

1 **Is there genetic variation in the response to competition intensity in juvenile**
2 **brown trout, *Salmo trutta*?**

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24 **ABSTRACT**

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Effects of intraspecific competition intensities on the relative performance (growth and movement) of juvenile brown trout *Salmo trutta* originating from nine different families were tested in tank experiments and in semi-natural streams. Both growth and movement differed consistently among families, indicating genetic variation in these traits. However, there were no significant interaction effects between the intensity of competition and family on performance in either of the two experimental systems. Thus, genetic variation in responses to competition intensity appeared to be limited in the population from which the juveniles used in this experiment originate.

Key words: density dependence; dispersal; environmental heterogeneity; genotypic selection; intraspecific competition; salmonids.

INTRODUCTION

Despite being heritable, under continuous selection and highly connected to fitness, genetic variation for life history traits is maintained within populations. This apparent paradox has received considerable interest in evolutionary ecology (Roff, 1992, 2002; Stearns, 1992) and several explanations have been proposed. These include the potential for temporal variation in selection pressures, balance between mutation rate and selection, selective advantage of heterosis, antagonistic pleiotropy, and frequency-dependent selection (reviewed in Roff, 1992). Finally, the environment can be spatially heterogeneous with regard to selection pressures (Levene, 1953; Roff, 1992). Since no single genotype can be superior under all environmental conditions, different genotypes will be selected for in different spatial locations within populations and this may contribute to maintenance of variation (Roff, 1992).

Several environmental variables typically vary over large spatial scales, and can thus be responsible for differences in selection pressures among distinct populations or sub-populations. Indeed, empirical studies have often investigated the effect of abiotic factors (such as latitudinal gradients, temperature and climate) on life-history trait variation (e.g. Williams & Moore, 1989; Weber & Schmid, 1998; Bronikowski, 2000; Allan & Pannell, 2009; Wagner & Simons, 2009). Uncovering environmental variation over smaller spatial scales (i.e. within populations) that could lead to differential local selection pressures, and thus contribute to the maintenance of within-population genetic variation, may be less straightforward (but see e.g. Kittelson & Maron, 2001). One biotic variable which may frequently vary substantially over small spatial scales is the local population density. By influencing the intensity of intraspecific competition it can affect local selective regimes. If competition is asymmetric the relative performance of individuals would likely rely on their competitive ability, with competitive individuals having an advantage at high density. However, having

traits connected to high competitive ability could be costly and may not pay off in the absence of competition. For example, under high levels of competition a fast growing individual could profit from high competitive ability as it will gain a cumulative size advantage (Arendt, 1997). In the absence of competition these benefits could be offset by costs, such as increased exposure to predators (Sundström *et al.*, 2004; Brodin & Johansson, 2004) and reduced tolerance to low oxygen conditions (Sundt-Hansen *et al.*, 2007). Traits associated with competitive ability can be heritable, and thus different genotypes may be optimal at different densities (Sinervo *et al.*, 2000; Joshi *et al.*, 2001).

Rather than being homogenously distributed within the spatial range inhabited by a population, individuals from a variety of organisms are often aggregated at some spatial scale (e.g. Taylor *et al.*, 1978; Perry, 1995). Spatial heterogeneity in population density has often been observed in both plants and other sessile organisms (e.g. Rees *et al.*, 1996; Law *et al.*, 1997), as well as in mobile animals (Hassell *et al.*, 1987; Brown *et al.*, 1995; Ray & Hastings, 1996; Wilkin *et al.*, 2006). Certain aspects of their biology may cause such local scale variation in density to be more pronounced in some organisms than in others. In particular, having a patchy propagule (offspring, seeds, eggs) distribution and high fecundity may potentially lead to high local densities in the juvenile stage even if overall population density is low. In such organisms spatial heterogeneity in population density, and hence intensity of intraspecific competition, is likely to be pronounced.

