rates

Density estimates of YOY char based on mark-recapture methods were only possible to obtain from Lake Ruozutjaure due to low captures of YOY char in Lake Vuorejaure and Suorujaure. Comparisons of the relative density estimates (trap and electrofishing captures) between the lakes suggested that the density of YOY char was 5–10 times higher in Lake Ruozutjaure than in Lakes Vuorejaure and Suorujaure (Table 4).

In all three lakes, YOY char were only captured in the near-shore habitat and no YOY char were ever captured in the benthic or the pelagic habitats (Table 4). Although the trap catches were low, the diving survey in September in Lake Ruozutjaure supported that the habitat use of YOY char was restricted to the near-shore habitat. YOY char (single or in small

groups) were only and frequently observed along the whole shoreline close to and just above stones and no YOY char were observed outside the stony near-shore region on benthic soft bottom areas or in the pelagic zone of the lake.

The diet of YOY char was dominated by benthic prey mainly benthic cladocerans and small chironomids in all three lakes. A progression towards an increased use of zooplankton was observed over time in all three lakes (Fig. 4).

The observed growth of YOY char in all three lakes was close to the predicted maximum growth by the Ratkowski growth model both in August and in September (Fig. 5).

### Size dependent attack rates and PSPM-predictions of small char performance

Within the size range examined, the attack rates of small char increased with size both when feeding on pelagic zooplankton (*Daphnia*; regression, attack rate ( $\text{L/s}$ ) =  $0.146 \text{ weight}^{0.50}$ ,  $r^2 = 0.61$ ) and benthic chironomid prey (regression, attack rate ( $\text{m}^2 \text{ s}^{-1}$ ) =  $0.0013 \text{ weight}^{0.31}$ ,  $r^2 = 0.38$ , Fig. 6).

We analyzed density dependence in growth and diets of YOY char assuming that their habitat use was restricted to the near-shore habitat. This was done to analyze whether resource limitation, if present, would be due to the restricted habitat use. Based on the estimated density of YOY char in Lake Ruozutjaure, the PSPM predicted that YOY char should grow at maximum rate. The estimated growth rates based on the PSPM agreed with the estimated growth rates based on the Ratkowski model (final size Ratkowski growth model at  $12^\circ\text{C} = 2.80 \text{ g}$  and  $\text{PSPM} = 2.85 \text{ g}$ ) in the near-shore habitat (Fig. 7a). The predicted diet of YOY char consisted of benthic prey with a small increase of zooplankton at the end of the season, which corresponded well with observed diets (Fig. 7b). Increasing the density of YOY char resulted in an earlier change in diet to include more zooplankton because of an earlier decrease in benthic prey resource levels. However, a reduced growth rate was only predicted at  $2 \times$  the ambient YOY char density (Fig. 7a, b and c). The predicted benthic resource level was fairly similar to observed resource levels in the lakes (Fig. 7c). The irregular pattern of the predicted diet for  $2 \times$  the

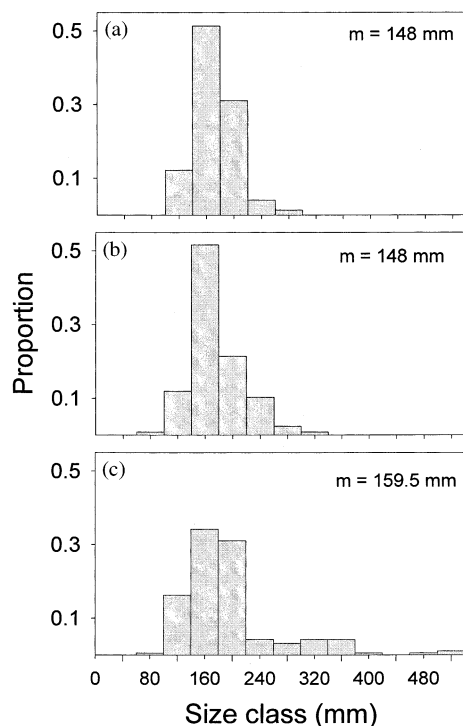


Fig. 3. Size distributions and median sizes (m) of arctic char in the study lakes based on multi-mesh gillnet catches. (a) Lake Vuorejaure ( $n = 74$ ), (b) Lake Ruozutjaure ( $n = 126$ ) and (c) Lake Suorujaure ( $n = 190$ ).



