



# Variation in aggressive behaviour and growth rate between populations and migratory forms in the brown trout, *Salmo trutta*

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(Received 31 October 2000; initial acceptance 13 January 2001;  
final acceptance 5 July 2001; MS. number: 6733R)

Aggressiveness of juvenile salmonid populations has been suggested to correlate positively with the time the fish spend in the stream. Consequently, resident populations are expected to be more aggressive than migratory populations. Aggressiveness and growth rate have been found to correlate positively at the individual level, but no studies have compared populations. We studied variation in aggressiveness and growth in 10 Finnish brown trout populations differing in their migratory behaviour (sea-run, lake-run and resident). Contrary to expectations, we found the sea-run populations to be more aggressive than the lake-run and resident populations. As all the study fish were reared under similar conditions, it is likely that the differences in aggression have a genetic basis. We also found a positive correlation between aggression and growth rate among the populations. This result supports earlier findings of a positive connection between aggressiveness and growth rate, but is, to our knowledge, the first time this phenomenon has been observed at the population level.

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There is now ample evidence that behavioural traits usually have a strong genetic component and can respond to selection (Boake 1994; Foster & Endler 1999). Consequently, when local or geographical selective regimes are different and strong enough, behaviour in different populations of a given species may evolve in different directions (Foster & Endler 1999). Hence, population comparisons are valuable in studies of behavioural evolution as they can provide insights into the causes of behavioural differentiation.

In salmonids there is considerable variation in life history patterns, growth rate, and age and size at maturation both between and within species (Schaffer & Elson 1975; Hutchings & Morris 1985; Elliott 1994; Skúlason & Smith 1995; Tallman et al. 1996). However, behavioural variation has received less attention. In juvenile salmonids, aggressive territory defence is an important

component of the behavioural repertoire. Territorial behaviour ensures adequate food supply in the stream, where juvenile fish feed mainly on drifting food (Chapman 1962; Keenleyside & Yamamoto 1962).

Salmonid fish also have variable migratory patterns both within and between species, and, depending on the migratory behaviour, the juveniles spend variable periods in their natal stream. In fish, resident populations are generally considered to be more aggressive than migratory ones (Bakker & Feuth-de Bruijn 1988; Hutchison & Iwata 1997), and migratory behaviour may be connected with the level of aggressiveness in the population and promote differentiation between populations. In some species, migratory forms have different levels of aggression; populations that migrate soon after hatching are less aggressive than those that spend more time in the stream (from a few months to several years; Rosenau & McPhail 1987; Taylor 1988, 1990). It has been suggested, therefore, that there should be a positive correlation between aggression and residence period in a stream (Taylor & Larkin 1986; Hutchison & Iwata 1997).

In salmonids there appears to be a positive connection between aggressiveness and growth rate at the individual level (Metcalf 1990; Nicieza & Metcalf 1999). This is partly due to the better competitive ability of the more aggressive, dominant individuals. The latter also have a

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higher standard metabolic rate (SMR; allowing participation in energetically costly behaviours) and as salmonids have indeterminate growth, high SMR favours high growth rate (Metcalf et al. 1995; Yamamoto et al. 1998). Furthermore, growth hormone injections increase not only growth but also aggressive behaviour and competitive ability (Johnsson & Björnsson 1994) and suggest a link between aggressive behaviour and growth performance. Studies on the connection between fast growth and aggressiveness at the population level may be a valuable source of further information; however, there have been none so far.

In this study we compared aggressive behaviour and growth rates of 10 Finnish brown trout populations representing three migratory forms. We investigated whether populations and migratory forms differed in aggressive behaviour and growth rate and whether aggressiveness and growth rate in the populations were related.

## METHODS

### Study Fish

We carried out the study at Saimaa Fisheries Research and Aquaculture in Enonkoski, eastern Finland. The 10 populations used in the study originated from distinct water systems across Finland (Fig. 1), and are separately maintained in the hatcheries of the Finnish Game and Fisheries Research Institute in southern and central Finland.

Brown trout, like many other salmonids, can be divided into three forms based on their migration behaviour. Anadromous trout migrate either to sea (sea-run form, *S. trutta* m. *trutta*) or to a lake (lake-run form, *S. trutta* m. *lacustris*) to feed at the age of 1–6 years, and return to their natal stream to spawn. In contrast, the resident form (*S. trutta* m. *fario*) stays in the home stream all its life (Elliott 1994). Some populations, however, can include both migrating and resident forms, which may interbreed freely with each other (Kallio-Nyberg & Koljonen 1991; Elliott 1994). We determined the migratory status of each population from the migratory form of the founder individuals (Kallio-Nyberg & Koljonen 1991). Three of our study populations represented the sea-run, four the lake-run and three the resident form. All the sea-run and three (Vuoksi, Rautalampi, Kuusinkjoki) of the lake-run populations migrate downstream, whereas one of the lake-run populations (Kitkajoki) migrates upstream because of natural migration barriers downstream. In Finnish brown trout populations smoltification and maturation are rare prior to the third year (2+, J. Piironen, unpublished data). As our study fish were yearlings (0+), it is unlikely that these life history events would affect our results.

All our study populations are threatened by overfishing and dam construction, and hatchery stocks were established to preserve them. Hatchery conditions, however, differ in many respects from those in the wild and there is a growing concern that hatchery rearing alters the genetic background of salmonid populations. Aggressive behaviour is one of the traits potentially affected by hatchery

selection (Fenderson et al. 1968), but how it is affected is not clear, as both increased (Fenderson et al. 1968; Swain & Riddell 1990) and decreased (Berejikian et al. 1996; Hedenskog et al., in press) aggression in hatchery strains have been found. Despite our efforts to use populations with a short hatchery history, they differed with respect to this parameter. Therefore, in a separate set of analyses, we included a variable describing hatchery background (Table 1). The number of parental fish used to produce the experimental generation varied between 50 and 500 among the populations.

Temperature and length of growing season are among the most important environmental factors that produce adaptive variation in physiological and life history traits in fish (Conover & Schultz 1995; Arendt 1997). Geographical location, especially latitude, causes intraspecific variation in metabolic processes (references in Hochachka & Somero 1971), digestive performance (Nicieza et al. 1994) and growth (Conover & Schultz 1995). Since high-latitude populations experience lower temperatures and shorter growing seasons than low-latitude populations, different populations may have adopted differing growth trajectories. To investigate whether this would be the case among our populations, we analysed aggressive behaviours and growth rates of the populations with respect to latitude of origin.

