

Body size, diet and growth of landlocked brown trout, *Salmo trutta*, in the subarctic River Laxá, North-East Iceland

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Received 17 November 2000

Accepted 11 September 2001

Key words: salmonids, streams, prey size, stomach contents, benthic production

Synopsis

Studies on diet preferences of stream-dwelling salmonids have mostly been limited to a relatively small range in body size. This study examined the influence of salmonid body size on prey size and diet composition, and its consequences for growth, in landlocked stream-resident brown trout, *Salmo trutta* (2.5–61.3 cm) in the Laxá River, N-E Iceland. The most common prey of the 1622 trout sampled, were blackflies, *Simulium vittatum*, chironomid midges and the freshwater snail, *Lymnaea peregra*, which represented 56.3%, 21.8%, 10.8% of the stomach content volume, respectively. In general, the Laxá trout showed a consistent, but moderate, shift towards larger prey with increased body size. The relatively stable growth and the large body size attained were probably due to the high production of small benthic invertebrates and only secondarily to the ontogenetic shift towards larger prey.

Introduction

The growth rate and body size attained by stream-resident salmonids is believed to be constrained by their feeding ecology (Bachman 1982). To maintain fast growth over a large range in body size, foraging models predict that salmonid fish should switch to larger prey as they increase in size (Bannon & Ringler 1986, Keeley & Grant 2001). These ontogenetic changes in food preferences, coupled with differences in prey size and productivity among streams, lakes and oceanic habitats, may be the evolutionary cause of fish migration between these habitats (Bachman 1982, Gross et al. 1988). These ideas, along with frequent reports of migrations of young salmonids from streams to lakes and estuaries (Northcote 1969, Hutchings 1986) and of a relatively small adult body size of stream-resident salmonids (Elliott 1988, Näslund et al. 1998), leave the impression that riverine habitats are unlikely to sustain nonmigratory populations of large salmonids (but see Holčík et al. 1988).

In salmonids, prey size is known to change with body size, as larger fish shift their preferences towards larger prey (Keeley & Grant 1997). In lakes, small salmonids feed primarily on invertebrates while large individuals are frequently piscivorous (Malmquist et al. 1992, Madenjian et al. 1998). In streams, relationships between prey size and body size of salmonids have been established for small fish (<14.5 cm), which generally feed on invertebrates (Keeley & Grant 1997). However, studies on the feeding habits of large stream-resident salmonids are rare, but do suggest that growth can be maintained at larger body sizes only if individuals switch to piscivory (Holčík et al. 1988).

This paper examines further the relationships among body size, diet and growth in stream-dwelling salmonids. The study population of resident brown trout, *Salmo trutta*, in the River Laxá in N-E Iceland exhibits a large range in body size (2.5 cm to >60 cm) and allows for two important contributions to knowledge. First, the population provides an opportunity to expand on the existing relationships between prey size

and body size of stream fishes. Second, the population allows for an exploration of the feeding habits and the ecological conditions that enable stream-resident salmonids to reach large body sizes.

Materials and methods

Study area and study population

The River Laxá runs from Lake Mývatn in N-E Iceland ($65^{\circ}35'N$, $17^{\circ}00'W$) with an approximate discharge of $33\text{ m}^3\text{ s}^{-1}$ (Ólafsson 1979, Rist 1979) (Figure 1). The study area extends from the lake outlet, ca. 35 km downstream to the waterfalls in the Laxárgljúfur Canyon, which prevents upstream migration of fish and sets a lower boundary for the study population (Gíslason 1994). Brown trout is by far the most abundant fish species in this section of the river, which also sustains small natural populations of Arctic charr, *Salvelinus alpinus*, and the three-spined stickleback, *Gasterosteus aculeatus* (Gíslason 1994). Below the Laxárgljúfur Canyon, the River Laxá also sustains a large population of anadromous Atlantic salmon, *Salmo salar*. Between 1973 and 1999 the study population of brown trout above Laxárgljúfur Canyon sustained a recreational fishery of an average of 3044 fish per year (range: 996–6458). By tradition, the study area can be divided roughly into two main management units, the upper fishing area (0–16 km from the lake outlet) and the lower fishing area (16–35 km from the lake outlet) (Figure 1). Similar management strategies apply to both fishing areas; all fish below 35 cm in length are released alive into the river and fly-fishing is the only fishing method allowed. A recent mark-recapture study has shown only limited movements of individuals between River Laxá and Lake Mývatn (Gíslason et al. 2002). Of 754 trout tagged in River Laxá over three years, 61% of the 71 recaptured individuals were found at their original tagging location and only one fish, tagged close to the lake outlet, was found in Lake Mývatn.

