

# State-dependent behavior and alternative behavioral strategies in brown trout (*Salmo trutta* L.) fry

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## Abstract

Animals generally adjust their behavior in response to bodily state (e.g. size and energy reserves) to optimize energy intake in relation to mortality risk, weighing predation probability against starvation. Here we investigated whether brown trout adjust their behavior in relation to feeding history (energetic status) and body size during a major early-life selection bottleneck, when fast growth also appear to be important. We manipulated growth using different food ration schemes over two consecutive time periods (P1 = 12 days, P2 = 23 days), excluding social effects through individual isolation. During these experimental periods the fish were fed either high or low food rations in a crossed design. In behavioral trials following the treatment, where acute hunger levels were standardized among all treatments, fish that were initially fed high rations (P1) and thereafter low rations (P2) had on average 15-21% higher swimming activity than the other groups, but large within-treatment variation rendered only weak statistical support for the effect. Furthermore, fish on low ration during P2 tended to be more aggressive than fish on high ration. Size was related to behavioral expression, with larger fish being more active and aggressive. Swimming activity and active aggression were positively correlated, forming a behavioral syndrome in the studied population. Based on these behavioral traits we could also distinguish two behavioral clusters, one consisting of more active and aggressive individuals, and the other consisting of less active and aggressive individuals. This indicates that two behavioral strategies may exist in young brown trout.

**Keywords:** animal personality, behavioral syndrome, compensatory growth, food restriction, mirror aggression, open-field activity, repeatability



## Introduction

Food restriction reduces body condition in animals, which in severe cases may lead to energy depletion and death from starvation. Thus, it is likely that food restriction alters the animal's behavior to reduce the risk of starvation, a pattern which has been observed in many different taxa. For instance, green sea turtles *Chelonia mydas* in poor body condition select more profitable, but also more risky, foraging areas than turtles in good body condition (Heithaus et al. 2007). Similarly, Atlantic salmon *Salmo salar* juveniles subjected to restricted feeding become less risk averse than well fed conspecifics, as shown by their increased diurnal activity out of shelter (Orpwood et al. 2006).

In growing animals, food restriction commonly leads to higher than normal foraging rates (hyperphagia) when food becomes available again, which aids in compensatory growth of the body (Ali et al. 2003; Dmitriew 2011). The occurrence of hyperphagia and compensatory growth following starvation suggest that growth rates are generally below their maximal levels under normal energetic conditions (Arendt 1997; Ali et al. 2003). The effects of food restriction on behavior are generally thought to be linked to the production-mortality trade-off hypothesis where behavior adjusts the foraging intensity optimally to minimize mortality risk (Gilliam and Fraser 1987; Fiksen and Jørgensen 2011). This trade-off incorporates two main feedback systems (Luttbeg and Sih 2010; Sih et al. 2015). On the one hand there is the negative 'starvation-threshold' feedback system consisting of starvation avoidance (SA) at the one end, and asset protection (AP) at the other (Sih 1980; Lima 1986; Pettersson and Brönmark 1993; Clark 1994; Heithaus et al. 2007; Luttbeg and Sih 2010). These feedback mechanisms (SA-AP) mean that lower-asset individuals (i.e. with relatively low predicted fitness, e.g. small body size or low energy reserves) will accept higher risks, because they need to increase their assets, while higher-asset individuals can afford to avoid risk at the expense of some of their assets (e.g. energy reserves). On the other hand there is a positive feedback mechanism based on state-dependent safety (SDS) (Clark 1994; Luttbeg and Sih 2010). Here, the high asset values (e.g. large energy reserves or body size) lead to higher competitive ability, and reduce risks due to predator gape-limits or increased vigor (Mittelbach 1981; Peterson and Wroblewski 1984; Werner and Gilliam 1984; Travis et al. 1985; but see Lima 1986). The

influence of these feedback systems could differ in strength in different environmental contexts (e.g. depending on population density, predator abundance, predator guild composition, or ontogenetic time constraints) (e.g. Ludwig and Rowe 1990). SDS and SA-AP may be elicited together, e.g. with larger individuals being more safe than smaller (SDS), but with SA-AP acting within each size class. If SA-AP is strong, then studies on individual behavioral consistency (a component of animal personality; see e.g. Bell 2007) need to take bodily state into account. Here, we investigate the relationships between bodily state (energy state as manipulated by recent feeding history, as well as body size) and behavior in young juvenile brown trout *Salmo trutta*. We also investigated the occurrence of personality in our experimental individuals.