In February 1998, 1000 eyed-stage eggs from each population were transferred to the Enonkoski hatchery from several hatcheries in southern and central Finland. The eggs from each population were incubated in separate troughs. After swim-up (when the fry start to search for exogenous food), the fish were reared in standard hatchery tanks (diameter 160 cm, flow 20–22 litres/min, 200 individuals, one tank per population) and fed trout pellets (nutraG EWOS, diameter 1.0 mm) ad libitum. The light:dark regime varied with the hatchery's daily routine, averaging 8:16 h. Mean  $\pm$  SD water temperature from mid-May to the start of the experiment (September) was  $15.9 \pm 1.4$  °C.

### Behavioural Trials

From each population, we used 32 individuals in aggression trials. Eight trials with four fish were run for each population. To recognize the fish individually, both during the behavioural observations and during the size measurements, we marked them with trial-specific cold-brands (Bourgeois et al. 1987) and by tail clipping within trials. Figure 2 illustrates the size and shape of the pieces of fin removed from the tail during tail clipping. Each fish had only one of the possible four marks. Tail clipping had no influence on the dominance rank of the fish ( $\chi^2_3=11.26$ ,  $N=316$ ,  $P=0.26$ ).

We selected four similar-sized (within 0.5 g) fish originating from the same population for each trial. The mean size of fish tested differed between populations but not between the migration forms (nested ANOVA: migration form:  $F_{2,306}=1.83$ ,  $P=0.415$ ; population:  $F_{7,306}=19.51$ ,  $P<0.001$ ; Table 2). The fish were anaesthetized with MS 222 (tricaine methanesulphonate), their total length (to the nearest mm) and weight (to the

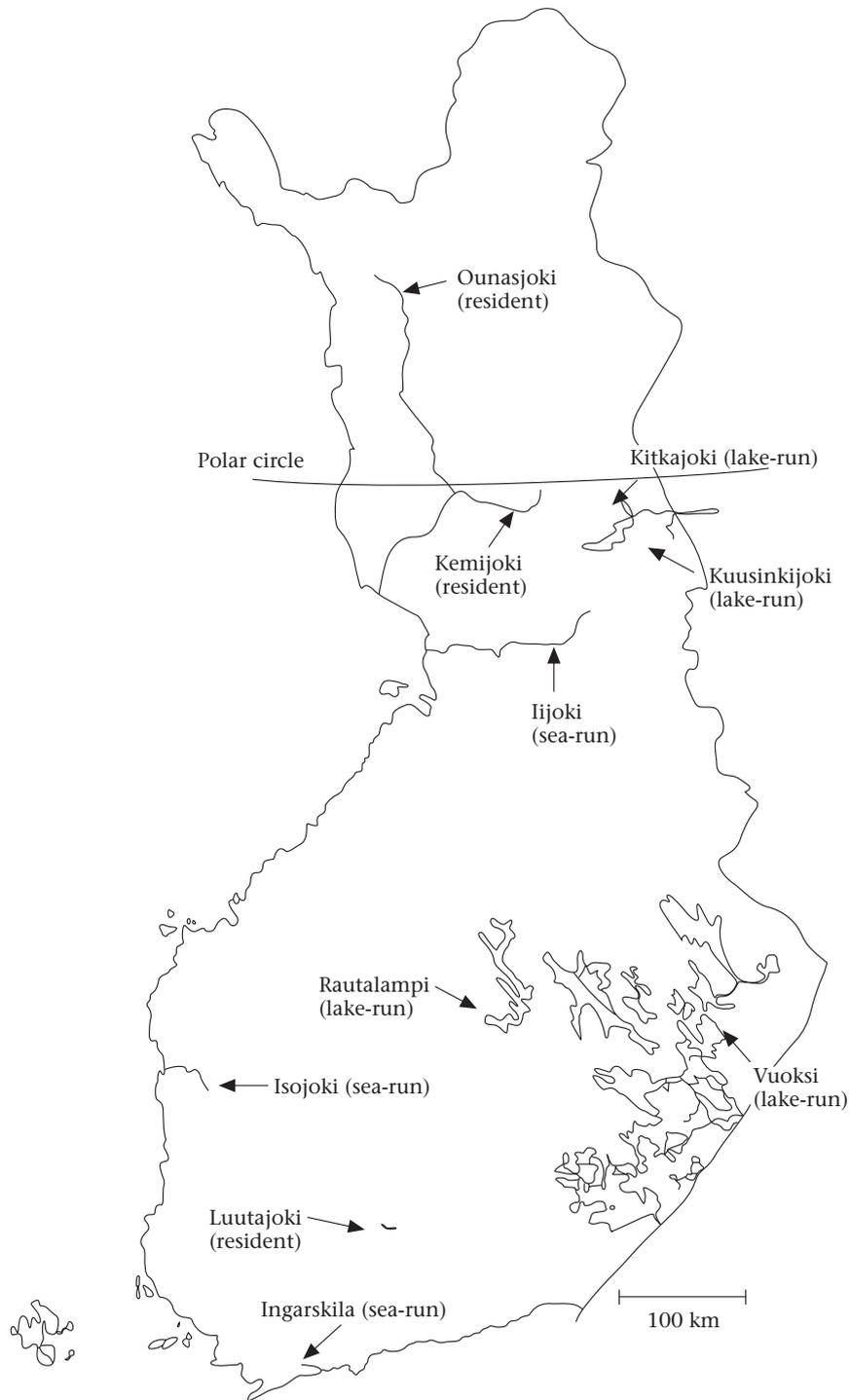


Figure 1. Map showing the locations and migratory status of the study populations in Finland.

nearest 0.1 g) were measured, and they were marked individually. The fish were then transferred to the trial aquarium, and left to acclimatize until the following day, when we started the observations.

