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Seasonal changes in the body composition of young riverine Atlantic salmon and brown trout

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The body composition of protein and fat in Atlantic salmon *Salmo salar* and brown trout *Salmo trutta* before and after winter was investigated in a temperate, small river, normally ice covered from the middle of November until the end of March. Fat, protein and specific energy declined greatly in winter but were replenished rapidly in spring. Rates of decline were slower for the smallest fish, which also had the lowest specific content of fat, protein, and energy, while the differences in absolute amounts were greatest for the largest fish. The mean specific fat content was reduced by 45–70% during winter, relative to the pre-winter period (September). Mean daily reductions in specific enegy of the larger size groups of brown trout ($3{\cdot}7 \times 10^{-3}$ kJ g^{-1} day^{-1}) were almost half of the corresponding values for the largest Atlantic salmon ($6{\cdot}3 \times 10^{-3}$ kJ g^{-1} day^{-1}) during winter. A minor reduction in protein content was found during winter, with mean reductions of 6–10% in comparison to those in September. During spring the fat content was replenished rapidly, particularly for the smallest salmon fry (a threefold increase from April to June). Fat content in the larger salmon and trout increased by about 1·8 times. Based on estimated metabolic rates, digested energy during wintertime may contribute about two-thirds of the brown trout fry's energy demand. For Atlantic salmon, the corresponding value is about 50%. The winter period put considerable stress on the young salmonids living in lotic environments, in particular for the smallest fry with the lowest energy content before winter and the largest losses during winter. This should make the fry more vulnerable to adverse abiotic and biotic factors.

Key words: *Salmo salar*; *Salmo trutta*; proximate composition; winter energetics; energy reserves; nutrition.

INTRODUCTION

In temperate and Arctic regions, there is marked seasonal variation in principal abiotic parameters like water temperature, water flow, light intensity and photoperiod, all of which influence freshwater organisms. Biotic parameters such as food availability, predation pressure and competition intensity change in response to the abiotic factors. Therefore many factors that influence freshwater organisms change with the seasons. Winter, defined as the period immediately following egg deposition by autumn-spawning salmonids (coincident with a decline in water temperature) and extending until the loss of all surface ice (Cunjak, 1996), is most probably a survival bottleneck for organisms living in temperate and Arctic regions. In these areas, the ice-covered period may be longer than the ice-free period, and must impose a considerable impact on resident organisms.

As a consequence of the methodological problems related to the harsh climatic conditions (Olsson, 1981), there are only a few investigations on the winter

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ecology of freshwater teleosts in Arctic and temperate regions, although winter is a critical period, especially for the youngest age groups of streamliving salmonids (Lindroth, 1965; Cunjak & Power, 1987; Fraser *et al*., 1993, 1995; Contor & Griffith, 1995; Graham *et al*., 1996; Valdimarsson *et al*., 1997; Valdimarsson & Metcalfe, 1998). Several behavioural and bioenergetic changes have been documented for young salmonids at the transitional stage from summer to winter. These include a change from diurnal to nocturnal activity (Heggenes *et al*., 1993) as they adopt a shelter-seeking behaviour during daytime instead of active feeding behaviour (Rimmer *et al*., 1984), and a general decline in growth (Elliott *et al*., 1995). When water temperatures drop below about 4–7° C, investment into new tissues appears to stop for young salmonids (Elliott, 1976, 1979, 1991; Elliott *et al*., 1995; Elliott & Hurley, 1997), but Higgins (1985) reported a specific growth rate of Atlantic salmon *Salmo salar* L., of about 0·02% at temperatures around 1° C, increasing rapidly at somewhat higher temperatures. For salmonids living in running waters, temperatures are around 0° C during the whole period when the rivers are covered with ice.

The present investigation was performed in a relatively small temperate river in middle Norway, where anadromous Atlantic salmon and brown trout *Salmo trutta* L., are the dominant fish species. The purpose was to measure seasonal changes in body composition of young salmonids and, in particular, to assess fat, protein and water content and thus the energy status of the young salmonids before, during and after winter. The determination of fat and protein content of the fish during winter can yield insights into the balance between acquired energy and the costs of metabolism. From only a few samples during winter, the loss in energy can be determined, thereby revealing the eventual impact of the winter period on the fish.

MATERIALS AND METHODS

STUDY AREA

River Humla (63°25′ N, 10°49′ E) is a lowland river with a total catchment area of 154 km^2, and an annual mean waterflow of 4·2 m^3 s^{-1}. The river originates from a small lake, *c*. 20-km from the river mouth (Fig. 1). The dominant fish species in the lower part of the River Humla are Atlantic salmon and brown trout, with a few flounder *Pleuronectes flesus* L., eel *Anguilla anguilla* L., and three-spined stickleback *Gasterosteus aculeatus* L. A 20-m high waterfall stops anadromous salmon and trout from ascending more than 4 km up the river, above which only resident brown trout are present. Fish in the River Humla grow somewhat faster than most salmonid stocks in central Norway, and consequently smolting age is lower than average for this region. Most Atlantic salmon smolts leaving the Humla are 3 years old, whereas most brown trout smolts are 2 years old.