Our primary aim was to investigate state-dependent behavior in young individuals. Like in many other animals with high fecundity, the early juvenile stage of brown trout is a major selective bottleneck (e.g. Degerman et al. 2001). Thus, the early life of trout is typically described as a critical period where individuals need to grow rapidly regardless of bodily state, due to selection against small sized individuals through predation or competition (Elliott 1990; Perez and Munch 2010). To explore whether or not these fish adjust their growth and behavior in relation to their bodily state, we manipulated food rations of individual trout and subsequently scored their behavior in standardized laboratory tests. Specifically, we tested effects of food ration on swimming activity, boldness and aggression. Activity and boldness were assumed to be related to risk taking, and aggression have been found to be important to obtain a territory, which is beneficial for foraging efficiency (Elliott 1990, 2002; Johnsson and Björnsson 1994; Johnsson et al. 1999). In line with studies on older stages of salmonid fish (e.g. Johnsson et al. 1996; Nicieza and Metcalfe 1997; Höjesjö et al. 1999; Vehanen 2003; Orpwood et al. 2006), expression of these behaviors was predicted to be relatively higher in low-asset fish (i.e. fish being starved), as foraging would be important to regain lost body growth for these individuals. Particularly, we predicted that the group being initially starved and subsequently re-fed for a short period of time would have the highest activity, boldness and aggression, as these fish were assumed to be in the midst of a compensatory growth phase. Compensatory growth has been observed repeatedly in older juveniles of brown trout from the same population as used in this study (Johnsson and Bohlin 2006; Sundström et al. 2013; Näslund et al. 2015a). Alternatively, the trout fry may mainly follow SDS, with larger fish being more active, aggressive and bold. A strong SDS effect could possibly drive all fish to maximize their individual capacity to express these behavioral traits, since the larger they get the safer and more competitive they are. Indeed, some studies indicate that young fish are maximizing growth with little capability to increase their foraging efforts (Pedersen 1997; Conceição et al. 1998; Peck et al. 2014). In contrast to many previous studies, we standardize acute hunger levels, to measure effects of energetic state only.

Our second aim of this study was to investigate whether our fish showed personality traits. Specifically we investigated whether they were consistent in their behavioral expression, whether different behavioral characters were correlated (indicative of behavioral syndromes, see Sih et al. 2004), and whether these characteristics of personality were related to bodily state (energetic state or body size). Distinct personalities are generally assumed to be the behavioral expressions of general life-history strategies (Stamps 2007; Réale et al. 2010). We predicted that behaviors would be correlated and repeatable, in line with previous studies of yearling brown trout (Höjesjö et al. 2011; Hoogenboom et al. 2012; Adriaenssens and Johnsson 2013; Kortet et al. 2014), with an explorative approach regarding the relationship with bodily state.

Our third aim of this study was to investigate whether brown trout fry group into separate behavioral strategies, or into a single continuum of behavioral expression. It has been suggested

that there are two, more or less distinct, behavioral strategies adopted by emerging salmonid fry (Héland 1999; Skoglund and Barlaup 2006). One behavioral strategy is to quickly establish and actively defend a territory (active and aggressive strategy), while the other is to hide and nocturnally disperse downstream from the nest and away from the main area of competition (passive and shy strategy). These strategies have been suggested to be independent of social environment, as the passive strategy has been observed also in isolated fish, i.e. in absence of a social hierarchy (Héland 1999). Generally, personality traits are often discussed as if they in a dichotomous way (e.g. fast vs. slow pace-of-life [Réale et al. 2010]; proactive vs. reactive coping style [Koolhaas et al. 1999]), but few studies investigate the actual distribution of behavioral traits in a population. Given the previous descriptions of brown trout fry behavior, being either active or passive, we predicted that behavioral clusters exist.

## Materials and methods

### Study population characteristics

We used fish from a natural population of sea trout, the anadromous form of the brown trout, from the coastal stream Norumsån in Sweden (N58° 2.589', E11° 50.759'). The adult sea trout spawns in rivers in late autumn, the eggs hatch in early spring, and fry emerges from the gravel in late spring (May-June) (Degerman et al. 2001). At this point the fry emerge to start to feed and establish territories (Elliott 1994; Héland 1999). In Norumsån, juveniles normally stay in the stream for one or two summers before migrating to the sea the following spring, typically at a size of 70 - 160 mm (Bohlin et al. 1993, 1996). However, depending on body condition in the previous year, up to half of the one-year old males, and a lower proportion of females, mature precociously and stay as stream residents (Dellefors and Faremo 1988; Bohlin et al. 1994). Thus, restricted growth at early stages may have extensive effects on life-history decisions.