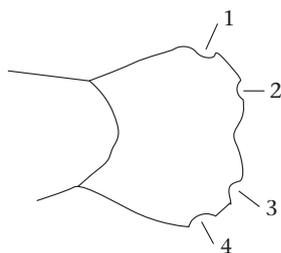
We conducted trials between 14 September and 29 October 1998, with 10 aquaria (40 × 25 cm, water depth 30 cm). The water temperature varied during the experiment ( $\bar{X} \pm \text{SE}$ ) = 7.6 ± 0.12 °C, minimum 5.9 and maximum 9.3. To avoid the confounding effects of season we

ran the trials on all the populations simultaneously. Fish density (40 fish/m<sup>2</sup>) was relatively high compared to the situation in the wild, but was chosen to ensure a competitive environment. It is well below the usual hatchery densities. Three sides and the top of the aquaria were covered with opaque plastic to avoid disturbance and to prevent fish from escaping. Water turnover in the aquaria was adjusted to 4 litres/min and the photoperiod was kept constant at 14:10 h light:dark.

**Table 1.** Scores used in describing hatchery history for the 10 study populations

| Score | Parents                                             | Source river of the population                                     | Background of parents                                                                                       |
|-------|-----------------------------------------------------|--------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------|
| 1     | All parents from hatchery stocks                    | Luutajoki (R)<br>Iijoki (S)<br>Ingarskila (S)                      | 1st H generation<br>3rd H generation<br>1st H generation                                                    |
| 2     | Some parents from hatchery stocks, some from nature | Isojoki (S)<br>Rautalampi (L)<br>Kuusinkijoki (L)<br>Kitkajoki (L) | W male×3rd H generation female<br>W male×H female<br>Parents from H and W<br>W male×1st H generation female |
| 3     | All parents from nature                             | Kemijoki (R)<br>Vuoksi (L)<br>Ounasjoki (R)                        | W<br>W<br>W                                                                                                 |

'W' indicates the parents originated from the wild; 'H' indicates they were of hatchery origin. The number of hatchery generations is given when the information was available. Migratory form of the population: R=resident; S=sea-run; L=lake-run.



**Figure 2.** Illustration of the marks left by the tail clipping, used to identify the fish in observations and in later measurements of growth.

**Table 2.** Mean fish length±SE in the different populations

| Population   | Length   |
|--------------|----------|
| Iijoki       | 9.6±0.15 |
| Isojoki      | 9.5±0.19 |
| Ingarskila   | 9.6±0.17 |
| Vuoksi       | 9.1±0.19 |
| Kuusinkijoki | 8.8±0.19 |
| Rautalampi   | 9.1±0.16 |
| Kitkajoki    | 7.2±0.11 |
| Kemijoki     | 9.6±0.15 |
| Ounasjoki    | 8.9±0.15 |
| Luutajoki    | 8.2±0.15 |

We made observations twice a day (0800 and 1600 hours), and one observation period lasted for 30 min. As food stimulates aggressive behaviour (Newman 1956), we fed the fish at the beginning of each observation period (the same type of food pellets as in the holding tanks). Food was provided in excess, and the fish were not fed outside the observation period. The pellets floated from a few seconds to 30 min on the water surface and they were provided in a circular floating plastic frame (diameter 8 cm), which prevented the pellets from running through the outlet. This ensured that the food was always provided at the same spot. Consequently, there were more profitable feeding locations to defend in the aquarium. We recorded the number of aggressive behaviours (nip, charge, chase, lateral display, frontal display and

approach; Keenleyside & Yamamoto 1962) and food items eaten by each fish. In addition, we divided aggressive behaviours into two categories: overt and mild aggression. Approach and charge, which were the least costly and risky behaviours, were classified as mild aggression. Nip, chase, frontal display and lateral display were more costly behaviours (chase), required physical contact (nip) or took place in a fighting situation, where both fish were motivated to fight (lateral displays). An observer sitting still 1 m from the aquaria recorded the behaviour.

At the end of each observation day, the dominant individual in each trial was determined based on the amount of aggression. An individual was regarded as dominant, if it (1) performed most aggression towards other fish, and also responded aggressively when attacked or (2) performed aggression towards others without receiving any. If the fish classified as dominant under (1) and (2) was not the same individual, the one that performed most aggression towards another fish was classified as dominant. We removed the dominant fish from the trial and repeated the procedure on successive days until only one fish was left. This was done for the purpose of another study (A. Laurila, S. Vilhunen & K. Lahti, unpublished data). However, in cases where dominance remained uncertain (because interactions were rare or general activity low within a trial), the maximum duration of each trial was set to 6 days and, consequently, the observation period per trial varied from 4 to 6 days.

## Growth

We monitored individual growth rates for all populations from the date they entered the behavioural trials (between 14 September and 29 October) until January 1999. We measured total length and weight for each fish before it entered the behavioural trials and a second time in January 1999. In between the measurements, the fish were kept in the same standard hatchery tanks (200 fish/tank and each population separately) as mentioned above. The specific growth rate (SGR, the percentage growth/day) for individually known fish was calculated according to Jobling (1994):

$$SGR = 100 \times [(\ln W_2 - \ln W_1) / T]$$

where  $W_1$  is the weight at the start of the behavioural trial and  $W_2$  is the weight in January 1999, and  $T$  is the length of the growing period in days, determined individually for each fish (note that although the start of the growing period varied between fish, aggression trials for the different populations were run in parallel). By January, the fish were no longer all recognizable with certainty, and the number of individuals from which SGR could be determined varied between 14 and 28 (mean 23) among the populations. The photoperiod during the growth period was first the natural one (to 62°N), but after early November it was a constant 8:16 h light:dark following the daily routines in the hatchery. The water temperature during the growth period was a mean  $\pm$  SE of  $4.8 \pm 0.35$  °C, minimum 1.5 and maximum 15.1.

## Data Analyses

As the behaviours of the four fish within an aquarium were not independent, we calculated mean aggression and foraging rates in the 30-min observation periods for each fish and used the mean value of the four fish in each trial as an observation. Aggressiveness and foraging were not normally distributed, and the data were ln transformed to normalize the distributions.