Most of the Humla's catchment area is located at altitudes <400 m, resulting in relatively high water temperatures during the summer period. The ice-covered period lasts normally from the middle of November until the end of March. A mild period at the end of November 1994 resulted in a flood. The ice was broken up, and made it possible to sample fish on 2 December. Thereafter the temperatures dropped and the river was covered with ice again within a week. The study site was located 300 m above the river mouth (Fig. 1), and consisted of a pool-riffle segment with a surface area of *c*. 800 m^2. The river substratum was heterogeneous, with coarser materials like cobble and boulder as dominant classes. Daily mean (recorded every 6 h) river temperatures (Fig. 2) were obtained from the Hydrological Department, Norwegian Water Resources

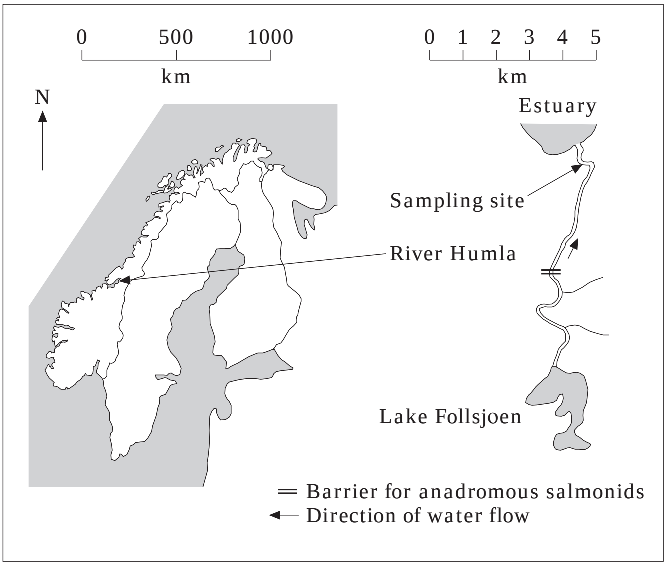

FIG. 1. Location of River Humla and the sampling site.

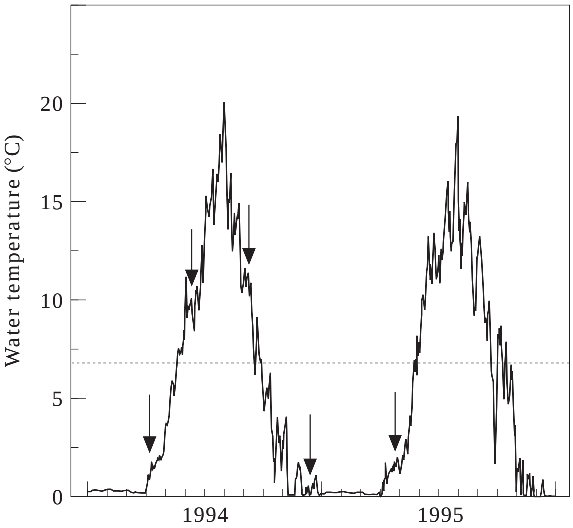

FIG. 2. Water temperatures (° C) in River Humla during January 1994–December 1995; arrows indicate sampling dates.

and Electricity Board. Due to failure of the logger during winter 1994/95, data for the nearby (10 km distant) Gråelva in Hegra were used. The daily mean temperature regimes of these two rivers were almost identical, as confirmed by nearly 2 years of comparison (Pearson's correlation, $r^2 = 0{\cdot}99$, $n = 524$).

STUDY DESIGN AND METHODOLOGY

Fish were captured using a 12-V backpack electroshocker (Bohlin *et al.*, 1989) during five sampling periods: April, June, September, December (1994) and April (1995) (Table I). The sampling from April in 2 successive years was made to test and verify the results

TABLE I. Sampling dates (day month year) and material of young Atlantic salmon and brown trout sampled in River Humla

Date	*n* of salmon	*n* of trout	*n* total
7 Apr. 94	91	33	124
12 Jun. 94	31	14	45
5 Sep. 94	91	51	142
2 Dec. 94	88	35	123
24 Apr. 95	69	18	87
Total	370	151	521

obtained after the wintering period. Species, total length (mm), and weight (g) were recorded in the field. The fresh weight obtained was used in the later calculations of water content and of the specific values of protein and fat. All fish were weighed in a standardized manner. To standardize the water content of each fish, after killing, they were laid in a water bucket. Each fish was then picked up with a pair of tweezers and allowed to drip off for *c.* 4 s. The head of the fish was held for *c.* 2 s in contact with blotting paper to get rid of droplets collecting at the head. After weighing, on an UWE scale (type NJW-150, precision: ± 0·005 g), the fish were packed individually in marked plastic bags and frozen.

For the fat and protein determination the fish were thawed for a few minutes and placed on numbered, pre-weighed, rectangular pieces of aluminium foil. These were folded to ensure a minimum of contact area between fish and foil to keep adhesion of fish tissues to the aluminium foil at a minimum. The foil and fish were weighed together (Precisa 100A-300M, precision: ± 0·001 g). The samples were then placed in a drying cabinet (55° C) for 1–5 days, after which stable dry weights were obtained. The empty aluminium foil was then weighed again to confirm that only negligible parts of the fish adhered.

Fat content was determined gravimetrically. Dried fish were divided into about 10-mm pieces and placed in individually numbered tea bags (dried in the drying cabinet). Fat extractions were performed in a solvent made up of petrol-ether (five parts) and chloroform (one part) (Dobush *et al.*, 1985). The fat extraction was executed in several steps, with fresh solvents used in the final steps (Gardiner & Geddes, 1980; Reznick, 1983). After fat extraction, each sample was dried again (55° C) before weighing.