Sampling

A total of 1622 brown trout, ranging from 2.5 to 61.3 cm in length, were sampled between 1 June and 31 August 1992. Of these, 490 fish were sampled from the recreational fisheries in collaboration with anglers, while 1132 juveniles were caught by electrofishing at seven sites (range: 26–197 m²), nine times over the summer (Figure 1). The seven sites covered

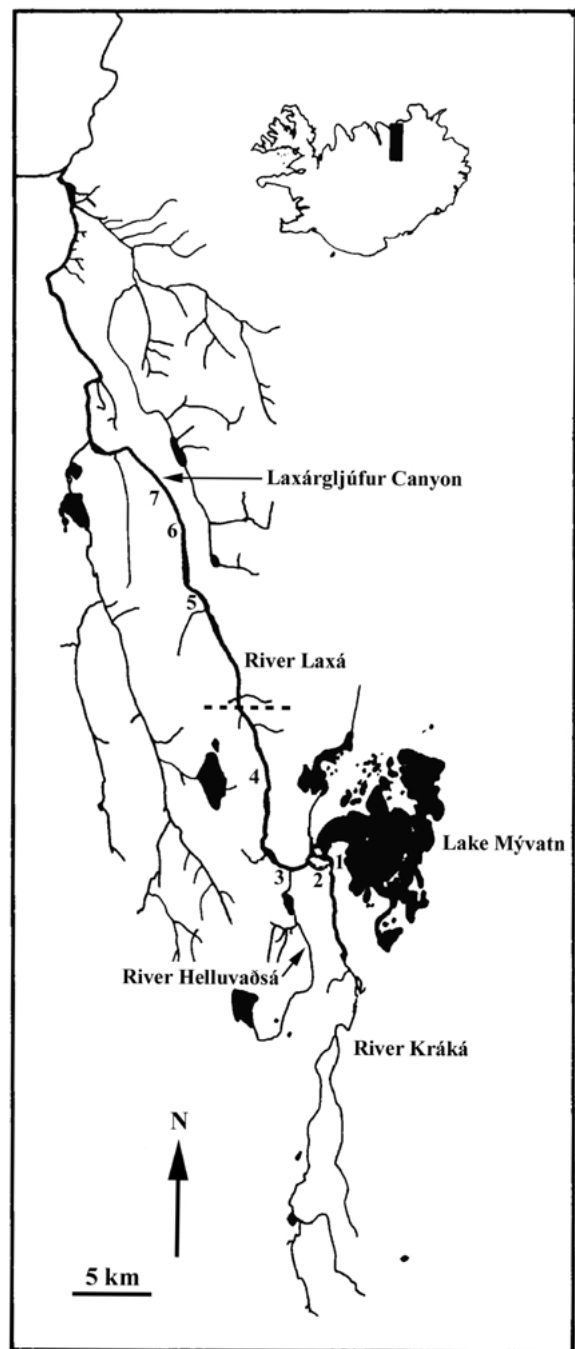


Figure 1. The study area in the River Laxá in N-E Iceland. The electrofishing sites are numbered from 1 to 7, and are located ca. 0.5, 2, 4.5, 11, 23, 29 and 33 km downstream from the Lake Mývatn outlet, respectively. The dashed line separates the upper and lower fishing area.

ca. 0.023% of the total 3.5 km² study area. For each fish, date, location, fork length (L_F), sex and sexual maturity (see below) were recorded. For 1270 fish, the stomach and the oesophagus were removed for stomach contents analysis. Fish scales were collected for age determination and back-calculation of growth.

Stomach contents analysis

For a total of 163 fish, prey items were measured for their maximum length (excluding antennae) and assigned to the appropriate 1 mm length category using a dissecting microscope (0–1 mm, 1–2 mm, etc.) (Newman & Waters 1984). For each fish, the mean, the maximum and the minimum prey lengths were calculated for the length distribution of each prey type. Juveniles used for this analysis were sampled at sites 2, 4 and 6 (Figure 1) on 2–3 June, 13–14 July and 20–21 August 1992. Larger fish were caught by anglers in various places along the river on and around the dates listed above (± 7 days). This sampling protocol ensured that different areas of the stream and the three study months were represented in the relationships between prey size and trout size.

The size of available prey was monitored over the summer by collecting benthic samples nine times at the seven sites. One to three stones were removed from the bottom per site while a net (mesh size 70 μ m) was held downstream. Each stone was scrubbed in water in a 10 l bucket and each sample was then sieved (mesh size 63 μ m) and stored in 70% alcohol (see Gíslason 1985). As with the stomach samples, prey were assigned to 1 mm length categories using a dissecting microscope.