We used nested ANCOVAs to analyse the differences in aggression and foraging between the migratory forms and populations as well as between the hatchery backgrounds (Table 1) and populations. The term population was nested either within the term form or the term background. Trial duration and temperature were used as covariates. We used nested ANCOVA with individual fish as observations to test the differences in specific growth rate ( $\ln(x+1)$  transformed) between the populations and forms as well as populations and hatchery backgrounds; length at the beginning of the experiment was used as a covariate. Pearson product-moment correlation was used in analysing the relationship between mean specific growth rate and aggressiveness (both  $\ln(x+1)$  transformed) among the 10 populations. Correlation analysis was also used to investigate the relationship between latitude and growth, and latitude and aggressiveness among the populations.

All the statistical tests conducted were two tailed.

## Ethical Note

Aggression among individuals did not result in physical damage, and, in general, escalated fights were rare. Fish were anaesthetized before being marked by cold branding and tail clipping. We used two methods because the cold-brand mark, which was necessary for recognizing the fish in later measurements, was not sufficiently visible in the aquarium to allow individual recognition. Cold branding is a commonly used marking method in fish hatcheries (Bourgeois et al. 1987), and it is a good way to mark individuals when they are too small to be, for example, marked with PIT tags. Liquid nitrogen was used to make a small ( $2 \times 2$  mm) rod of iron cold. This was pressed lightly to the skin of the fish, on one side above

and below the lateral line, for about 2 s leaving a tiny mark. The anaesthetized fish did not react physically to it. The procedure is quick and appears not to stress the fish. We did not find any signs of irritation, infection or disease in the marked area, nor was there any mortality in the experiment due to marking. The fish started to recover from the anaesthetic after 1–3 min of the marking and were left in smaller containers for ca. 1 h before we put them into the experimental aquaria. The fish were observed feeding normally on the day after the marking. The cut fins and branded skin both grew back quickly as indicated by the fact that we were able to recognize only 71.5% of the study fish when we remeasured them in January 1999, that is, despite the low water temperature, the marks had completely disappeared in 28.5% of the fish. In all, two fish died when they jumped out of the experimental aquarium. No other mortality occurred during the experiment.

## RESULTS

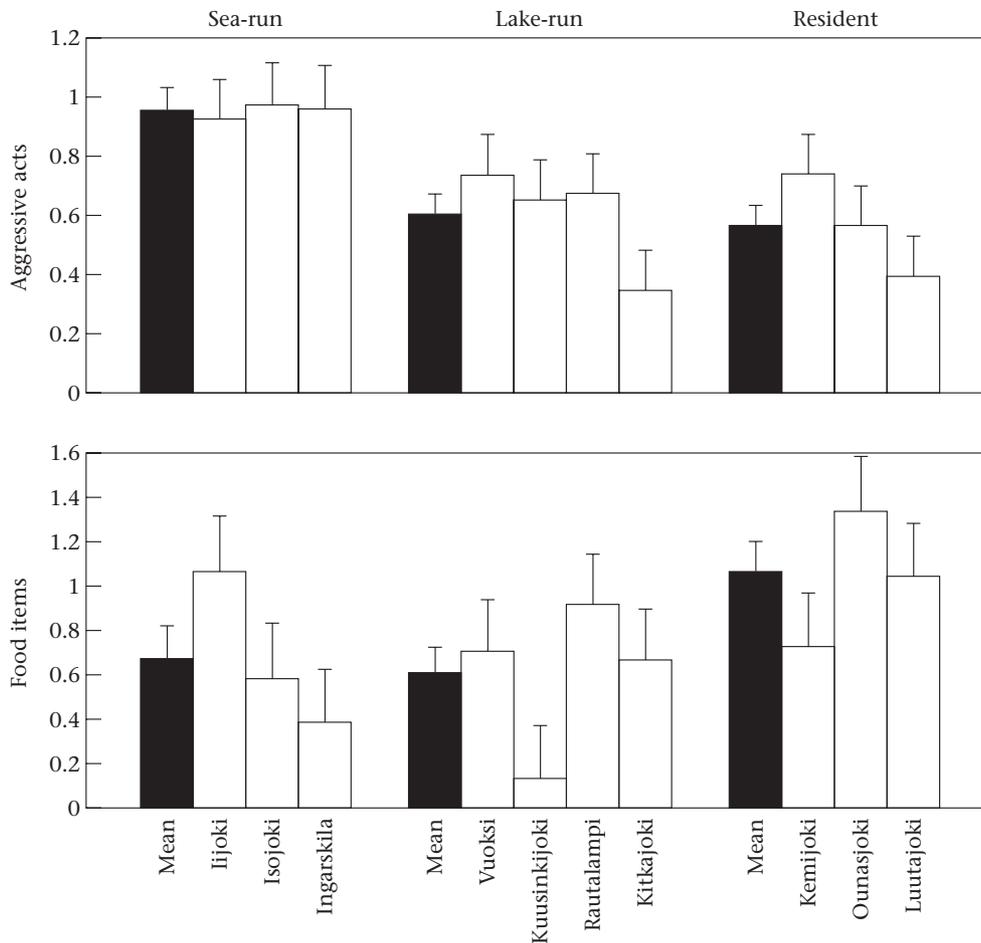
Aggressiveness varied between the populations (Fig. 3). However, migration form explained most of this variation (Fig. 3, Table 3). The forms differed significantly in total aggressiveness, and the sea-run form was more aggressive than the lake-run (Tukey test:  $P=0.04$ ) and the resident (Tukey test:  $P=0.03$ ) forms. Migration form also explained most of the variation in overt aggression, but not in mild aggression (Fig. 4, Table 4). Populations differed in their body size, and as size of the fish may influence their aggressiveness (Abbot et al. 1985), we tested this possibility in another set of analyses where trial-specific mean body length was included in the model as a covariate. However, body size did not influence either total aggression ( $F_{1,66}=0.10$ ,  $P=0.76$ ) or the other aggression types, and the results remained qualitatively unchanged. Foraging rate did not differ significantly between populations or forms (Fig. 3, Table 3).

Hatchery background did not have a significant effect on aggressive behaviour and, as the term form was now not included in the model, population became a significant explanatory variable (Tables 3 and Table 4). Neither did hatchery background have a significant effect on foraging rate (Table 3).