The mean constituents of 521 Humla fish were: water (79·6%), protein (15·5%), fat (2·0%) and ash (2·7%), with carbohydrates contributing only 0·1–2·4% (Craig, 1977; Jonsson *et al.*, 1997). Therefore, protein was determined as the weight difference between the fat-free samples and the ash after combustion (12 h at 550° C). The combustion was done in aluminium foil cylinders (diameter 3–7 cm, height 9·5 cm). Further details are in Gardiner & Geddes (1980) and Reznick (1983).

For smaller fish (<10 g), the laboratory procedure was changed from the standard procedure. As aluminium foil oxidizes, reliable results were obtained only when the fish were combusted in numbered porcelain crucibles. After combustion, the crucibles were cooled in a dessicator, preventing the absorption of atmospheric water. The smallest fry analysed this way was 0·410 g (fresh weight).

Total energy content was determined as the sum of the caloric values of the different tissues, where fat was assigned a value of 39 kJ g^{-1} and protein 24 kJ g^{-1} (Jobling, 1995). All weights with the exception of fresh weights, are given as dry weights (precision: 0·0001 g). Percentage protein and fat have been calculated based on fresh weight.

The fish were divided into groups based on the weight–frequency distribution (Table II), corresponding with the age grouping determined in an earlier study (Bremset & Berg,

TABLE II. The division in weight groups of Atlantic salmon and brown trout in River Humla

Species	Group	Weight range (g)	n
Atlantic salmon	S1	<2·0	90
	S2	2·0–5·0	119
	S3	>5·0	161
Brown trout	T1	<3·2	74
	T2	3·2–7·5	29
	T3	>7·5	48

The S1 and T1 groups refer to young-of-the-year of salmon and trout, respectively; the S2 and T2 groups refer largely to yearlings; whereas the S3 and T3 groups refer largely to older parr (Bremset & Berg, 1997). The S3 and T3 group generally leave the river as smolts in spring (after the April sampling).

1997). Only fish weighing <25 g have been analysed. The few mature parr present in the September and December samples, were not used in the further analyses.

RESULTS

The distribution of three parameters: fresh weight, specific (per unit fresh weight) fat content, and total energy deviated significantly ($P<0{\cdot}001$, Kolmogorov–Smirnov test) from normality. The log-transformed ($X+1$) values of these three variables did not deviate significantly from normality, and were used in the further statistical analyses. The time period was divided into winter from September to April, and spring/summer from April to June. Atlantic salmon and brown trout were compared during the different periods by an analysis of covariance (ANOVA) with fish weight as a covariate. Non-significant interaction effects were removed serially to obtain the final model.

The fish sampled in April in 2 different years were generally low in fat content (mean 1·2%) while the water content was relatively high (mean 80·9%). Multiple comparisons between the two April analyses of specific content of fat (%), protein (%) and water (%) in each of the three size groups of salmon and trout revealed significant differences (Mann–Whitney U-test, Bonferroni-adjusted) in the protein and water content of only the S3-group. For the other comparisons there were no statistical differences. In the later statistical comparisons the two April materials were grouped together.

FAT CONTENT

The most pronounced seasonal differences were found in specific fat content during winter (Fig. 3) of both Atlantic salmon and brown trout. For the smallest salmon, the S1 group, the mean specific fat content in April (0·91%) was 44% less than the September value (1·63%). Correspondingly, mean specific fat content in April was 62–68% less than the value in September for the large salmon (S2 and S3), which had mean fat content of 1·30% and 1·53%, respectively in April. For

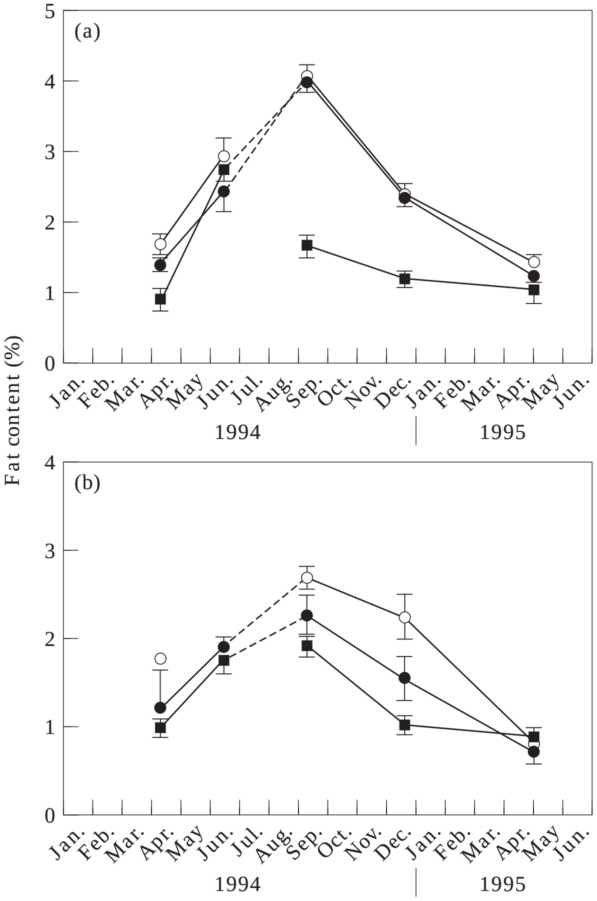

FIG. 3. Mean fat content of (a) Atlantic salmon and (b) brown trout in accordance with seasonal sampling periods (April 1994–April 1995). The break in lines from June to September accord to the change in age status during the early summer period. S.E. bars are indicated for each mean value, and sample size is given in Table I. (a), ■, Body mass <2·0 g; ●, 2·0–5·0 g; ○, >5·0 g. (b), ■, Body mass <3·2 g; ●, 3·2–7·5 g; ○, >7·5 g.