### Capture and housing

We captured 144 recently emerged fry on one of the stream's main spawning grounds on June 5, 2012, using electrofishing (L-600; Lug AB, Sweden; straight DC, 200-300 V) and brought them to the laboratory. All fish were initially put in one 70 l holding aquarium, equipped with sand and plastic fanwort plants, for seven days. During this time we supplied the fish with thawed chironomid larvae, approximately 5-10 larvae per fish and day. During treatments fish were housed individually in ten 55 l polypropylene storage boxes with removable transparent lids (Nordiska Plast, Sweden), each modified to contain 12 equally sized compartments (bottom area: 100 × 150 mm; water depth: 100 mm; see drawing in electronic supplement, Fig. S1). Water (average temperature: 11.5°C; range: 10.3 - 11.9°C) flowed through all compartments, supplied by the in-house circulating system. All compartments had 5 mm of sand as bottom substrate. During the experiment the boxes were covered with lids to prevent escape by jumping. Rearing boxes were lit by fluorescent tubes with the armature covered by black garbage bags to reduce light intensity (illuminance above the boxes was ca. 100 lux).

### Food manipulation (treatment)

At the start of the experiment the fish were randomly split into two feeding groups ( $n = 60$ ): high food ration (H) and restricted food ration (L); see Table 1. These rations were given over 12 days

**Table 1:** Food rations for the treatment groups during the experiment.

Day of experiment	Number of chironomids per fish per day				
	HH	HL	LH	LL	
0	5	5	5	5	
1-12	10	10	2	2	
13-17	10	2	10	2	
18-27	12	3	15	3	
28-35	12	4	18	4	
36*	Satiation	Satiation	Satiation	Satiation	
37*	Trial 1	12	4	18	4
38*		Satiation	Satiation	Satiation	Satiation
39*	Trial 2	-	-	-	-
Total (1-35)	386	192	368	96	
% of HH ration (1-35)	100%	50%	95%	25%	

\* Behavioral trial period

(Period 1). At the end of Period 1, twelve fish had died (H: 4; L: 8). Furthermore, eight fish which had been on high ration but lost in mass were removed from the experiment as they did not fulfil the criteria for the treatment (i.e. being well fed). The two feeding groups were split in half by random assignment of the remaining fish, creating two sub-groups from each initial feeding group. One sub-group from each initial feeding group was given high food rations, and the other sub-groups were given restricted rations, see Table 1. These latter rations were provided over 23 days (Period 2). This resulted in four treatment groups ( $n$  denote final sample size): (i) continuous high food ration (HH;  $n = 23$ ); (ii) continuous restricted food ration (LL;  $n = 21$ ); (iii) initially high food ration, switched to restricted food ration (HL;  $n = 23$ ); and (iv) initially restricted food ration, switched to high food ration (LH;  $n = 22$ ). The supplied food consisted of thawed chironomid larvae (Akvarieteknik, Sweden). Chironomids constitute a major part of the natural food eaten by brown trout at the early fry stage (Nilsson 1956; Skoglund and Barlaup 2006). Food rations were the same for all fish within a treatment. Thus, the smallest fish received slightly more food relative to their mass than the larger fish, but the maintenance rations should regardless represent a very restricted food intake for all fish. Food rations were based on a previous experiment (Näslund et al. 2015b) and during the course of the experiment the rations were adjusted for growth and bodily condition of the fish, based on daily visual inspection (Table 1). Leftover bloodworms were removed using a disposable pipette the day after each feeding before the provision of new food; the pipette was also dipped in compartments without leftovers to standardize disturbance. The food manipulation lasted for 35 days.

### Growth monitoring

We recorded wet mass (precision: 0.01 g; Kern EW 3000-2M, Kern & Sohn GmbH, Germany) and took digital photographs (Canon EOS 40D; lens: EF-S 17-85 IS USM [at 70 mm focal length]; Canon Inc., Japan) of all fish at three time points: (i) the day before the start of the food manipulation (day 0; June 9); (ii) the day we switched the food ration for the HL and LH groups (day 12); and (iii) the day prior to the last day of food manipulation (day 34). Mass was recorded before feeding, leaving fish unfed for 24 h prior to the weighing. From the digital photographs we measured fork length (from the tip of the snout to the end of the central caudal fin ray; precision: 0.1 mm) using ImageJ 1.45 (<http://imagej.nih.gov/ij/>). During handling the fish were anaesthetized with 2-phenoxyethanol ( $0.5 \text{ ml} \cdot \text{l}^{-1}$ ).

Growth rate in wet mass ( $M$ ) was analyzed as specific growth rate ( $SGR_M$ ; % change per day):

$$SGR_M = 100 \cdot (\ln(M_{t_1}) - \ln(M_{t_0})) \cdot (t_1 - t_0)^{-1} \quad (1)$$

where  $t_0$  and  $t_1$  are the initial and final time-point in days, respectively.

Growth rate in fork length ( $L$ ) was analyzed as absolute growth rate ( $AGR_L$ ; mm per day):

$$AGR_L = 100 \cdot (L_{t_1} - L_{t_0}) \cdot (t_1 - t_0)^{-1}. \quad (2)$$

## Growth analyses

Abbreviations for models, dependent variables and factors are found in Table 2.