Table 4. Catches (numbers/100 m shoreline) of YOY char by electrofishing at the different sampling dates in the study lakes. Total catch per unit effort (CPUE) of YOY char using minnow traps in the littoral (L), benthic (B) and pelagic (P) habitats and estimated density (numbers/ha) of YOY char at the September sampling date. × no traps set in the pelagic. \* No density estimate possible to obtain due to low captures.

	Electrofishing (100 m <sup>-1</sup> )			Minnow traps (CPUE)			Density (ha <sup>-1</sup> ± 95% CL)
	July	Aug	Sept	L	B	P	
Vuorejaure	0.1	0.2	0.5	1	0	0	*
Ruozutjaure	1.2	12.5	14.0	7	0	0	471 (284-897)
Suorujaure	0.2	0.6	1.8	2	0	×	*

ambient YOY char density is due to an early depletion of the macroinvertebrate resource and the subsequent depletion of zooplankton resource and thereafter diet patterns only reflect the consumption of the production of resources. To conclude, using the ambient YOY char density in Lake Ruozutjaure no resource limitation in YOY char was predicted despite a restricted habitat use. Actually, resource limitation in YOY char was only predicted to be present at a density of 2 × the ambient density even if YOY char restrict their habitat use to the near-shore habitat.

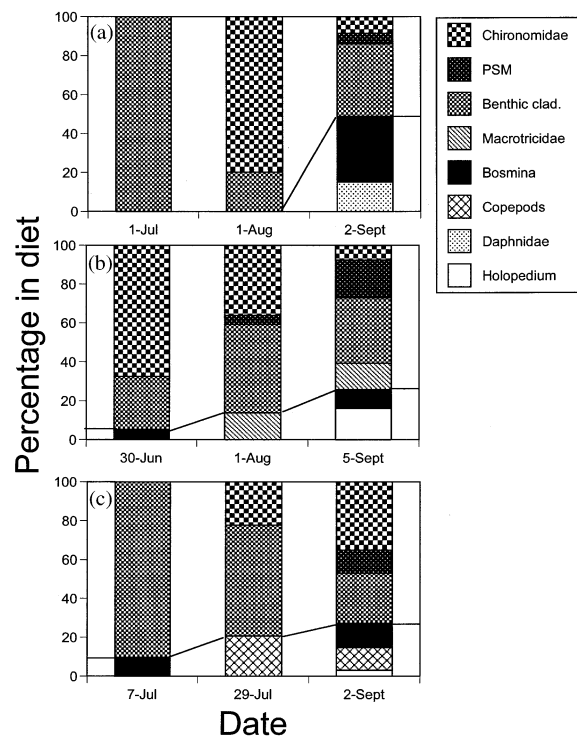


Fig. 4. Seasonal changes in the diet of YOY char. (a) Lake Vuorejaure (n = 2, 3, 10, respectively, for the different sampling dates), (b) Lake Ruozutjaure (n = 10, 10, 10) and (c) Lake Suorujaure (n = 10, 10, 10). PSM = predator sensitive macroinvertebrates which include the taxa Ephemeroptera, Trichoptera and Coleoptera. Lines indicate proportion of pelagic zooplankton in diet where *Holopedium*, *Daphniae*, *Bosmina* and copepods are considered as pelagic zooplankton prey.

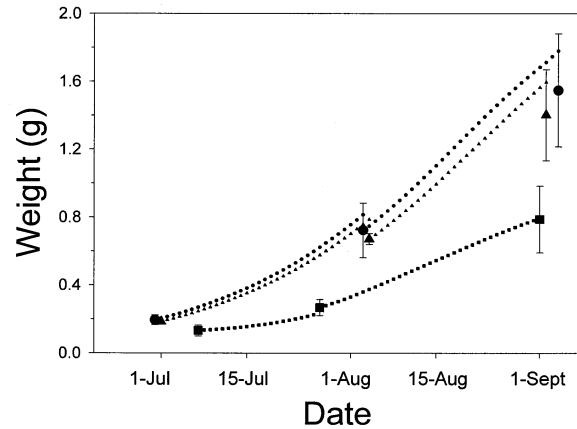


Fig. 5. Weight (mean ± 1 SD) of YOY char in the study lakes at different sampling dates in Lake Ruozutjaure (circles), Lake Vuorejaure (triangles) and Lake Suorujaure (squares). Dotted lines represents estimated maximum weights based on the Ratkowski growth model. Initial start weights in the model are based on the mean weights in each lake at the first and second sampling occasions.