the smallest brown trout, the T1 group, the specific fat content in April (mean 0·98%) was reduced by about 50%, relative to September. The reduction was identical for T2, while the largest trout (T3) showed a 65% reduction. The fat content increased by a factor of 3 from April to June for the smallest salmon (S1), whereas the larger salmon increased by a factor of 1·8–1·9. The fat content of trout (T1 and T2) increased similarly to that of salmon from April to June by a factor of 1·8.

Analysis of covariance of the (log transformed) specific fat content with fresh weight as a covariate, revealed highly significant effects ($P<0{\cdot}001$) of weight, sampling period (Table I) and species (Fig. 3) during both winter and spring/summer. The statistical details for winter were: the specific fat content was highly significantly ($P<0{\cdot}001$; $F_1=109$) positively related with fresh weight. The variation in fat content differed significantly between sampling periods ($P<0{\cdot}001$; $F_2=82$) and between species ($P<0{\cdot}001$; $F_1=47$). For spring/summer (April–June)

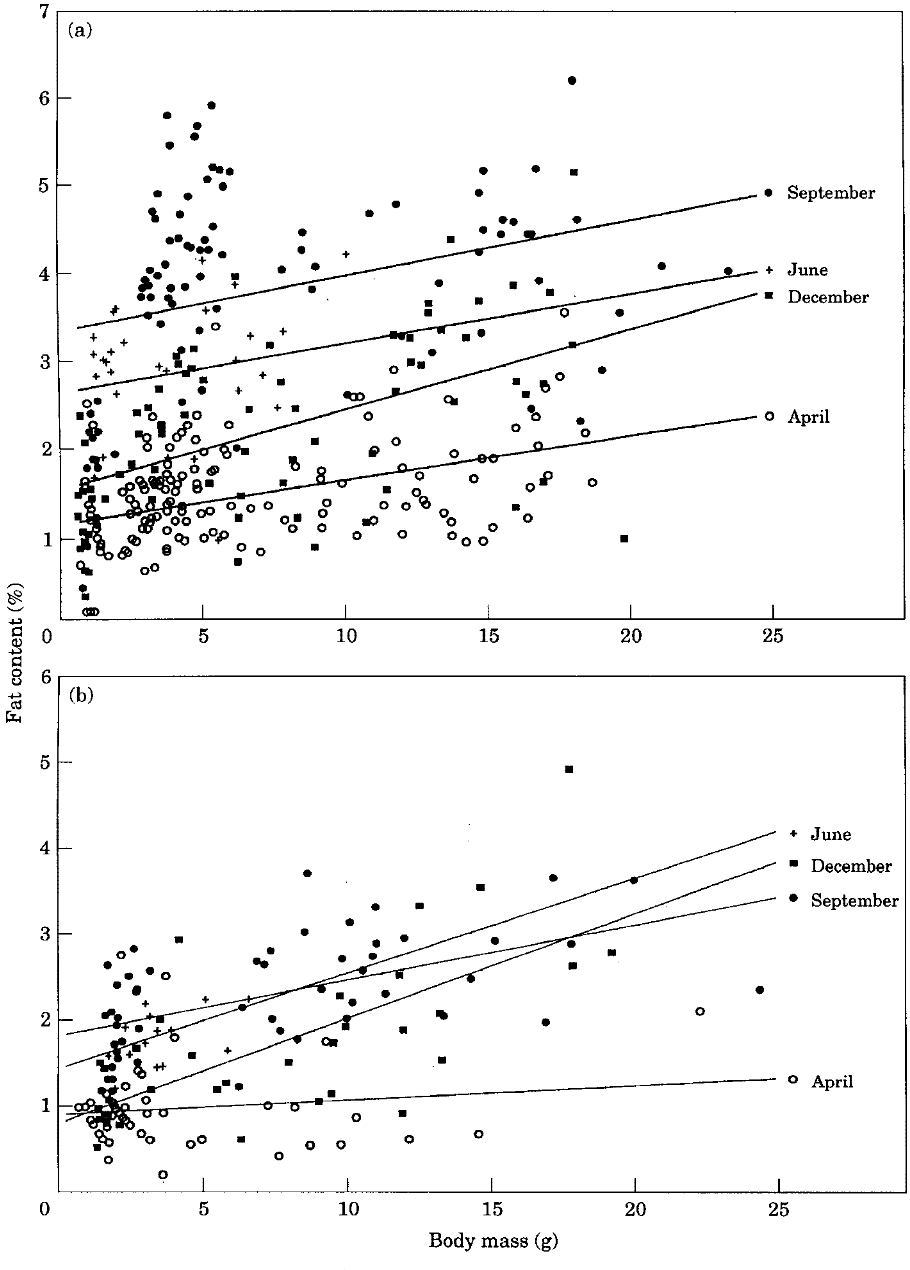

FIG. 4. The relationship between specific fat content and body weight of (a) Atlantic salmon and (b) brown trout from the four sampling periods with the corresponding regression line indicated for the different sampling periods.