Populations differed in their growth rate; however there were no differences in growth rate between migration forms (Fig. 5, Table 5). Both the populations having the highest (Vuoksi) and the lowest (Kitkajoki) growth rate were lake-run. There was a positive correlation at the population level between specific growth rate and aggressiveness ( $r_8=0.87$ ,  $P=0.001$ ; Fig. 6). Hatchery background did not affect growth rate (Table 4). There was no significant correlation between aggressiveness and original latitude of the populations ( $r_8=-0.013$ ,  $P=0.97$ ) nor between latitude and growth rate ( $r_8=-0.094$ ,  $P=0.80$ ).

## DISCUSSION

There are three main causes of phenotypic variation between populations: (1) differences may have a genetic



**Figure 3.** Mean number of aggressive acts and food items eaten (least square means+SE,  $\ln(x+1)$  transformed) in a 30-min observation period for each of 10 brown trout populations. ■: Mean values for each migration form.

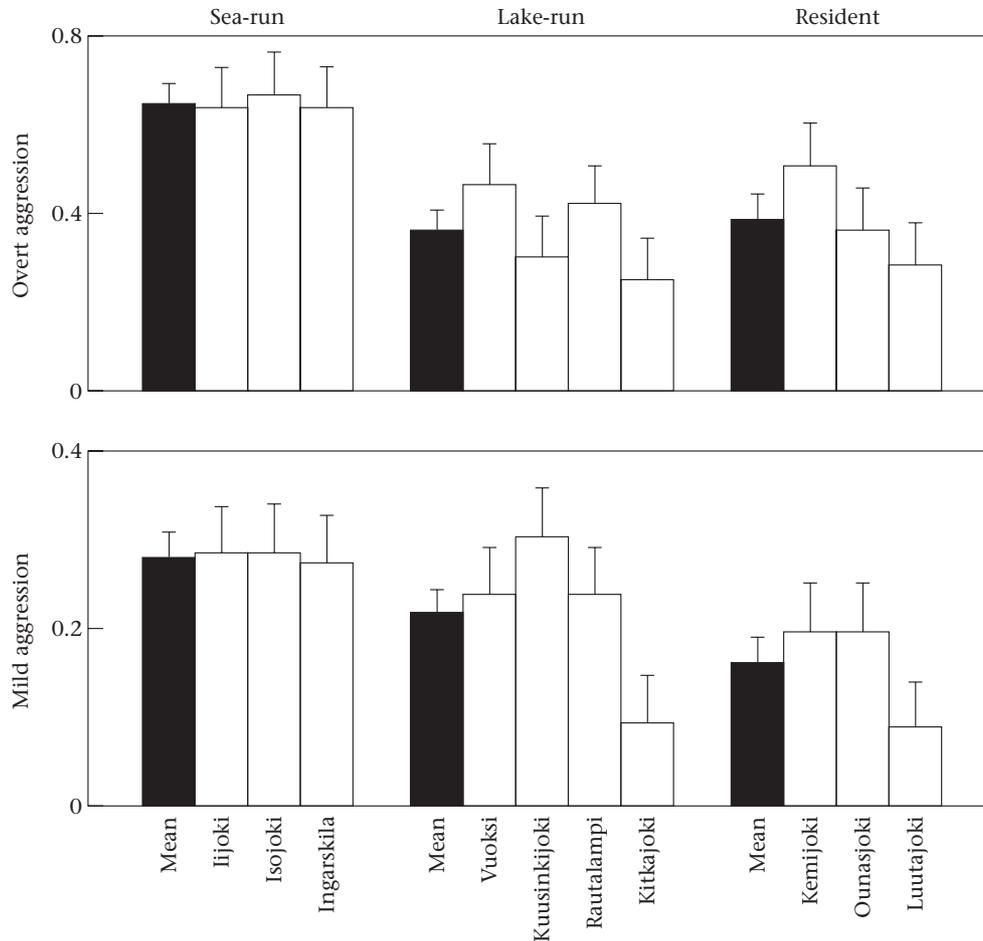
basis; (2) similar genotypes may differ because they experience different environments; and (3) variation can result from the interaction of both genetic differences and environmental factors. We found that brown trout populations differed in their aggressiveness. As all populations were reared under similar conditions and they experienced the same handling procedures, we suggest that the differences in behaviour between populations have a genetic basis. However, the fish were reared in only one environment and we do not know about the possible interactions between genetic and environmental influences. Also, we cannot exclude the influence of maternal effects on the variation in aggressive behaviour.

It has been suggested that resident populations are the most aggressive group of salmonids, because resident fish are under greater selective pressure for aggression, as they increase their survival, growth and reproduction by investing in territorial behaviour (Hutchison & Iwata 1997). In our study, however, migrating sea-run populations had higher aggression rates than lake-run and resident populations. We also found significant differences in overt aggression between the forms, whereas there was no difference in mild aggression. Overt aggressive behaviours are likely to be energetically more costly, and probably more risky than mild aggression.

**Table 3.** Nested ANCOVA table for the effects of migration form and hatchery background (analysed separately) on total aggressiveness and foraging

| Source                  | <i>df</i> | <i>F</i> | <i>P</i> |
|-------------------------|-----------|----------|----------|
| <b>Aggression rate</b>  |           |          |          |
| Form                    | 2,7       | 6.55     | 0.025    |
| Population (Form)       | 7,67      | 1.12     | 0.360    |
| Hatchery background     | 2,7       | 0.16     | 0.855    |
| Population (Background) | 7,67      | 3.12     | 0.007    |
| Covariates              |           |          |          |
| Temperature             | 1,67      | 13.17    | 0.001    |
| Observation days        | 1,67      | 64.05    | <0.001   |
| <b>Foraging rate</b>    |           |          |          |
| Form                    | 2,7       | 1.64     | 0.261    |
| Population (Form)       | 7,67      | 2.06     | 0.060    |
| Hatchery background     | 2,7       | 0.93     | 0.438    |
| Population (Background) | 7,67      | 2.40     | 0.030    |
| Covariates              |           |          |          |
| Temperature             | 1,67      | 7.04     | 0.010    |
| Observation days        | 1,67      | 7.12     | 0.010    |

Temperature and number of observation days were used as covariates in all analyses.



**Figure 4.** Mean number of overt (nip, chase, frontal display, lateral display) and mild (approach, charge) aggressive acts (least square means+SE,  $\ln(x+1)$  transformed) in a 30-min observation period for each of 10 brown trout populations. ■: Mean values for each migration form.