One group of organisms that has received considerable attention with regard to spatial variation in local density are the stream-spawning salmonid fishes. The eggs of such species (e.g. brown trout, *Salmo trutta* L. and Atlantic salmon, *Salmo salar* L.) are deposited in distinct nests in the streambed gravel. After hatching juveniles emerge from the gravel and

99 establish feeding territories (Titus, 1990; Elliott, 1994; Milner *et al.*, 2003). The high
100 fecundity of salmonids, together with this patchy distribution of eggs and the restricted
101 movement of the juveniles leads to spatial heterogeneity in the local density, and hence levels
102 of competition experienced by the juveniles varies over space (Einum & Nislow, 2005; Einum
103 *et al.*, 2006, 2008; Foldvik *et al.*, 2010). Selection on traits providing competitive advantages
104 may therefore be hypothesised to vary accordingly, thereby contributing to the maintenance
105 of within-population genetic variation. In the present study this hypothesis is tested by
106 comparing the relative performance (growth and movement) of individuals from different
107 full-sib *S. trutta* families under different competitive intensities in both semi-natural streams
108 (by manipulating fish density) and in tanks (by manipulating feeding regime).

110 METHODS

111 Eighteen adult *S. trutta* (nine males and nine females) from a 1st generation hatchery reared
112 strain (i.e. offspring of wild parents) from the Tunhovd population (60°22'59N, 08°51'57E)
113 were used to produce nine full-sib family groups in the fall of 2006 at the Norwegian Institute
114 for Nature Research (NINA) Research Station, Ims, south-western Norway. All experiments
115 were also conducted at this location. During May 21-25 2007, approximately 2 months after
116 onset of exogenous feeding, a random sample of the resulting juveniles (mean fork length, L_F
117 $\pm S.D.$: 41.2 ± 2.6 mm) were anaesthetized (benzoat), photographed for later measurements of
118 L_F (using ImageJ v. 1.41), assigned to different treatments (see below) and marked
119 accordingly with visible implant elastomer tags (VIE).

121 FAMILY-SPECIFIC GROWTH RATES UNDER CONTRASTING FEEDING REGIMES

122 To estimate family specific growth rates under two contrasting feeding regimes, five
123 individually VIE marked juveniles from each family were put into each of ten tanks (450 mm

x 450 mm, 600 mm deep with a water level of 300 mm) and 1) fed *ad libitum* with EWOS (Bergen, Norway, www.ewos.com) commercial pelleted food (five tanks), or 2) given a reduced ration of a natural prey (chironomid larvae) allowing a mean energy intake half way between maintenance and maximum (five tanks). For this second treatment rations were calculated according to Elliott (1976) and Elliott *et al.* (1995), taking into consideration fish body size and expected water temperatures (ration range: 80 – 135 mg individual⁻¹ day⁻¹). To increase the potential for competitive interactions and dominance in the reduced diet treatment, the fish were fed twice each day by placing an ice cube containing half of the daily ration of chironomid larvae in a tube which was placed vertically in the tank such that its lower opening protruded 100 mm below the water surface. Thus, as the ice thawed larvae were gradually made accessible for the fish at a certain location within the tank. The experiment was started on May 25 and ended after thirty-one days, when the fish were killed by an overdose of anaesthetics and subsequently identified and L_F measured.

FAMILY-SPECIFIC RESPONSE TO HIGH AND LOW DENSITY

On May 25, juveniles which were VIE marked according to family-group were released simultaneously at either high or low density close to the inlets of the two parallel artificial streams (107 x 1.5 m). The high and low density streams received 20 and 100 individuals from each of the nine families, respectively. The streams contained gravel suitable for juvenile salmon rearing and had fish traps at the outlets. Water to the streams was drawn from a nearby lake and both streams had a water discharge of ~16 l s⁻¹. Only natural food items entering through the inlet water or present in the substrate were available for the fish. During the course of the experiment the fish were allowed to move into the fish traps. The traps were checked every day and movers were killed and frozen for subsequent processing. Thirty-one

days after the fish were released, three pass electro-fishing was conducted and all fish were identified and L_F measured.

STATISTICS

All statistical analyses were conducted in R, v. 2.10.0. (R Development Core Team 2009).

Linear mixed models (using the *lme* function in the *nlme* package; Pinheiro *et al.*, 2009) were used to model variation in individual growth rate in the tank experiment.