the details were: the specific fat content was highly significantly ($P<0{\cdot}001$; $F_1=30$) positively related with fresh weight. The variation in fat content differed significantly between sampling periods ($P<0{\cdot}001$; $F_1=121$) and between species ($P<0{\cdot}001$; $F_1=19$). For the winter period there were also significant interactions between species and period ($P<0{\cdot}001$; $F_2=7$) and between weight and period

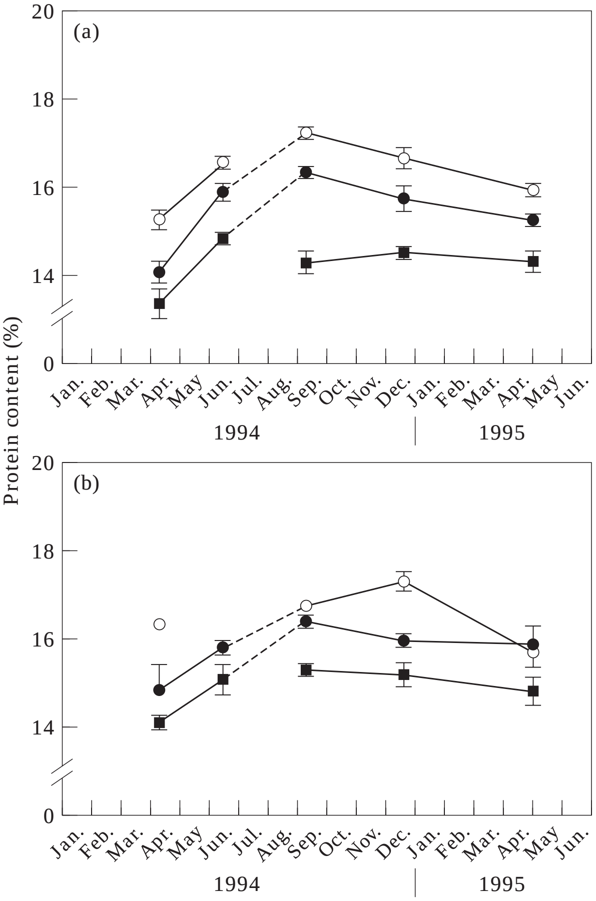

FIG. 5. Mean specific protein content of (a) Atlantic salmon and (b) brown trout in accordance with seasonal sampling periods (April 1994–April 1995). The break in lines from June to September accord to the change in age status during the early summer period. S.E. bars are indicated for each mean value, and sample size is given in Table I. (a), ■, Body mass <2·0 g; ●, 2·0–5·0 g; ○, >5·0 g. (b), ■, Body mass <3·2 g; ●, 3·2–7·5 g; ○, >7·5 g.

($P<0{\cdot}012$; $F_2=4{\cdot}5$). The combined effects of all significant parameters had an r^2 of 0·59 for the winter period and 0·44 for the summer period.

The larger fry of both trout and salmon in December had a relatively low reduction in fat (Fig. 4). The slope of the linear regression of specific fat on weight in the December sample was somewhat steeper than in the other periods.

PROTEIN AND WATER CONTENT

For specific protein content there was a reduction of 6% for the smallest salmon, S1, from September to April (Fig. 5). For the larger salmon the reduction during winter was 10%. For trout, corresponding reductions in protein content ranged from 6 to 7% for the different size groups. Specific protein content increased rapidly from April to June for all investigated groups.

Analysis of covariance of the (log transformed) specific protein content with fresh weight as a covariate, revealed highly significant effects ($P<0{\cdot}001$) of weight and sampling period during both the winter and the spring/summer (April–June) period (Fig. 5). The statistical details for the winter period were: the specific protein content was highly significantly ($P<0{\cdot}001$; $F_1=263$) positively related with fresh weight. The variation in protein content differed significantly between sampling periods ($P<0{\cdot}001$; $F_2=47$) but notably not significantly between species ($P\approx0{\cdot}30$). The corresponding details for the spring/summer period were: the specific protein content was highly significantly ($P<0{\cdot}001$; $F_1=103$) positively related with fresh weight. The variation in protein content differed significantly between the two sampling periods ($P<0{\cdot}001$; $F_1=28$), but not between species ($P\approx0{\cdot}76$). For the winter period there was a significant interaction between species and period ($P<0{\cdot}02$; $F_2=3{\cdot}8$). This interaction was similar to that of specific fat, where the smallest fry decreased in specific protein less rapidly than did the larger fry. During spring/summer there was a significant ($P<0{\cdot}001$) interaction between fry weight and period, as the larger fry had a more rapid ($P<0{\cdot}05$, coefficient of inclination difference) increase in their specific protein content. The combined effects of these parameters had an r^2 of 0·54 for the winter period and 0·37 for the summer period.

For both protein and water there were similar (but opposite) significant ($P<0{\cdot}001$) trends between fish size and content (%) of their protein, specific protein or water in both salmon and trout. The correlation (r) between water and protein content was as high as 0·87 ($n=369$) for salmon and 0·91 ($n=167$) for trout. A similar significant ($P<0{\cdot}001$) negative correlation was found between the percentage of water and the percentage of fat in both salmon ($r=0{\cdot}78$) and trout ($r=0{\cdot}79$). Multiple regression between water content (%) and protein (%) and fat (%) content increased r to values as high as 0·93 (salmon) and 0·94 (brown trout). In some periods, notably September and April, the protein content (%) of S1 salmon was significantly ($P<0{\cdot}05$; t-test) lower than that of the T1 trout.