If aggressiveness is a beneficial trait in resident populations, why was the resident form less aggressive than the sea-run form? There may be several explanations for this result. Perhaps most importantly, regardless of the migration form, all our study populations spend several years in the stream. In species where migration may occur relatively soon after hatching, the populations with earlier migration are expected to behave less aggressively than later migrating or resident populations, as the behaviour shifts from territorial to schooling at the time of migration (Roff 1988). However, when considering populations that spend several years in the stream, the benefits of aggressiveness might no longer be pronounced only in resident populations. Migratory brown trout commonly have high densities right after swimming up from the gravel, but by autumn the density has been reduced by up to 80% (Elliott 1986). The decrease in population size is mostly a result of territorial behaviour; only a few dominants can occupy and defend a territory and a large proportion of the fish are forced to move downstream (Titus & Mosegaard 1991; Elliott 1994). Hence, it seems likely that migratory populations of brown trout may also enhance their fitness by investing in territorial defence. In Atlantic salmon, *Salmo salar*, fish that have high social

**Table 4.** Nested ANCOVA table for the effects of migration form and hatchery background (analysed separately) on the rates of overt and mild aggressive acts

| Source                  | df   | F     | P      |
|-------------------------|------|-------|--------|
| <b>Overt aggression</b> |      |       |        |
| Form                    | 2,7  | 9.30  | 0.012  |
| Population (Form)       | 7,67 | 0.97  | 0.457  |
| Hatchery background     | 2,7  | 0.39  | 0.690  |
| Population (Background) | 7,67 | 3.20  | 0.006  |
| Covariates              |      |       |        |
| Temperature             | 1,67 | 15.80 | <0.001 |
| Observation days        | 1,67 | 73.04 | <0.001 |
| <b>Mild aggression</b>  |      |       |        |
| Form                    | 2,7  | 2.35  | 0.166  |
| Population (Form)       | 7,67 | 1.61  | 0.148  |
| Hatchery background     | 2,7  | 0.05  | 0.950  |
| Population (Background) | 7,67 | 2.69  | 0.016  |
| Covariates              |      |       |        |
| Temperature             | 1,67 | 5.15  | 0.026  |
| Observation days        | 1,67 | 34.98 | <0.001 |

Temperature and number of observation days were used as covariates in all analyses.

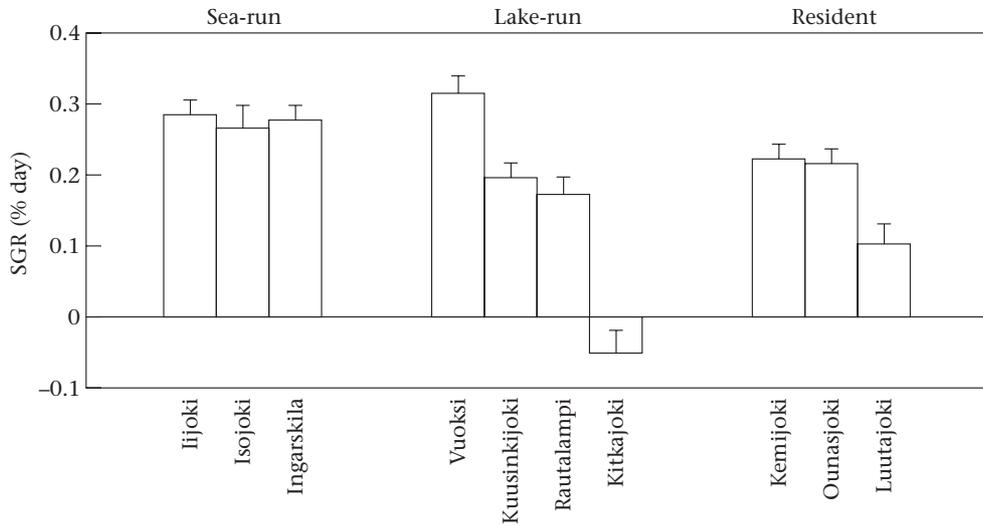


Figure 5. Adjusted least squares means of specific growth rates (SGR+SE, %/day) shown separately for 10 brown trout populations.

status are more aggressive and migrate at a younger age (Metcalf et al. 1989; Nieceza & Metcalfe 1999) and, consequently, they have long-term fitness benefits (earlier maturation, decreased overwinter mortality) compared to later migrating fish (Schaffer & Elson 1975; Hutchings & Morris 1985). Assuming that migratory brown trout in our populations gain similar benefits from early migration, selection can be expected to favour aggressiveness in these populations as well.

Furthermore, differences in the quality of the habitats where these populations originate may produce differences in behaviour through local adaptation. Several environmental factors in the habitat affect the aggressiveness of fish populations, such as food availability (Rosenau & McPhail 1987; Dunbrack et al. 1996), predation risk (Huntingford 1982; Magurran & Seghers 1991) and current velocity (Grant & Noakes 1988; Swain & Holtby 1989). Rivers with sea-run trout populations may share an environmental factor selecting for increased aggression. Unfortunately, we do not have enough information either on the habitat quality of the rivers or on the habitat selection of the populations, and this question remains open for further investigation.

The alternative hypothesis that the hatchery history of the populations would affect the amount of aggression

was rejected. However, hatchery-reared fish can show different and even deficient behaviour independent of parental background (Olla et al. 1994). Hence, while our results clearly show differences between the populations and migratory forms, care should be taken when extrapolating them to nature. Similarly, aggressive interactions between fish, compared to other activities, may be relatively rare in nature, and the effects of differential aggressive behaviour may be mainly visible in the consequences manifested, for example, as differences in density or growth rate. However, disentangling these effects from environmental variation (habitat quality, etc.) is difficult.

Migratory species are predicted to grow faster, mature later and be larger than nonmigratory species (Roff 1988). Although our populations differed in growth rate, we did not find any differences between migratory forms. This is

Table 5. Nested ANCOVA table for the effect of migration form and hatchery background on specific growth rate

| Source                      | df    | F      | P      |
|-----------------------------|-------|--------|--------|
| <b>Specific growth rate</b> |       |        |        |
| Form                        | 2,7   | 1.15   | 0.370  |
| Population (Form)           | 7,215 | 14.02  | <0.001 |
| Length                      | 1,215 | 126.13 | <0.001 |
| <b>Hatchery background</b>  |       |        |        |
| Population (Background)     | 7,215 | 14.24  | 0.001  |
| Length                      | 1,215 | 126.13 | 0.001  |

Fish length at the beginning of the experiment was used as a covariate.