A model including family-group, treatment and the interaction between these was made to check for effects on final L_F . Initial individual L_F was included as a covariate and tank as a random factor (random intercept). To enable estimation of family-specific intercepts between initial L_F and final L_F (i.e. a proxy for family-specific growth rate) the interaction between initial L_F and family was not allowed for in the full model. The variance of the residuals from this model differed among families. To account for this the *varIdent* function was applied, which led to a decrease in AIC ($\Delta AIC = 22.3$, calculated using REML). Evaluation of fixed effects was done according to the protocol recommended in Zuur *et al.* (2009), and thus based on sequential removal of fixed effects with subsequent ANOVA comparisons until log-likelihoods (based on ML) decreased significantly ($P < 0.05$).

Differences among families in relative movement rates from the two streams throughout the experimental period were also tested for. For each focal family and stream, the expected number of movers (i.e. expected if relative movement from the two streams was not different from that of the rest of the families) were calculated based on 1) the total number of movers from the focal family and 2) the proportion of the total observed movement (sum from both streams) that occurred at high and low density, respectively, after the family in question was

excluded. The observed number of movers at high and low density for the focal family was then compared to these expected numbers of movers using a Chi-squared test.

Variation in final L_F of the fish left in the streams until the end of the experiment was modelled using the generalised least squares (*gls*) function (in the *nlme* package; Pinheiro et al., 2009). Stream (high or low density treatment), family-group and mean initial family L_F were included as main effects in the initial model. Interactions between stream and family-group as well as between stream and initial L_F were also included. To account for heterogeneity of residual variance among families the *varIdent* function was applied. This led to a decrease in AIC ($\Delta AIC = 7.8$, calculated using REML). Significance of the explanatory variables in this model was assessed using the backwards model selection procedure as described for the *lme* models. Family 2 was excluded from this analysis since no individuals from this family were left in the low-density stream at the end of the experiment.

Next, model selection of *gls* models was used to test whether family-specific probabilities for movement depended on stream, the relative family growth rates estimated in the tank experiment, mean initial L_F , or two-way-interactions among these. Family proportions of the individuals moving at different points in time or staying until electro-fished were arcsine-square root transformed prior to statistical analyses.

To analyze whether the effect of relative family growth rates estimated from the tank experiment, stream or the interaction between these had an effect on L_F of the fish remaining in the streams at the end of the experiment, linear mixed effects models (*lme*) were used. To control for family specific traits other than the estimated specific growth rate that could influence final L_F , family was included as a random variable (random intercept). The model including the random term was significantly better the model that did not (ANOVA

comparisons of log-likelihoods calculated using REML, $P < 0.05$). Again, to evaluate the significance of the fixed effects, the backwards model selection procedure was used.

RESULTS

FAMILY-SPECIFIC GROWTH RATE UNDER CONTRASTING FEEDING REGIMES

In the tank experiment all families grew better when given food in excess than when subject to a restricted monopolizable feeding regime (Fig. 1). Further, the mean coefficient of variation in growth (final L_F – initial L_F) was significantly lower in the tanks with food in abundance (CV = 30%) than in the tanks with a restricted feeding regime (CV = 99%, t-test, $P < 0.001$). The higher growth variation in the latter treatment indicates greater levels of competition when the food was monopolizable and restricted than when food was given in excess. The linear mixed model with tank as a random factor that included the main effects of all the explanatory variables (family, treatment and initial L_F) performed best in explaining variation in final L_F (Table I, decrease in AIC > 2 between consecutive models, increase in AIC > 22.4 for removal of further terms). The lack of an interaction between family-group and treatment in this model implies that the relative growth of the different families did not depend on treatment. The estimates of relative family growth rates given by this model were used as parameters in a movement model.

FAMILY-SPECIFIC MOVEMENT AND GROWTH AT HIGH AND LOW DENSITY

In the artificial streams a large fraction of the fish moved into the fish-traps during the first four days of the experiment (Fig. 2). During this period a significantly higher proportion (56%) moved at high density compared to at low (38%) (2-sample test for equality of proportions, $P < 0.01$). Between day 12 and 18 a second movement wave occurred, during which 31% and 42% of the fish that had not moved during the first 11 days moved from high

and low density, respectively (Fig. 2). The difference between these proportions was not significant ($P > 0.05$). When the streams were electro-fished at the end of the experiment, 22% of the initial number of fish were left at high density and 24% at low ($P > 0.05$).