For 1-yr old char, strong resource limitation was predicted to be present at ambient density after 15–20 days if 1-yr old char habitat use was assumed to be restricted to the near-shore (Fig. 8). Actually, to obtain maximum growth rate in the near-shore habitat a decrease in density of 1-yr old char of one order of magnitude was needed (Fig. 8). Correspondingly, our field data show that 1-yr old char used the offshore habitat. The offshore habitat use of 1-yr old char did not only increase over time but was also density dependent as the use of the offshore habitat was higher in Lake Ruozutjaure (high density of 1-yr old char) than in Lake Vuorejaure (low density, Fig. 8).

## Discussion

### Habitat use and size dependent resource limitation

We found no evidence for that YOY char used the offshore benthic or pelagic habitats as diving observations, minnow trap catches and diets all suggest that YOY char habitat use was restricted to the near-shore. Both our model approaches to estimate the extent of

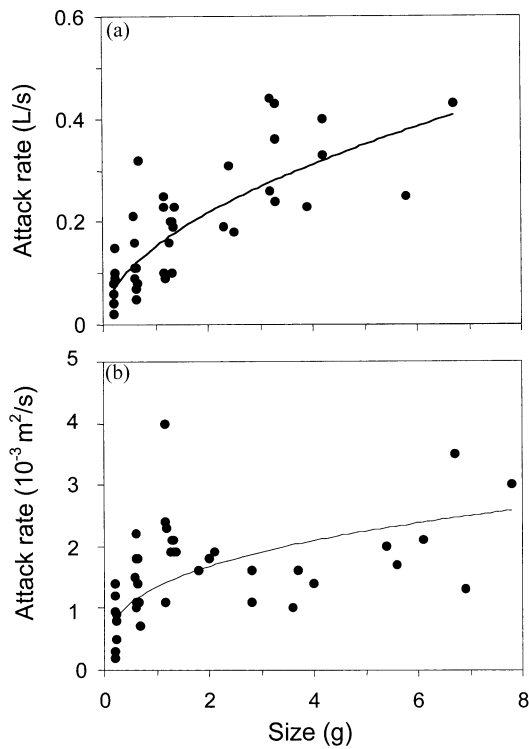


Fig. 6. The attack rate as a function of size (Weight) of small arctic char feeding on (a) zooplankton and (b) chironomids.

resource limitation further suggested that YOY char were not resource limited and that the restricted habitat use to the near-shore did not incur a foraging cost. Considering diets, YOY char were mainly feeding on benthic prey such as benthic cladocerans and small chironomid larvae. This corresponded well with the predicted diet based on our estimates of size-dependent foraging capacities and resource dynamics in the lakes, rendering further support to our conclusions of no resource limitation in YOY char in the near-shore habitat. Although the use of zooplankton by YOY char increased over time in all three lakes, the diet of char was still dominated by benthic or near-shore prey in September. Furthermore the pelagic zooplankton categories found in our lakes were also present in the near-shore habitat. Thus, the increase in zooplankton in the diet in September does not have to reflect a gradual change in habitat use.

The fact that YOY char in the two closely adjacent lakes (Lakes Ruozutjaure and Vuorejaure) had similar growth rates despite large differences in YOY char density (almost 10-fold) further supports the lack of resource limitation in YOY char and suggests that YOY char growth is not density dependent within a relative large density range. Estimated near-shore density ( $0.5 \text{ m}^{-2}$ ,  $0.3\text{--}1.0 \text{ m}^{-2}$ , 95% CL) of YOY char in Lake Ruozutjaure is also comparable to YOY char