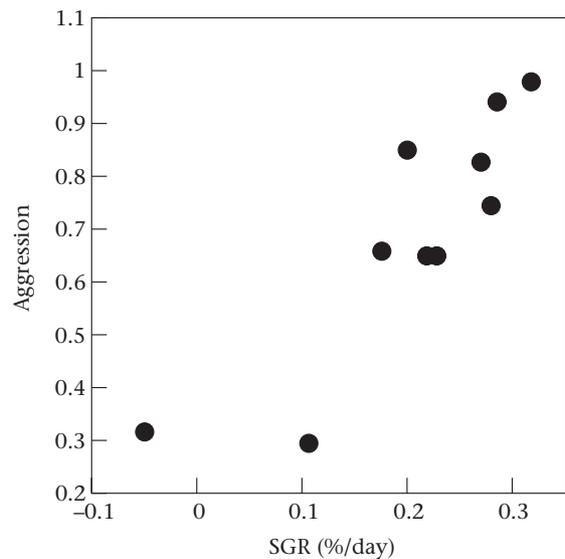


Figure 6. Relationship between specific growth rate, SGR (adjusted least squares means, %/day) and mean aggressiveness (ln(x+1) transformed). Each point represents one trout population.

in accordance with previous results showing no difference between the growth rates of resident and migratory forms of brown trout (Elliott 1994). When reared under identical conditions, high-latitude populations of ectothermic animals have genetically higher growth rates than low-latitude populations (Conover & Schultz 1995). Although our study populations originated from a geographically wide area from north of the Polar circle to southernmost Finland, no relationship between latitude and growth rate was found. Timing of our growth study is a potential explanation for this result, as the growth period was from autumn until January. Fish that live in temperate or boreal environments usually grow slowly or not at all in winter (Wootton 1998).

There was a positive correlation between aggression and growth rate: populations that had high growth rates also showed high levels of aggression. As our analyses were conducted at the population level they suggest a positive genetic correlation between these traits. At the individual level, high aggressiveness is known to promote high growth rate through prior access to food resources, despite the costs of aggressive behaviour (Nicieza & Metcalfe 1999). However, the causes and consequences of large size in dominant individuals remain still partly unresolved. Quantitative genetic studies conducted within populations are likely to shed more light on the nature of genetic correlation between aggression and growth rate and, hence, the integration of the two characters.

### Acknowledgments

We thank Finnish Game and Fisheries Research Institute's aquaculture units in Kuusamo, Laukaa, Paltamo and Taivalkoski for allowing us to use their trout stocks in the study. Saimaa Fisheries Research and Aquaculture provided excellent working facilities. T. Aho helped to transport the eggs and S. Vilhunen assisted in fish maintenance. Constructive comments by J. Dannewitz, N. Metcalfe, N. Peuhkuri, E. Ranta, O. Smith and two anonymous referees improved the manuscript. This study was funded by the Academy of Finland (to A.L. and E. Ranta) and the Finnish Ministry of Education (K.L.).

### References

- Abbot, J. C., Dunbrack, R. L. & Orr, C. D. 1985. The interaction of size and experience in dominance relationships of juvenile steelhead trout (*Salmo gairdneri*). *Behaviour*, **92**, 241–253.
- Arendt, J. D. 1997. Adaptive intrinsic growth rates: an integration across taxa. *Quarterly Review of Biology*, **72**, 149–177.
- Bakker, T. C. M. & Feuth-de Bruijn, E. 1988. Juvenile territoriality in stickleback *Gasterosteus aculeatus* L. *Animal Behaviour*, **36**, 1556–1558.
- Berejikian, B. A., Mathews, S. B. & Quinn, T. P. 1996. Effects of hatchery and wild ancestry and rearing environments on the development of agonistic behaviour in steelhead trout (*Oncorhynchus mykiss*) fry. *Canadian Journal of Fisheries and Aquatic Sciences*, **53**, 2004–2014.
- Boake, C. R. B. (Ed.) 1994. *Quantitative Genetic Studies of Behavioral Evolution*. Chicago: University of Chicago Press.
- Bourgeois, C. E., O'Connell, M. F. & Scott, D. C. 1987. Cold-branding and fin-clipping Atlantic salmon smolts on the Exploits River, Newfoundland. *North American Journal of Fisheries Management*, **7**, 154–156.
- Chapman, D. W. 1962. Aggressive behaviour in juvenile coho salmon as a cause of emigration. *Journal of the Fisheries Research Board of Canada*, **19**, 1047–1079.
- Conover, D. O. & Schultz, E. T. 1995. Phenotypic similarity and the evolutionary significance of countergradient variation. *Trends in Ecology and Evolution*, **10**, 248–252.
- Dunbrack, R. L., Clarke, L. & Bassler, C. 1996. Population level differences in aggressiveness and their relationship to food density in a stream salmonid (*Salvelinus fontinalis*). *Journal of Fish Biology*, **48**, 615–622.
- Elliott, J. M. 1986. Spatial distribution and behavioural movements of migratory trout, *Salmo trutta*, in a Lake District stream. *Journal of Animal Ecology*, **55**, 907–922.
- Elliott, J. M. 1994. *Quantitative Ecology and the Brown Trout*. Oxford: Oxford University Press.
- Fenderson, O. C., Everhart, W. H. & Muth, K. M. 1968. Comparative agonistic and feeding behaviour of hatchery-reared and wild salmon in aquaria. *Journal of the Fisheries Research Board of Canada*, **25**, 1–14.
- Foster, S. A. & Endler, J. A. (Eds) 1999. *Geographic Variation in Behaviour*. Oxford: Oxford University Press.
- Grant, J. W. A. & Noakes, D. L. G. 1988. Aggressiveness and foraging mode of young-of-the-year brook charr, *Salvelinus fontinalis* (Pisces, Salmonidae). *Behavioral Ecology and Sociobiology*, **22**, 435–445.
- Hedenskog, M., Petersson, E. & Järvi, T. In press. Agonistic behaviour in newly emerged brown trout (*Salmo trutta* L.) of sea ranched and wild origin. *Aggressive Behavior*.
- Hochachka, P. W. & Somero, G. N. 1971. Biochemical adaptation to the environment. In: *Fish Physiology*. Vol VI (Ed. by W. S. Hoar & D. J. Randall), pp. 100–156. New York: Academic Press.
- Huntingford, F. A. 1982. Do inter- and intra-specific aggression vary in relation to predation pressure in sticklebacks? *Animal Behaviour*, **30**, 909–916.
- Hutchings, J. A. & Morris, D. W. 1985. The influence of phylogeny, size and behaviour on patterns of covariation in salmonid life histories. *Oikos*, **45**, 118–124.
- Hutchison, M. J. & Iwata, M. 1997. A comparative analysis of aggression in migratory and non-migratory salmonids. *Environmental Biology of Fishes*, **50**, 209–215.
- Jobling, M. 1994. *Fish Bioenergetics*. London: Chapman & Hall.
- Johnsson, J. & Björnsson, B. Th. 1994. Growth hormone increases growth rate, appetite and dominance in juvenile rainbow trout, *Oncorhynchus mykiss*. *Animal Behaviour*, **48**, 177–186.
- Kallio-Nyberg, I. & Koljonen, M.-L. 1991. Kalakantarekisteri. lohi, taimen ja nierä. Riista- ja kalatalouden tutkimuslaitos. *Kalatutkimuksia–Fiskundersökningar*, **26**, 15–115. (In Finnish.)
- Keenleyside, M. H. & Yamamoto, F. T. 1962. Territorial behaviour of juvenile Atlantic salmon (*Salmo salar* L.). *Behaviour*, **19**, 139–169.
- Magurran, A. E. & Seghers, B. H. 1991. Variation in schooling and aggression amongst guppy (*Poecilia reticulata*) populations in Trinidad. *Behaviour*, **118**, 214–234.
- Metcalfe, N. B. 1990. Aquaculture. In: *Managing the Behaviour of Animals* (Ed. by P. Monaghan & D. Wood-Gush), pp. 125–154. London: Chapman & Hall.
- Metcalfe, N. B., Huntingford, F. A., Graham, W. D. & Thorpe, J. 1989. Early social status and the development of life-history strategies in Atlantic salmon. *Proceedings of the Royal Society of London, Series B*, **236**, 7–19.
- Metcalfe, N. B., Taylor, A. C. & Thorpe, J. E. 1995. Metabolic rate, social status and life-history strategies in Atlantic salmon. *Animal Behaviour*, **49**, 431–436.