For each of 1270 fish, a stomach contents analysis was conducted by identifying and separating prey into four categories: (1) blackflies, *S. vittatum* (larvae + pupae + imago), (2) chironomid midges (L + P + I), (3) a freshwater snail, *Lymnaea peregra* and (4) 'other' prey. The proportion of each category was determined using only intact prey items, except in the case of some larger prey (e.g. fish), which could also be recognized in a more digested state. For most larger fish ($n = 536$, range: 12.1–61.3 cm) the proportion of each main prey category was estimated by eye to the nearest 5% of the total volume. Later, these visual estimates were verified for a subsample of 30 fish by measuring the volume of each category to the nearest 0.1 ml by submersion into a known volume of ethanol. Since stomachs of most smaller fish ($n = 734$, range: 2.7–22.9 cm) contained

Table 1. Statistics for the regression of \log_{10} prey weight (mg) on \log_{10} prey length (mm) for five common trout prey types in the River Laxá.

Prey type	Slope	Y intercept	n	R ²	p value
<i>Simulium vittatum</i> (L) ^a	3.385	0.006	8 ^c	0.998	<0.001
<i>Simulium vittatum</i> (P) ^b	1.995	-0.654	27	0.841	<0.001
Chironomidae (L) ^a	3.189	0.005	30	0.950	<0.001
Chironomidae (P) ^b	3.023	-1.985	37	0.969	<0.001
<i>Lymnaea peregra</i> ^b	2.575	-0.440	28	0.963	<0.001

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^cThe data points are means of at least 40 larvae measured in each of eight 1 mm length categories (i.e. 1–2 mm, 2–3 mm, etc.).

very few food items, the relative volume of the four categories could not be estimated accurately by eye. Hence, for a consistent comparison of stomach contents composition over the whole size range of trout, prey of the smaller fish were counted and transformed to volume using the following criteria and simplifying assumptions. First, for each trout, prey numbers were converted to volume for *S. vittatum*, chironomids and *L. peregra*, assuming a constant mass–volume ratio of 1.05 for all prey (Hynes & Coleman 1968), and using relationships between (1) prey length and prey weight (Table 1) (Smock 1980) and (2) trout length and mean prey length (see results). Second, because of a similar size and shape of pupae and adults for both *S. vittatum* and chironomids, and the scarcity of the adult form in the stomachs, the relationships for pupae were applied to the adults of the same category. Third, since prey numbers for the 'other' category could not be transformed using the above methods, the proportion of volume for this category was assumed to be equal to its proportion of the total prey number; this assumption is reasonable for small fish where the vast majority of 'other' prey were similar in size to the prey in the other three categories (Hynes 1950). Hence, for each fish where the proportion of the four prey categories could not be estimated visually, the proportion of the 'other' category was established first as the proportion of the total prey number (e.g. 5%) and the remaining percentage (e.g. 95%) was divided among the other three prey categories according to their relative volume. The stomach fullness of 1611 fish was scored from 0 to 5 (0 = empty, 1 = 0–25%, 2 = 25–50%,

3 = 50–75%, 4 = 75–100%, 5 > 100%, i.e. stomach extended). For a subsample of 554 fish, the total volume of the stomach contents was also measured to the nearest 0.1 ml by submersion into a known volume of water.

Growth, condition and sexual maturation

Age was determined for 1579 fish by examining size frequency distributions ($n = 1064$) and reading scales ($n = 515$) (Bagenal & Tesch 1978). Size at age was estimated for 447 individuals (age 2–9) by back-calculating trout length from the inter-annular distances of their scales (Pierce et al. 1996). One to six scales per fish were pressed onto a transparent plastic strip and read using a Canon 100 microfiche projector (magnification = $32.5\times$). The slope of the log–log relationship of trout weight (W) on trout length (L_F) was 2.997 (95% C.L. = 2.991–3.003). Therefore, the condition factor (K) was calculated for each fish using the standard formula: $K = 100 \times W \text{ (g)} \times L_F \text{ (cm)}^{-3}$ (Bagenal & Tesch 1978).

Sex and maturity were determined for a total of 1290 fish by a visual examination of the gonads. Because of difficulties in determining maturation of fish caught early in the season, and males in particular, the statistical analysis was limited to females and based only on samples from July and August. Females were rated either as immature (gonad length < 1/4 of the length of the abdominal cavity) or as becoming sexually mature (gonad length > 1/4 of the length of the abdominal cavity).

Statistical analysis

The original data on the proportion of stomach contents for the four prey categories could not be normalized using standard transformations. Therefore, the data were normalized by calculating the mean proportion of each prey category for 5 cm trout length intervals (2.5–7.5 cm, 7.5–12.5 cm, etc.), separately for the upper and lower fishing areas. An analysis of covariance (ANCOVA) was then used to test if the mean proportion of each prey category differed between fishing areas (factor) or varied with trout length (covariate). In general, this approach is conservative and reduces the chance of observing anomalous statistical differences in the proportion of prey among the predicting variables. Stomach fullness scores were normally distributed and both parametric and non-parametric tests

yielded the same results, so only the parametric test results are reported. Logistic regression was used to determine the probability of sexual maturation for a given female body length (NCSS 1995).