The specific water content (Fig. 6) had its highest value in spring for all groups of salmon and trout. The highest water content was found in the smallest salmon fry, with values of water content up to 86%.

ENERGY

Specific energy content (fat and protein energy content) in the different groups (Fig. 7) corresponded closely with the seasonal differences in fat content. The specific energy content in April was reduced 30% relative to the September values for the largest salmon (S3), compared to about 28% less for trout. Mean daily specific energy loss for the winter period (about 220 days) was $2{\cdot}18\times10^{-3}$ kJ g^{-1} day^{-1} for the S1 Atlantic salmon, increasing to $6{\cdot}5\times10^{-3}$ kJ g^{-1} day^{-1} for S2 salmon (mean weight 3·7 g) and $6{\cdot}2\times10^{-3}$ kJ g^{-1} day^{-1} for the largest salmon parr (mean weight 11·9 g). Specific energy losses during the entire winter (220 days) were 0·48 kJ g^{-1}, 1·44 kJ g^{-1} and 1·36 kJ g^{-1} for salmon in the respective size classes. The corresponding daily values for trout were $3{\cdot}0\times10^{-3}$ kJ g^{-1} day^{-1} (T1), $3{\cdot}4\times10^{-3}$ kJ g^{-1} day^{-1} (T2 mean weight 5·7 g) and $4{\cdot}2\times10^{-3}$ kJ g^{-1} day^{-1} (T3 mean weight 12·0 g). Specific energy losses during the entire winter were 0·66 kJ g^{-1}, 0·75 kJ g^{-1} and 0·91 kJ g^{-1} for trout in the respective size classes. The daily values for

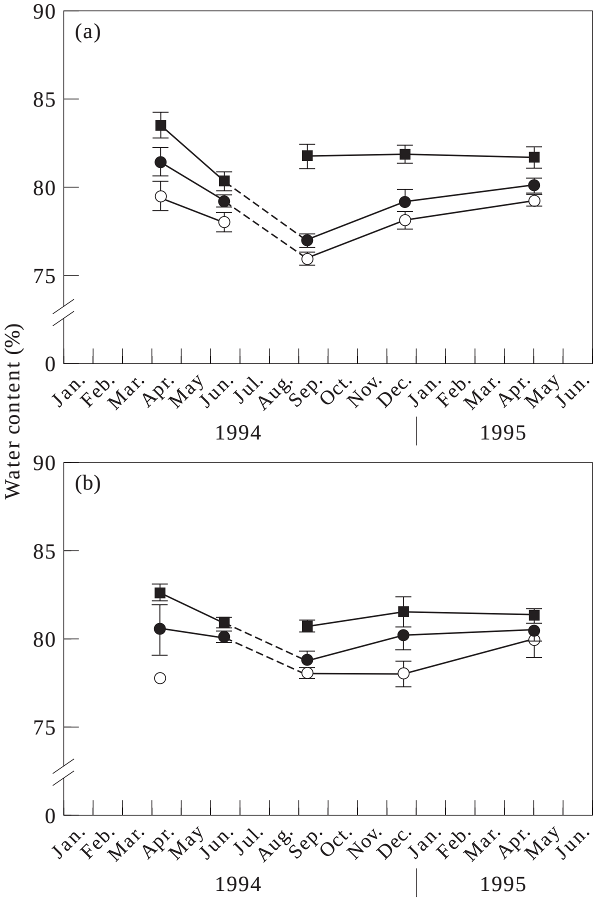

FIG. 6. Mean water content of (a) Atlantic salmon and (b) brown trout in accordance with seasonal sampling periods (April 1994–April 1995). The break in lines from June to September accord to the change in age status during the early summer period. S.E. bars are indicated for each mean value, and sample size is given in Table I. (a), ■, Body mass <2·0 g; ●, 2·0–5·0 g; ○, >5·0 g. (b), ■, Body mass <3·2 g; ●, 3·2–7·5 g; ○, >7·5 g.

the two largest size groups of trout were almost half of the corresponding values found for salmon.

The build-up of energy after winter was most rapid for the smallest salmon. There was newly hatched cohort arriving as the smallest fish after June, while the fish in the different groups grew into the next group during summer, between June and September. Thus, the larger fry of both salmon and trout had their largest specific energy content in September. For trout the increase in energy after winter was more gradual.

DISCUSSION

The content of protein and fat was determined after the winter in two consecutive years. The similarity between these two samples and their differences from the other periods show that there was a period of energy depletion in