- Newman, M. A. 1956. Social behaviour and interspecific competition in two trout species. *Physiological Zoology*, **29**, 64–81.
- Nicieza, A. G. & Metcalfe, N. B. 1999. Cost of rapid growth: risk of aggression is high for fast-growing salmon. *Functional Ecology*, **13**, 793–800.
- Nicieza, A. G., Reiriz, L. & Brană, F. 1994. Variation in digestive performance between geographically disjunct populations of Atlantic salmon: countergradient in passage time and digestion rate. *Oecologia*, **99**, 243–251.
- Olla, B. L., Davis, M. W. & Ryer, C. H. 1994. Behavioural deficits in hatchery-reared fish: effects on survival following release. *Aquaculture and Fisheries Management*, **25**, 19–34.
- Roff, D. A. 1988. The evolution of migration and some life history parameters in marine fishes. *Environmental Biology of Fishes*, **22**, 133–146.
- Rosenau, M. L. & McPhail, J. D. 1987. Inherited differences in agonistic behaviour between two populations of coho salmon. *Transactions of the American Fisheries Society*, **116**, 646–654.
- Schaffer, W. M. & Elson, P. F. 1975. The adaptive significance of variations in life history among local populations of Atlantic salmon in North America. *Ecology*, **56**, 577–590.
- Skúlason, S. & Smith, T. 1995. Resource polymorphisms in vertebrates. *Trends in Evolutionary Ecology*, **10**, 366–370.
- Swain, D. P. & Holtby, B. 1989. Differences in morphology and agonistic behaviour in coho salmon (*Oncorhynchus kisutch*) rearing in a lake or its tributary stream. *Canadian Journal of Fisheries and Aquatic Sciences*, **46**, 1406–1414.
- Swain, D. P. & Riddel, B. E. 1990. Variation in agonistic behaviour between newly emerged juveniles from hatchery and wild populations of coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences*, **47**, 566–571.
- Tallman, R. F., Saurette, F. & Thera, T. 1996. Migration and life history variation in Arctic charr, *Salvelinus alpinus*. *Ecoscience*, **3**, 33–41.
- Taylor, E. B. 1988. Adaptive variation in rheotactic and agonistic behaviour in fry of chinook salmon, *Oncorhynchus tshawytscha*, from ocean- and stream type populations. *Canadian Journal of Fisheries and Aquatic Sciences*, **45**, 237–243.
- Taylor, E. B. 1990. Phenotypic correlates of life-history variation in juvenile chinook salmon, *Oncorhynchus tshawytscha*. *Journal of Animal Ecology*, **59**, 455–468.
- Taylor, E. B. & Larkin, P. A. 1986. Current response and agonistic behaviour in newly emerged fry of chinook salmon, *Oncorhynchus tshawytscha*, from ocean- and stream-type populations. *Canadian Journal of Fisheries and Aquatic Sciences*, **43**, 565–573.
- Titus, R. G. & Mosegaard, H. 1991. Selection for growth potential among migratory brown trout (*Salmon trutta*) fry competing for territories: evidence from otoliths. *Canadian Journal of Fisheries and Aquatic Sciences*, **48**, 19–27.
- Yamamoto, T., Ueda, H. & Higashi, S. 1998. Correlation among dominance status, metabolic rate and otolith size in masu salmon. *Journal of Fish Biology*, **52**, 281–290.
- Wootton, R. J. 1998. *Ecology of Teleost Fishes*. 2nd edn. Dordrecht: Kluwer Academic.