Results

Body size and prey size

An average of 20.7, 10.1, 5.9, 10.2 and 8.6 prey items were measured for length per fish for these five prey types respectively: blackflies, *Simulium vittatum* (L + P), chironomid midges (L + P), and the freshwater snail, *L. peregra*. The mean length of prey increased significantly ($p < 0.001$) with trout length for all five prey types examined (Figure 2, Table 2). In all cases, prey length increased in a declining way with increasing trout length; i.e. the slopes of the log–log regressions were all <1.0. In general, prey length appeared to increase faster with trout length for prey types with a greater range in size (Spearman's $r = 0.949$, $n = 5$, $p = 0.014$). For example, the slope of the log–log regression of mean prey length on trout length ranged from 0.063 for *S. vittatum* (P), the prey type most uniform in size (2.5–6.5 mm) to 0.529 for *L. peregra*, the prey type with the greatest range in body size (1.5–12.5 mm). Similarly, the strength (i.e. R^2) of the prey length–trout length relationship increased with the prey size range (Spearman's $r = 0.949$, $n = 5$, $p = 0.014$), ranging from $R^2 = 0.187$ for *S. vittatum* (P) up to $R^2 = 0.787$ for *L. peregra*. The maximum and the minimum prey lengths increased with trout length for all prey types ($p < 0.001$), except for *S. vittatum* (P) where there was no relationship between minimum prey length and trout length ($p = 0.573$).

Prey length was measured for an average of 24.3 items for three benthic prey types, *S. vittatum* (L), chironomids (L) and *L. peregra*, found in 51, 61 and 61 benthic samples, respectively. For all three prey types, prey items were generally larger in the diet than in the benthic samples. The mean prey lengths of *S. vittatum* (L), chironomids (L) and *L. peregra* in the benthos were 3.55, 3.88 and 4.07 mm, respectively. The log–log regression of mean prey length on trout length shows that the length at which the trout switch from eating smaller prey than the mean available, to eating prey larger than the mean in the benthos, varied among the three prey types (Figure 2). For chironomids

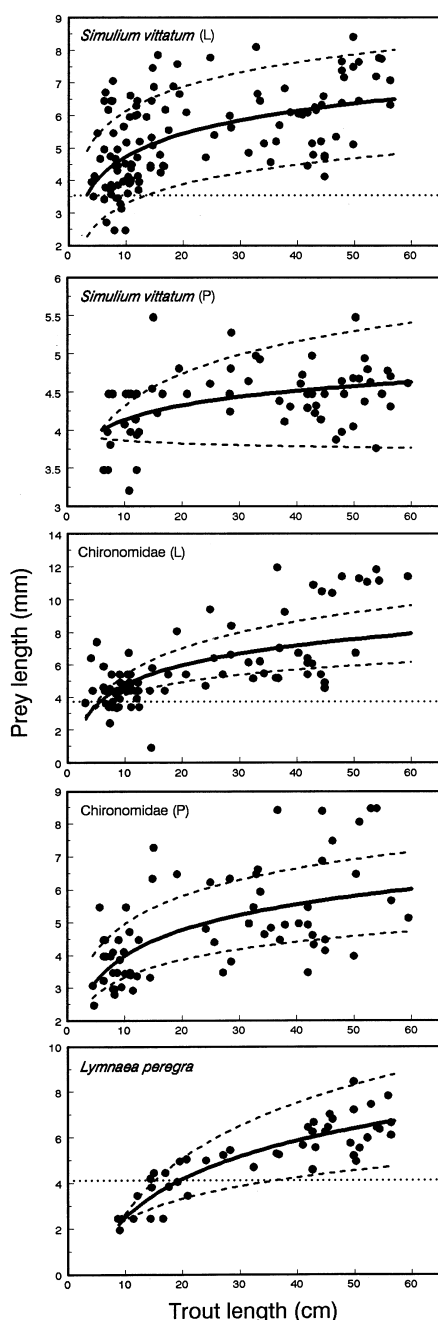


Figure 2. The relationships between mean, maximum and minimum prey length and brown trout length for five common prey types in the River Laxá. The solid circles represent the mean prey length observed for each fish. The solid lines depict the log-log regression line of mean prey length on trout length. The upper and lower dashed lines show the log-log regression line of maximum and minimum prey length on trout length, respectively. The dotted lines represent the mean benthic prey length for the corresponding prey type.