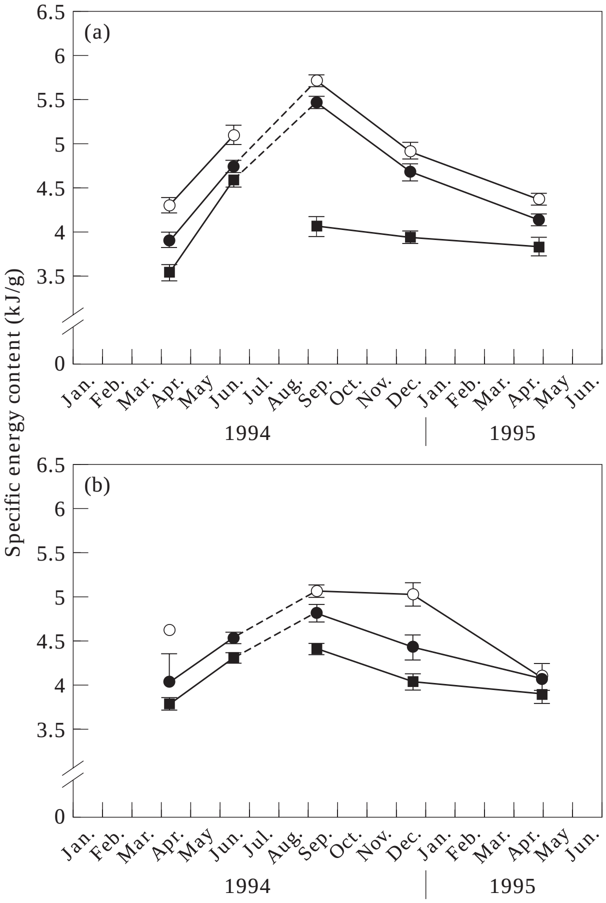

FIG. 7. Mean specific energy content of (a) Atlantic salmon and (b) brown trout in accordance with seasonal sampling periods (April 1994–April 1995). The break in lines from June to September accord to the change in age status during the early summer period. S.E. bars are indicated for each mean value, and sample size is given in Table I. (a), ■, Body mass <2·0 g; ●, 2·0–5·0 g; ○, >5·0 g. (b), ■, Body mass <3·29 g; ●, 3·2–7·5 g; ○, >7·5 g.

salmon and trout during winter. This depletion was most rapid among the largest fry, which had the highest specific fat levels before winter. The corresponding loss among the smallest fry might nevertheless have more severe consequences, as these have least fat and energy in both autumm and spring.

The winter period puts considerable constraints on fishes living in lotic environments (Cunjak & Power, 1987; Valdimarsson & Metcalfe, 1998). As a consequence, stream-dwelling salmonids seek sheltered habitats in the winter (Cunjak, 1996; Valdimarsson *et al.*, 1997). Physical space, specifically the amount of suitable habitat features like low-velocity areas and instream cover (Valdimarsson & Metcalfe, 1998), is the primary factor regulating stream fish populations in winter (Cunjak, 1996), because reduced metabolic demands at low water temperatures lessen the need for feeding and defending territories (Chapman, 1966). The winter-induced change in behaviour and habitat use recorded in several riverine salmonids, may be governed by a need to minimize energy expenditure and hide from predators, as suggested by several authors (Bustard & Narver, 1975; Rimmer *et al*., 1984; Cunjak & Power, 1987; Metcalfe & Thorpe, 1992; Gibson, 1993; Riehle & Griffith, 1993; Gregory & Griffith, 1996; Valdimarsson *et al*., 1997; Valdimarsson & Metcalfe, 1998). In spite of the changes in feeding and other behavioural adaptations during the winter, salmonids lose considerable amounts of energy. The decrease in somatic energy by fish in the River Humla was large for all size groups. Atlantic salmon had a somewhat larger reduction in energy, but also had a higher initial level of energy. The lower limit of fat content necessary for survival of small salmonid fry is not known. Of 105 fry with fat content <1%, only nine had <0·4%, and of these were six individuals with no fat detected. The solvent mixture used for the extraction of fat extracts neutral lipids, which act as energy reserves. Structural lipids such as those in the brain and other neural tissues are made up of phospholipids, which are not extracted with the solvent mixture used (Dobush *et al*., 1985; Randall *et al*., 1991).

There was a relatively rapid decrease in fat and specific energy content from September to December, while the decrease from December to April was less steep. The specific energy content of the larger brown trout fry in September was similar to that of resident and anadromous brown trout spawners (Jonsson & Jonsson, 1997; Berg *et al*., 1998). If there is selective mortality during winter, its rate would probably increase late in the winter season when the fat resources are depleted (Riehle & Griffith, 1993). Eventual seasonally selective mortality of fat-depleted fish might explain the differences between early and late winter reductions in fat and relative energy content (i.e. the fish with the lowest fat content die and only those with higher fat content remain to be sampled).

After the river ice thawed in spring, water temperatures increased rapidly and there was a rapid build-up of fat in the young salmonids. Growth rate is determined by temperature and food consumption (Elliott *et al*., 1995; Elliott & Hurley, 1997). The minimum temperature for growth of Atlantic salmon and brown trout is reported to be just below 7° C (Elliott, 1991; Elliott *et al*., 1995; Elliott & Hurley, 1997), but Higgins (1985) and Higgins & Talbot (1985) reported a rapid increase in growth rate of Atlantic salmon in spring at temperatures between 1° C and about 7° C. Similar results for brown trout were provided by Koskela *et al*. (1997) under rearing conditions with water temperatures down to 2° C. They predicted that the specific growth rate in weight would be zero at water temperatures <0° C, whereas increase in length would cease at approximately 0·6° C. Feeding by salmonids continues during winter (e.g. Cunjak & Power, 1987; Cunjak, 1988; Heggenes *et al*., 1993; Koskela *et al*., 1997). Surplus energy for growth of juveniles in the River Humla, and rivers with similar temperature regimes would commence in April (Fig. 2). In running water, the biomass of potential prey items (Bell *et al*., 1994) is at its maximum during spring (Allan, 1995). Studies by Allan (1985) and Jensen (1990) have revealed growth rates of young salmonids at this time around the theoretical maximum predicted by the growth model of Elliott *et al*. (1995). The difference in fat between winter and spring was greater for salmon than for trout. The mean weight of the smallest salmon was only about half of that of trout, and the increase in fat relative to body mass was thus similar for the two species.