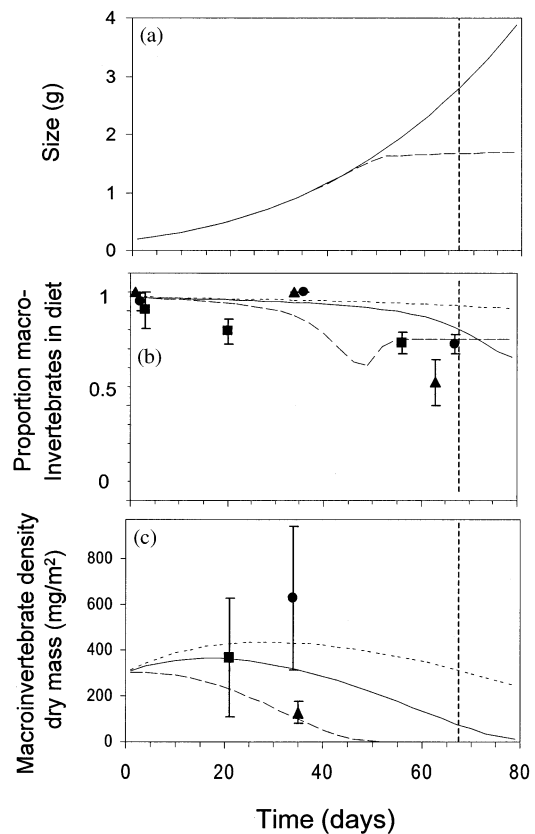


Fig. 7. (a) Predicted growth of YOY char from the PSPM-model. The solid line represents the growth rate based on the ambient density in Lake Ruozutjaure in the near-shore habitat ( $0.5 \text{ individuals m}^{-2}$ ). Solid line overlaps completely with growth at  $0.5 \times$  ambient density and long dashed lines represent growth at  $2 \times$  ambient density in the near-shore habitat. Vertical line indicates last sampling date in Lake Ruozutjaure. (b) Predicted change in the proportion of benthic prey in diet over time at ambient density (solid line),  $0.5 \times$  ambient density (short dashed line) and at  $2 \times$  ambient density (long dashed line) in the near-shore habitat. Symbols show observed proportions of benthic prey in the diets of YOY char in Lake Ruozutjaure (circles), Lake Vuorejaure (triangles) and Lake Suorujaure (squares). (c) Predicted changes in benthic resource densities over time at the three different densities in the near-shore habitat, ambient density (solid line),  $0.5 \times$  ambient density (short dashed line) and at  $2 \times$  ambient density (long dashed line). Symbols (as in b) represent empirical estimates of the benthic near-shore resource.

densities ( $0.17\text{--}1.3 \text{ m}^{-2}$ ) estimated in the near-shore habitat from a study by Ranta-aho (1988). In contrast to YOY char, our model results suggest that 1-yr old char would become strongly resource limited if they would restrict their habitat use to the near-shore habitat only. The predicted strong density-dependent resource limitation in 1-yr old char, if constrained to the near-shore habitat, is in correspondence with our field data on habitat use as 1-yr old char decreased their use of the near-shore habitat over time and that the near-shore habitat use was also density dependent (L. Ruozutjaure versus L. Vuorejaure).

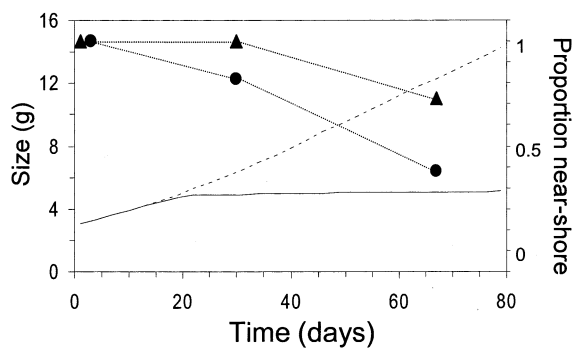


Fig. 8. Predicted growth of 1-yr old char from the PSPM-model. Ambient density of 1-yr old char in Lake Ruozutjaure ( $0.5 \text{ individuals m}^{-2}$ , solid line) and  $0.1 \times$  the ambient density (dashed line). Symbols show observed proportion of 1-yr old char in the near-shore habitat in Lake Ruozutjaure (circles) and Lake Vuorejaure (triangles) based on trap catches. Total number of 1-yr old char captured at each sampling occasion was for Lake Ruozutjaure (16, 433 and 428 respectively) and for Lake Vuorejaure (3, 2 and 45 respectively).