(L) and *L. peregra* the calculated 'switch length' was at $L_F = 5.0$ cm and $L_F = 20.7$ cm, respectively. However, for *S. vittatum* (L), the 'switch length' was calculated at only $L_F = 2.3$ cm, indicating that over their whole range in body size (2.5–61.3 cm) trout were, on average, eating larger larvae than in the benthic samples.

Body size, diet composition and stomach fullness

For the 30 fish where the proportion of the prey categories in the stomachs was estimated both visually and by measuring volume directly, the two methods yielded estimates that differed on average only by 2.8% (1.2–3.8% depending on the prey category). *S. vittatum* are by far the most common prey in the Laxá trout stomachs and represent on average 56.3% of the total prey volume (Figure 3). The remaining three prey categories; chironomids, *L. peregra* and 'other' made up on average 21.8%, 10.8% and 11.1% of the total prey volume, respectively. The 'other' category represents a wide array of organisms of benthic and allochthonous origin. The most common of these prey items were small invertebrates, such as the muscid, *Limnophora riparia* (L + P + I) found in 191 trout and unidentified dipterans found in 192 trout. However, the 'other' category also included larger prey, such as Trichoptera (L + P + I), juvenile salmonids, three-spined sticklebacks and a harlequin duckling, *Histrionicus histrionicus*, but these prey types were rare and observed in 136, 12, 3 and 1 of the 1270 fish, respectively.

S. vittatum were significantly more prominent in the stomachs of trout from the upper area of River Laxá (64.9%) compared with the lower area (47.6%) (Figure 3; ANCOVA: $F_{1,21} = 14.71$, $p < 0.001$). The proportion of *S. vittatum* in the stomachs did not change significantly with trout length (ANCOVA: $F_{1,21} = 0.02$, $p = 0.89$). For the second most common prey category, chironomids, the percent of the total prey volume was greater in the lower area of the river (27.0%) compared with the upper area (16.6%) (ANCOVA: $F_{1,21} = 7.47$, $p = 0.012$) and decreased significantly with increasing trout length (ANCOVA: $F_{1,21} = 29.82$, $p < 0.001$). The two remaining prey categories, *L. peregra* and 'other' showed similar patterns; the proportion of both categories increased significantly with trout size (ANCOVA: $F_{1,21} = 18.83$, $p < 0.001$ and $F_{1,21} = 8.50$, $p = 0.008$, respectively), but did not differ between the upper and lower stream area (ANCOVA: $F_{1,21} = 1.29$, $p = 0.27$ and $F_{1,21} = 2.39$, $p = 0.137$, respectively).

Table 2. Statistics for the regressions of mean, maximum and minimum \log_{10} prey length (mm) on \log_{10} fork length (cm) for five common prey types of brown trout in the River Laxá.

Prey type	Slope (SE.)	Y intercept (SE.)	n	R ²	p value
<i>Simulium vittatum</i> (L)					
Mean	0.191 (0.027)	0.483 (0.035)	120	0.293	<0.001
Maximum	0.159 (0.028)	0.628 (0.036)	120	0.210	<0.001
Minimum	0.229 (0.040)	0.287 (0.051)	120	0.214	<0.001
<i>Simulium vittatum</i> (P)					
Mean	0.063 (0.016)	0.554 (0.024)	66	0.187	<0.001
Maximum	0.127 (0.019)	0.509 (0.027)	66	0.420	<0.001
Minimum	-0.014 (0.025)	0.601 (0.036)	66	0.005	0.573
Chironomidae (L)					
Mean	0.308 (0.036)	0.374 (0.045)	85	0.474	<0.001
Maximum	0.360 (0.037)	0.373 (0.047)	85	0.531	<0.001
Minimum	0.235 (0.044)	0.388 (0.056)	85	0.253	<0.001
Chironomidae (P)					
Mean	0.245 (0.037)	0.353 (0.050)	67	0.396	<0.001
Maximum	0.216 (0.044)	0.477 (0.058)	67	0.269	<0.001
Minimum	0.208 (0.049)	0.312 (0.065)	67	0.217	<0.001
<i>Lymnaea peregra</i>					
Mean	0.529 (0.042)	-0.086 (0.063)	45	0.787	<0.001
Maximum	0.622 (0.060)	-0.130 (0.090)	45	0.714	<0.001
Minimum	0.378 (0.065)	0.020 (0.097)	45	0.443	<0.001