Family-specific proportions of the number of fish released that moved at high and low density were positively correlated during the first movement wave (day 1-4) (Fig. 3a, $r_s = 0.85$, $P < 0.01$). What seems to be a similar pattern, although non-significant, was observed during the second movement wave (day 12-18, Fig. 3b, $r_s = 0.62$, $P > 0.05$). Finally, family-specific proportions of the total number released that were recaptured during electro-fishing were significantly positively correlated (Fig. 3c, $r_s = 0.75$, $P < 0.05$).

Observed numbers of movers at high and low density did not differ significantly from the expectations for any of the families (Table II). Thus, there was no pattern suggesting family differences in response to density in terms of movement rates.

A model including the main effects of family and stream performed best in explaining variation in final L_F of the fish remaining in the streams at the end of the experiment (Table III, sequential ANOVA comparisons of log-likelihoods of preceding models, $P > 0.05$; removal of further terms, $P < 0.01$). The lack of an interaction between family-group and stream in this model implies that the relative growth of the different families did not depend on stream (high or low density treatment).

EFFECT OF FAMILY-SPECIFIC GROWTH RATE ON MOVEMENT AND GROWTH AT
HIGH AND LOW DENSITY

None of the main effects (relative family growth rate, family mean initial L_F or density) or interaction terms remained in the *gls* models best explaining variation in movement rates during the two waves or proportions staying in the streams until electro-fished (ANOVA comparisons of log-likelihoods, Bonferroni corrected for multiple comparisons, all $P > 0.05$). Family-specific movement probabilities were therefore not related to the relative family growth rates as estimated in the tank experiment.

Overall, final L_F of stayers in the low-density stream were larger than of those in the high-density stream (mean \pm *S.D.*, low density: 55.2 ± 3.5 mm; high density: 50.4 ± 4.7 mm). The mixed effects model that best described L_F of individual stayers included the main effect of density treatment, but not the relative family growth rate estimates or the interaction between these (*S.D.* for the random intercept = 1.01 and *S.D.* of residual variation = 4.37; low density = 55.28 ± 0.75 (*S.E.*), $t = 73.29$, $P < 0.001$; high density relative to low density = -4.88 ± 0.73 (*S.E.*), $t = -6.65$, $P < 0.001$; n is 244 individuals from 9 groups).

DISCUSSION

By manipulating the level of intraspecific competition both in tank experiments and semi-natural streams family-specific effects on the relative performance (growth and movement) were tested for. Overall, both growth and movement were found to vary considerably among families, indicating genetic variation in these traits. This is consistent with previous studies (growth: Bailey & Loudenslager, 1986; Gjerde, 1986; Vøllestad & Lillehammer, 2000; Vøllestad & Quinn, 2003; movement: Webb *et al.*, 2001). Yet, no significant interaction effects between competition regime and family origin on performance were detected in either of the two experimental systems. Thus, in contrast to previous studies performed on organisms such as plants and shrimps (e.g. Shaw, 1986; Coman *et al.*, 2004), the relative

performance of individuals from different families was not conditioned by the strength of competition. This result does not lend support to the hypothesis that spatial heterogeneity in population density can be responsible for maintaining within-population genetic variation for traits influencing competitive ability.

Two potential explanations for the lack of family-by-competition interactions in the present study are suggested. First, the treatments could have failed in generating sufficient differences in levels of competition. In the stream experiment, high density-dependent movement during the initial period (day 1-4) caused a substantial reduction in the density contrast, which may have reduced the power to detect such an interaction. Yet, although there was no evidence for density-dependent movement following this initial period, the differences in density were sufficient to produce effects on final body size, and hence growth rates. Furthermore, the treatments in tanks (i.e. given non-monopolizable food in excess or restricted rations of monopolizable food) had pronounced effects on both mean growth and variation in growth. Thus, the different treatments were clearly successful in creating contrasting strengths of competition in both experimental systems.