An individual's response to changing resource levels is dependent on the size scaling of foraging capacities (encounter and handling) and energetic constraints (Werner 1994, Persson et al. 1998, 2000b). It has been hypothesized that the likelihood for resource limitation will increase with body size due to that the handling capacity increases faster with body size than the encounter capacity (Werner 1994, Persson et al. 1998, 2000b). Our estimates of foraging capacities in char support this hypothesis as the allometric scaling of attack rates (chironomids 0.31 and zooplankton, 0.5, Fig. 6) were lower than the corresponding size scaling of the handling capacity (0.66, Table 2). As a consequence, small individuals, constrained more by their low handling capacity relative to encounter capacity, will feed at maximum rates at lower resource levels than large individuals (Lundberg and Persson 1993, Werner 1994, Byström et al. 2003). In many cases we therefore expect growth rates in small individuals to be close to maximum and less density dependent. Still, the variation in the size-scaling of encounter and handling capacities between species as well as system specific resource levels ultimately set the size limit at which different species will start to become resource limited (Byström and Garcia-Berthou 1999, Cowan et al. 2000, Persson et al. 2000b). Based on these arguments we expect that the size-threshold, when resource limitation becomes evident, will vary both between species and systems. It is therefore not surprising to find contradictory evidence for the existence of resource limitation and density dependent growth in YOY fish (Jenkins et al. 1991, Elliott 1994, Post et al. 1998a, Jenkins Jr. et al. 1999, Post et al. 1999, Cowan et al. 2000, Persson et al. 2000b, Byström et al. 2003, Biro et al. 2003).

### Habitat use, cannibalism and size-dependent trade-offs in foraging gain and predation risk

Individual habitat use is besides foraging gain also affected by predation risk (Sih 1982, Werner and Gilliam 1984, Lima and Dill 1990, Houston et al. 1993, Lima 2002). The near-shore habitats in lakes are generally considered to be low risk habitats due to the higher structural complexity compared to the pelagic and benthic offshore habitats which lack physical refuges from predation (Werner and Hall 1988, Post et al. 1998b, Biro et al. 2003). However, the use of low risk near-shore habitats has in many situations been shown to incur a cost in terms of reduced growth due to increased competition among refuging prey (Werner and Hall 1988, Eklöv and Persson 1995, Biro et al. 2003).

Despite the restricted habitat use of YOY char, we found no evidence for resource limitation suggesting that the restricted habitat use did not incur a cost in terms of reduced growth. Similarly, Byström et al. (2003) found no evidence for that the habitat use of small perch (*Perca fluviatilis*) was a result of a foraging gain-predation risk trade-off as small perch fed at maximum rates in all habitats. The habitat use was instead related to habitat specific variation in predation risk only. When a foraging gain predation risk trade-off has been demonstrated, the trade-off has either been shown to first develop late in the growth season in YOY fish (Persson et al. 2000b, Biro et al. 2003) or concerned larger juvenile fish (1-yr and older), which both are more prone to resource limitation due to their larger size and digestive capacity but still vulnerable to predation (Werner and Hall 1988, Eklöv and Persson 1995, Langeland and L'Abée-Lund 1998).

Based on the results from this study, we suggest that variation in resource levels between habitats is less important for small individuals as foraging gain may be at maximum levels even at relatively low resource levels leading to that the habitat use of small individuals is more likely to depend on predation risk only. In contrast, variation in resource densities may have substantial effects on foraging gains of large individuals at the same time as predation risk is small. The habitat use of larger individuals should therefore depend mainly on foraging gains. Therefore intermediately sized individuals are the ones that are more likely to face a trade-off situation between predation risk and foraging gain as the likelihood for resource limitation becomes higher at the same time as these individuals are still vulnerable to predation. Correspondingly, a trade-off between habitat dependent food availability and predation risk has also been suggested to exist for larger juvenile char (L'Abée-Lund et al. 1993, Langeland and L'Abée-Lund 1998).

Finally, our results may shed light on the observed size-dependent cannibal-victim relationship in char. In contrast to other cannibalistic systems e.g largemouth

bass (Post et al. 1998a), rainbow trout (Post et al. 1999, Biro et al. 2003) and perch (Persson et al. 2000a, b, Byström et al. 2003), cannibalism on YOY char is generally low and cannibalism is commonly directed towards older/larger juveniles (Riget et al. 1986, Amundsen 1994, Hammar 1998, Byström unpubl. results from the study lakes). The demonstrated absence of resource limitation in the low risk near-shore habitat for YOY char and the predicted strong resource limitation in 1-yr old char at observed densities (if they were to use the near-shore habitat only) can be advanced as explanatory mechanisms for the observed victim size patterns in char. Analogously, in species where cannibalism is mainly directed towards YOY fish, resource limitation has been observed in YOY fish during the latter part of the summer (Post et al. 1998a, 1999, Persson et al. 2000a and b, Biro et al. 2003). Thus, in these systems YOY are likely to face a growth-predation risk trade-off, which in turn may increase the frequency of cannibalism on YOY fish.

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