While subjective, the stomach fullness scores were a good predictor (partial $R^2 = 0.596$) of the measured stomach content volume for the 554 fish where both variables were obtained (ANCOVA: $F_{4,548} = 355.77$, $p < 0.001$). Hence, after controlling for trout length (ANCOVA: $F_{1,548} = 258.30$, $p < 0.001$) an average trout in this analysis (39.4 cm) had a mean stomach volume of 0.28, 1.03, 2.29, 4.88 and 10.89 ml, for scores of 1, 2, 3, 4 and 5, respectively. Most trout, of the 1611 sampled, had stomachs that were rated more than half full and the mean and median stomach fullness scores were 2.98 and 3, respectively. Stomach fullness scores differed significantly across the 5 cm trout length categories (two-way ANOVA: $F_{11,1587} = 5.92$, $p < 0.001$) but did not vary between the fishing areas (two-way ANOVA: $F_{1,1587} = 0.13$, $p = 0.719$). A Bonferroni corrected t-test of all possible comparisons across the length categories showed that the only significant difference in stomach fullness could be traced to 10 cm (mean score \pm S.E. = 3.09 ± 0.06) and 25 cm (3.54 ± 0.16) fish, which had significantly ($p < 0.05$) higher scores than 5 cm (2.72 ± 0.06) and 55 cm (2.44 ± 0.17) fish. Stomach fullness did not show an overall change with trout length (Pearson product-moment correlation $r = -0.009$, $n = 1611$, $p = 0.719$).

Growth, condition and sexual maturation

The Laxá trout grew fairly consistently throughout life, with a mean yearly length increase of 6.3 cm (Figure 4a) and fastest growth at 8.2 cm yr^{-1} in their third and fourth years (i.e. 2+ and 3+ growth). Growth leveled off with age, as fish in their seventh, eighth and ninth season had mean increments of 5.3, 4.5 and 3.8 cm, respectively (i.e. 6+, 7+ and 8+ growth). The overall growth patterns of the trout differed slightly, but significantly, between the two fishing areas. Early in life (age < 3 years), the fish in the upper area were larger than those from the lower area (t-tests: $p < 0.05$), but this pattern is reversed later in life (age = 4–7 years; t-tests: $p < 0.05$). The same growth pattern was observed in the original length-at-age data (i.e. without using the back-calculated length). There was a significant interaction between age and fishing area, indicating that length increased faster with age in trout from the lower compared with the upper area (two-way ANOVA: $F_{9,1559} = 68.5$, $p < 0.001$).

The condition factor of the Laxá trout did not differ between the two fishing areas (Figure 4b; two-way ANOVA: $F_{1,1536}$, $p = 0.299$), but varied significantly with age (two-way ANOVA: $F_{9,1536}$, $p < 0.001$). The

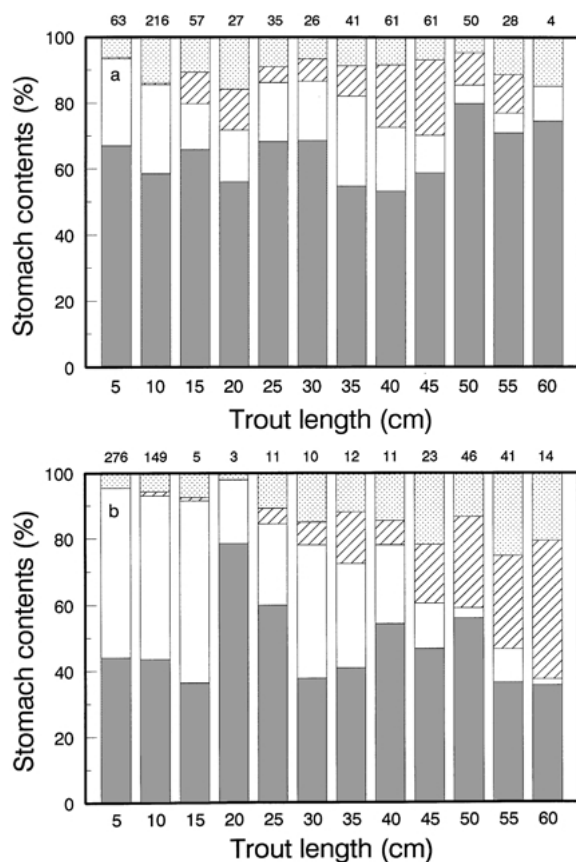


Figure 3. The effect of body size on the relative stomach content volume of the four main prey categories in brown trout in (a) the upper and (b) the lower fishing area of the River Laxá. The four prey categories are *S. vittatum* (solid), Chironomidae (open), *L. peregra* (hatched) and 'other' prey (dotted). The numbers above each bar represent the sample size of trout in each length category. For most length categories the proportion of volume was estimated visually, but length categories 5–20 cm also contain many fish where the proportion of volume had to be transformed from prey numbers.

age-related differences in condition can be traced primarily to the relatively poor condition of older fish. More specifically, Bonferroni corrected t-tests of all possible comparisons across the 10 age classes showed that 7+, 8+ and 9+ fish had significantly ($p < 0.05$) lower condition factor than six, five and three of the seven preceding age-classes, respectively.