A second, and perhaps more likely, explanation for a lack of a family-by-competition interaction could be that stabilising selection for the optimal competitive ability during the juvenile life stage can be intense and spatiotemporally consistent in wild populations. If so, this would lead to low genetic variation in traits influencing competitive abilities, and manipulations of traits as well as intensity of competition would be required to detect the effects of potential trade-offs. Due to the high fecundity and patchy egg distribution of salmonids, high density of juvenile *S. trutta* after emergence from the gravel may be ubiquitous in some populations. The *S. trutta* juveniles used in the current study originate from the population in Lake Tunhovd, which is a relatively large lake (approximately 25 km²)

within which most of the feeding (including piscivory) and growth of sub-adults and adults occur. Lake Tunhovd provides favourable growing conditions, resulting in relatively large and highly fecund adults (many between 2-6 kg), whereas access to spawning areas in its tributaries is limited (Åge Brabrand, Freshwater Ecology and Inland Fisheries Laboratory, Natural History Museum, University of Oslo, pers. comm.). Accordingly, early-life competition among juveniles after emergence from nests can be expected to be consistently high in this population. Thus, experienced levels of competition may rarely be sufficiently low to select for trait values that are beneficial under low competition during this early juvenile stage in this population.

The authors are not aware of previous vertebrate studies experimentally testing for within-population genetic variation in competitive ability. This is true even for juvenile salmonids, in which genetic variation has been the subject of much attention (reviewed in Garcia de Leaniz *et al.*, 2007). Other studies have shown relative performance of juvenile salmonids to depend on phenotypic traits under different levels of competition, but these have focused on the maternal effect of egg size rather than the genetic characteristics of the offspring (Hutchings, 1991; Einum & Fleming, 1999). Such effects include both maternal age- and size-dependent traits (e.g. egg size increase with female size in salmonids, reviewed in Fleming, 1996; Heath & Blouw, 1998) as well as environmental influences on mothers that have accumulated throughout their lives (Fleming, 1996; Mosseau & Fox, 1998; Bonduriansky & Day, 2009). Therefore, variation in such traits may be pronounced even under strong stabilising selection. Since maternal effects generally are believed to be limited to the first period after hatching in fish (Heath & Blouw, 1998; Perry *et al.*, 2004), and the juveniles used in this study had been feeding exogenously for more than a month before the experiment was initiated, such effects were not expected to be pronounced. Thus, even if the families may well have had different

competitive abilities associated with them due to maternal effects at an earlier stage, this would not be expressed in the present study where the focus was on genetic effects. The consistent among-family variation in growth rates across competitive regimes revealed in the tank experiment allowed for a test of whether this trait had an effect on performance (movement or final body length) in the semi-natural streams. Contrary to our expectations no effect of the relative family growth rate estimates was revealed. This result adds to studies that have failed in finding a correlation between individual performance in lab experiments and under more natural conditions (Niva & Jokela, 2000, Martin-Smith & Armstrong, 2002; Harwood *et al.*, 2003). These results do imply that relative performance among families, such as growth, may depend highly on environmental conditions, and that traits beneficial in one environment can be less beneficial, or even incur costs in another. Yet, there is currently no support for the hypothesis that the relative performance of different genotypes of juvenile salmonids depends on population density or competition intensity within a single type of environment.

The present results indicated a lack of genetic within-population variation in response to competitive intensity. It seems possible that the spatial heterogeneity in local juvenile densities may not have been sufficient for differential genetic selection among patches to occur for our population. If so, this would prevent spatial variation in level of competition to contribute to maintaining genetic variation. Yet, previous studies of maternal effects in salmonid fishes have shown strong effects of the intensity of competition on the relative performance of different phenotypes (e.g. Hutchings, 1991; Einum & Fleming, 1999). It would therefore be surprising if offspring genetics in general plays no role in determining their response to competition intensity. Thus, it may prove fruitful to test for genetically based

variation in response to competition intensities for populations or species that have evolved under different ecological settings from those of the population used in the present study.