The correlation between protein and water is as expected, as protein binds a correspondingly high amount of water in the body tissues (Jobling, 1995), while fat has no such water binding property (Jobling, 1995; Koskela *et al*., 1997). There was a significant multiple correlation between protein, fat and water content. With the low value of fat during the spring, the body of the smallest salmon fry consisted largely of proteins and bones (ash), with a correspondingly high level of water. The highest level detected was about 86% water.

Protein content also declined during the winter. The largest fish had a proportionally larger loss, which was matched by a large gain in protein content after the winter. Fat and protein losses have been detected as reductions of condition during the winter (Cunjak & Power, 1987), while Cargnelli & Gross (1997) reported that larger individuals emerged from winter in better condition. The smallest fish had the quickest rebuilding of their energy stores in spring, which can be expected on basis of their smaller body size (Jobling, 1995), while larger fish increased their fat content continuously over the summer period above that of the small fry. This trend apparently reflects a trade-off (Calow, 1985; Stearns, 1992), in which small fry give priority to protein build-up compared to fat build-up to increase size and thus reduce predation risk and competition with other fish. Within a large range of sizes in salmonid fishes, there appear to be positive correlations between body size and fat content (Simpson, 1992; Kadri *et al*., 1995).

The seasonal differences in specific energy largely reflected the seasonal fluctuations in fat content. The difference in daily reductions in specific energy between the smallest trout and salmon can be attributed largely to the size differences. The larger size groups of brown trout had mean daily reductions in specific energy which were half of those of the larger Atlantic salmon fry. These differences are probably a product of species-specific metabolic costs and/or energy gained through feeding. There is poor knowledge of species-specific differences in behaviour and energetics between Atlantic salmon and brown trout at low temperatures. A number of authors (Fraser *et al*., 1993, 1995; Heggenes *et al*., 1993; Contor & Griffith, 1995; Valdimarsson *et al*., 1997; Valdimarsson & Metcalfe, 1998) have described the nocturnal feeding of brown trout, rainbow trout *Oncorhynchus mykiss* (Walbaum) or Atlantic salmon during winter. Trout may save energy relative to salmon as salmon generally tend to forage in areas with higher water velocity than trout (Gibson, 1993), thus increasing the metabolic costs of foraging behaviour, but this is merely a speculation under winter conditions.

A crude estimate of metabolic costs was performed to estimate the role of ingestion during the winter. There is a marked deficiency in the literature on metabolic costs of salmonid fry at temperatures near 0° C. The temperature effects on metabolism have been measured down to 3·8° C (Elliott, 1982) for 20-g trout [standard metabolism 326 J day^{-1} (78 cal day^{-1})]. Extrapolation of Elliott's curve to 1° C, yields a standard metabolism of about 210 J day^{-1}. Standard metabolism (R_s, the energy equivalent to that released in the course of metabolism in unfed and resting fish) measured by Elliott (1982) may be slightly high, as the fish could move (Elliott, 1975, 1976), and his values may correspond better with fish in natural environments. Our largest size group of trout had a mean weight of 12·0 g, which should correspond to a reduction in maintenance ration of about 25% (Elliott, 1975). Based on a basal metabolic need of 157 J day^{-1}, a 12-g trout expends a minimum of 34·5 kJ winter^{-1} (winter = 220 days). Energy loss during winter in the Humla was 0·91 kJ g^{-1} for the largest trout fry, corresponding to about 11 kJ winter^{-1}. Therefore, the digestive energy input during the winter must contribute about two thirds of the fish's energy needs. This crude estimate is the first for digestive energy input during winter for brown trout. For Atlantic salmon no corresponding metabolic rates have been ascertained, and direct metabolic comparison between trout and salmon is not possible because of a lack of standardization of size, temperature and experimental procedure (Beamish, 1964; Wiggs *et al.*, 1989; Butler *et al.*, 1992; Beaumont *et al.*, 1995). If metabolic rates are similar between trout and salmon during winter, digestive energy input for salmon during winter would be about 50%.

The winter period with its low freshwater temperatures appears to put considerable stress on the young of Atlantic salmon and brown trout, both of which are considered to be coldwater fish species (Nathanailides, 1996). The winter fat depletion may be balanced by behavioural tactics ranging between anorexia or feeding (Metcalfe & Thorpe, 1992; Valdimarsson *et al.*, 1997; Valdimarsson & Metcalfe, 1998). The gradual decrease in energy in the fish in the River Humla during winter does not support such a balance. Bull *et al.* (1996) found that an elevation of appetite to restore lost reserves was dependent not on current energy state, but on projected energy state at the end of the winter. The fish were held at a water temperature of 6° C in contrast to the Humla fish at 0° C. The winter decrease in fat content and the general reduction in fish energy content may make the fish more vulnerable to ecological factors like parasitism, predation or adverse abiotic factors (e.g. pollution). Factors that may have little effect during periods of higher water temperatures can thus become lethal during winter. Lemly (1996) has described a winter situation where the fish have increased their respiratory demand, and has called this phenomenon the winter stress syndrome. With this in mind we hope that the present study will stimulate further investigations pertaining to the winter ecology of freshwater fishes.

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