The probability of sexual maturation in female trout was well described by a logistic regression model: $\ln[p(1-p)^{-1}] = 0.27 L_F(\text{cm}) - 9.56$, where p is the probability of being rated as becoming sexually mature ($\chi^2 = 386.1$, $n = 405$, $df = 1$, $p < 0.001$). According

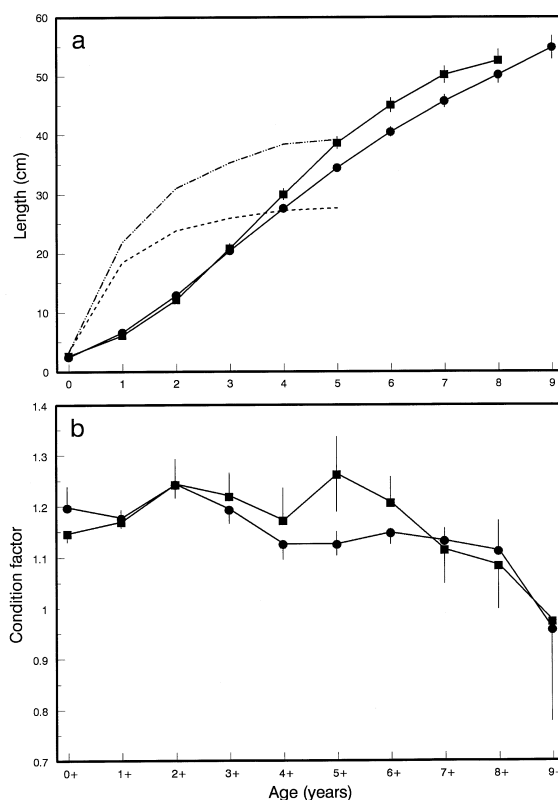


Figure 4. Brown trout length (a) and condition factor (b) as a function of age in the River Laxá. The solid circles and solid squares represent fish caught in the upper and lower fishing area, respectively. The error bars show the 95% confidence intervals. The extra growth curves in (a) are from Allen (1962), and show the growth of brown trout in the main water (chained) and the road branch (dashed) of the Horokiwi Stream in New Zealand.

to this model, the inflection point ($p = 0.5$) is at a length of 35.4 cm, meaning that fish >35.4 cm in length have a $>50\%$ chance of being rated as becoming sexually mature, and vice versa. Trout from the two fishing areas did not differ in length at sexual maturation since the addition of the fishing area as a factor did not improve the logistic model significantly ($p = 0.996$). Also, it is likely that 35.4 cm is a slight underestimation of the true size at sexual maturity because the fish were sampled in July and August.

Discussion

The growth of stream-resident salmonids frequently levels off at a relatively small body size (20–40 cm) (Figure 4a) (Allen 1962, Elliott 1988, Näslund et al. 1998). Compared with other stream populations, the

Laxá trout is unusual both in terms of how large individuals grow, and because the growth is relatively stable over a large range in body size (but see Holčík et al. 1988). In fact, many life history characteristics of the study population, such as body size, longevity and size at maturity, are more similar to those observed for anadromous brown trout (Jonsson et al. 1991). From the perspective of feeding ecology, stream-resident salmonids can maintain growth at larger body sizes only if they have access to either a sufficient supply of large prey items or an extremely abundant supply of smaller prey (Allen 1962, Bachman 1982).

In this study, prey size generally increased over a wide range of trout size, as trout selected larger prey of each prey type, and shifted from relatively small prey types (midges) to larger prey types (freshwater snails). However, while these ontogenetic changes in prey choice would be expected, they were less dramatic than predicted by the available models of optimal prey size in stream-dwelling salmonids. For example, based on calculations from Bannon & Ringler's (1986) and Wankowski's (1979) foraging models on salmonids, Keeley & Grant (1997) estimated that optimum prey length (mm) = 1.15 fork length (cm). If these predictions are extrapolated over the range in trout length used in this study, fish at 5, 20, 40 and 60 cm should feed on prey with a mean length of 5.75, 23, 46 and 69 mm, respectively. Thus, in this study most fish larger than 10–15 cm are eating prey considerably smaller than expected. Similarly, Keeley & Grant (1997) showed that even at only 14.5 cm, stream-dwelling Atlantic salmon fed on prey smaller than predicted by these models. The observed size-dependent changes in prey choice are also less than observed in the stream-resident Danube salmon, *Hucho hucho* (Holčík et al. 1988) and many lake-dwelling salmonid populations (Madenjian et al. 1998), where large individuals become mainly piscivorous. Obviously, the low frequency of piscivory in this study (1.2%) may be an underestimation if fish are digested and evacuated faster from the stomachs than hard-shelled invertebrates (e.g. Andersen 1999). In our study, however, most insect prey have thin exoskeletons and should be digested at similar rates as soft-bodied fish (Andersen 1999). Furthermore, our sampling may already be slightly biased towards larger organisms (e.g. fish) since these could be recognized, and were included in the stomach analysis, even when found in a very digested state.