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FIGURE CAPTIONS

Fig. 1. Mean ($\pm S.E.$) of the mean family growth (final L_F – initial L_F , mm) in different tanks under the restricted ($n = 5$ tanks) and the maximum ($n = 5$ tanks) feeding regime. Numbers denote families.

Fig. 2. Number of juvenile brown trout moving each day and the number left at the end of the experiment (day 31) in the (a) high and (b) low density stream.

Fig. 3. Relationship between family proportions of brown trout juveniles at low and high density that (a) moved within the first four days ($r_s = 0.85$, $P < 0.01$), (b) stayed in the streams until day 11 and moved during day 12-18 ($r_s = 0.62$, $P > 0.05$) and (c) stayed in the streams until the end of the experiment ($r_s = 0.75$, $P < 0.05$). Numbers denote families.

514 **Table I.** Summary of the best linear mixed effects model explaining variation in final body
515 length (L_F , mm) of juvenile brown trout, *Salmo trutta* in the tank experiment. Tank is included
516 as a random factor (random intercept). The fixed effects parameters are given as treatment
517 contrasts with Family 1 and the maximum feeding regime as intercept. Estimated parameters
518 for Random is *S.D.* of the random intercept in the model, with *S.D.* of residual variation given
519 in brackets. *n* is 390 individuals from 10 groups.

	Parameter \pm <i>S.E.</i>	<i>T</i>	<i>P</i>
Random	0.65 (2.87)		
Intercept	46.72 \pm 0.61	76.06	< 0.001
Initial L_F (mm)	0.03 \pm 0.001	20.07	<0.001
Family 2	2.11 \pm 0.66	3.21	< 0.01
Family 3	2.50 \pm 0.71	3.51	< 0.01
Family 4	1.92 \pm 0.75	2.56	< 0.05
Family 5	0.27 \pm 0.58	0.47	> 0.05
Family 6	0.48 \pm 0.52	0.91	> 0.05
Family 7	-0.57 \pm 0.54	-1.05	> 0.05
Family 8	0.38 \pm 0.68	0.56	> 0.05
Family 9	0.88 \pm 0.54	1.64	> 0.05
Treatment (Restricted diet)	-7.93 \pm 0.50	-15.9	< 0.001

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Table II. Numbers of individual brown trout, *Salmo trutta* juveniles from each family moving at low (LD) and high density (HD), together with the proportion of total movers of the remaining families moving at LD (LD Prop) and HD (HD Prop), respectively (expected movement rates). Chi-square tests compare observed numbers of individuals from each family moving at high and low density with expected numbers.

Family	LD	HD	LD Prop	HD Prop	χ^2	<i>P</i>
1	14	91	0.16	0.84	0.55	> 0.05
2	18	92	0.16	0.84	0.06	> 0.05
3	13	75	0.16	0.84	0.06	> 0.05
4	15	75	0.15	0.85	0.09	> 0.05
5	16	77	0.15	0.85	0.23	> 0.05
6	11	62	0.16	0.84	0.02	> 0.05
7	9	58	0.16	0.84	0.29	> 0.05
8	16	64	0.15	0.85	1.47	> 0.05
9	11	70	0.16	0.84	0.32	> 0.05

Table III.

Summary of the generalised least square model that best explains variation in final lengths (L_F , mm) of juvenile brown trout, *Salmo trutta* staying in the streams until electrofished. Parameters are given as treatment contrasts with Family 1 and the low density stream as intercept. $n = 237$ individuals; Family 2 was excluded from this analysis since no individuals from this family were left in the low density stream when the experiment was finished.

	Parameter \pm S.E.	t	P
Intercept	55.47 ± 1.6	34.57	< 0.001
Family 3	-2.35 ± 1.89	-1.25	> 0.05
Family 4	1.16 ± 1.85	0.62	> 0.05
Family 5	1.45 ± 1.77	0.81	> 0.05
Family 6	-1.24 ± 1.72	-0.72	> 0.05
Family 7	0.74 ± 1.6	0.46	> 0.05
Family 8	-1.50 ± 1.66	0.9	> 0.05
Family 9	-0.82 ± 1.66	-0.49	> 0.05
Stream (High density)	-4.86 ± 1.66	-7.27	< 0.001