Perhaps a more important factor contributing to the growth and body size of fish in the study

population is the extremely high productivity of the River Laxá ecosystem. Between 1977 and 1985, the mean benthic production of the most common prey, *S. vittatum*, ranged from 11 to 896 g (afdw) m⁻² y⁻¹ [90–7340 g (ww) m⁻² y⁻¹] at three sites in the river (Gíslason & Gardarsson 1988). The chironomid production in River Laxá was estimated at two study sites in 1978 and 1979 from 6 to 20 g (afdw) m⁻² y⁻¹ (Gíslason 1994). Consequently, if benthic production reflects the available drifting prey in River Laxá, prey density is probably one or two orders of magnitude higher than in most salmonid streams in Iceland (Gíslason et al. 1998), or elsewhere (Wotton 1988, Benke 1993). A higher density of drifting prey should increase the net energy gain of individuals at any given current velocity, and the range in body size at which stream-dwelling salmonids can continue growing (Bachman 1982).

There are slight, but consistent, differences in the growth patterns of trout between the two fishing areas in River Laxá. These differences are not caused by the size at sexual maturation since this variable did not differ between the two areas, but may be caused by differences in prey size and abundance. For example, greater abundance of small prey in the upper fishing area relative to the lower area (Gíslason 1985) may contribute to fast growth early in life. Alternatively, brown trout in the lower area may grow faster later in life since they feed on larger prey (i.e. closer to the optimum), which should be energetically more beneficial (Bannon & Ringler 1986).

This study has implications for the management of the River Laxá fisheries. In 11 years between 1971 and 1987, 11 000–75 000 juvenile Atlantic salmon were released in the study area per year to enhance numbers of salmon returning to the river (reviewed in Gíslason 1994). These procedures, especially if Atlantic salmon are released in higher numbers, may be detrimental to the brown trout for two reasons. First, the growth and survival of the brown trout appears to depend on prey availability, as the number of trout caught each year is correlated with blackfly production in the previous year (Gíslason 1994). Second, the trout depend on small prey over their whole range in body size and may compete for food with juvenile Atlantic salmon, which selects prey of similar size (Keeley & Grant 1997). Introduced juvenile salmon may not only compete with trout of similar size, but may have negative effects on the growth and the condition of larger brown trout with similar feeding habits.

The study population challenges the general consensus that stream-dwelling fishes can reach large body sizes only by migrating to presumably more energetically favourable habitats, such as lakes or estuaries. The brown trout in River Laxá maintains stable growth over a large range in body size by shifting gradually towards larger prey, and perhaps more importantly by having access to very high numbers of small prey. This study also provides further evidence that brown trout switches from pure drift feeding to epibenthic feeding with increased body size (Tippetts & Moyle 1978). The consumption of freshwater snails by the Laxá trout increases gradually with trout size, but this prey is rarely, if ever, caught drifting in the water column (Elliott 1973, Keeley & Grant 1997). Therefore, the general energetic rules of the existing foraging models (e.g. Bachman 1982, Bannon & Ringler 1986) which assume that stream-salmonids feed only on drifting organisms may not apply over a larger range in fish size. Clearly, a more comprehensive synthesis is needed to explain how foraging behaviour, prey size and stream productivity contribute to the growth and body size of stream-resident salmonids.

Acknowledgements

We thank Á. Einarsson at the Lake Mývatn Research Station for his help and the logistical support; H. Jónsdóttir, E. Ásgeirsdóttir and S. Jónsdóttir for collecting samples from the anglers; Á. Guðmundsson and E. Einarisdóttir for processing stomach samples; J.S. Ólafsson for his help in identifying prey items; G. Guðbergsson for advice on aging and back-calculating growth from fish scales; and A. Einarsson, A. Garðarsson, I. Girard, J.W.A. Grant, I. Imre and two anonymous reviewers for comments. This work was funded by The Science Foundation of Iceland, The University of Iceland Research Fund, The Icelandic Aluminium Co. Ltd. and The Lake Mývatn Research Station. While writing the paper, S.Ó. Steingrímsson was supported by a Concordia University Graduate Fellowship and an NSERC grant to J.W.A. Grant. All sampling of brown trout was conducted in accordance with Icelandic laws, i.e. the Act of salmon, trout, and char fisheries no. 76/1970.

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