Initial and final size (fork length and wet body mass) was analyzed using a GLMM (Gaussian distribution, identity link function) with the factors TR and DATE and their interaction TR  $\times$  DATE. Growth was analyzed separately for Period 1 and Period 2 using GLM (Gaussian distribution, identity link function), including TR and FL at the start of each period. The interaction TR  $\times$  FL was tested for significance in all growth analyses, but sequentially removed if there was low evidence for effects of this term (i.e.  $p > 0.1$ ).

One LL fish grew substantially faster than all other LL ( $SGR_M = 1.9\%$ ; cf. Fig. 1b) fish during the second experimental period, and was removed from all analyses investigating treatment effects, as it was likely erroneously fed.

## Behavioral trials

Behavioral trials were conducted on the second (trial 1; day 36) and fourth (trial 2; day 38) day after the end of the feeding treatment. To measure effects of bodily state rather than immediate hunger effects, all fish were fed once to satiation the day before trials. On trial days fish were given rations corresponding to the final feeding treatment rations after the trial. On each trial day, single fish were put into opaque white trial arenas (area:  $28 \times 19$  cm, water level: 5 cm; Slugs, Ikea,

**Table 2:** Descriptions of abbreviations used to describe statistical analyses.

Statistical methods	
LM	Linear model
GLM	Generalized linear model
GLMM	Generalized linear mixed model
ICC	Intraclass correlation
PCA	Principal component analysis
Dependent variables	
$SGR_M$	Specific growth rate in wet mass (% per day)*
$AGR_L$	Absolute growth rate in fork length (mm per day)*
$Act1/Act2$	Swimming activity score, trial 1/trial 2**
$Boldn1/Boldn2$	Boldness score, trial 1/trial 2**
$AAggr1/AAggr2$	Active aggression score, trial 1/trial 2**
$PAggr1/PAggr2$	Passive confrontation score, trial 1/trial 2**
Independent factors	
TR	Food treatment*** Categorical between-subject factor (fixed; four levels)
FL	Fork length (mm) at the time of the trials Continuous factor
DAY	Trial day****
DATE	Categorical within-subject factor (fixed; two levels) Date of size-measurement***** Categorical within-subject factor (fixed; three levels)
* see Materials and methods: Growth monitoring	
** see Materials and methods: Behavioral analyses	
*** see section "Food manipulation" in Materials and methods	
**** see section "Behavioral trials" in Materials and methods	
***** see section "Growth monitoring and analyses" in Materials and methods	

The Netherlands), where behavior was recorded from above, using web-cameras (Creative VF0520; Creative Labs, Singapore) mounted on the ceiling. Nineteen fish could be recorded simultaneously. Over one trial, water temperature in the trial arena generally rose from 12.0 – 12.3°C to 13.7 – 14°C.

### Trial protocol

Three consecutive behavioral tests (modified versions of the tests used in Adriaenssens and Johnsson 2013) were conducted on each trial day. First the fish were left to swim around in the barren white environment for 15 minutes (*forced open-field test*). Secondly, we lowered down a novel object (trial 1: M6 hardware nut glued to a red 10 × 10 mm plastic bead; trial 2: stainless steel screw 3 × 10 mm) into one corner of the arena, using a clear nylon line attached to the object, and left the fish for another 15 min (*novel-object test*). Lastly, we put a mirror into the container (hiding the novel object behind the mirror) into one of the short sides of the container and let the fish interact with the mirror image for 10 min (*mirror-aggression test*), after which the trial ended and the fish was put back into its home tank.

### Behavioral analyses

Behavior was scored manually from recorded videos using Adobe Premier CS3 (Adobe Systems Inc., USA). Abbreviations for statistical models, dependent variables and independent factors are found in Table 2.

In the open-field test we scored swimming activity (*Act1/Act2*). The trial arena was divided by lines into a grid of 12 equal-sized rectangles (70 × 63.3 mm; Fig. 2a). The number of line-crossings, between the 10th and the 15th minute after release into the arena, was recorded as a measure of activity. The whole body had to cross the line to count as a crossing.

In the novel-object test we scored boldness (*Boldn1/Boldn2*). Four zones were delimited (Fig 2b), based on the distance to the novel object: zone 1 (0 – 84 mm distance), zone 2 (85 – 169 mm distance), zone 3 (170 – 254 mm distance), and zone 4 (> 255 mm distance). The location of the head of the fish was scored every tenth second between the 10th and the 15th minute after the novel object was put into the arena. The mean score was used as a measure of boldness.

In the mirror-aggression test we scored aggression toward a mirror image. A “confrontation-zone” was delimited at 3 cm distance from the mirror (Fig. 2c). If the fish was inside this zone with its head, it was scored as confronting the mirror reflection, except for when the body was facing away from the mirror at an angle of > 45°. If the fish was swimming actively against the mirror, or swimming towards the mirror at an angle of > 45° inside the zone, the behavior was scored as being actively aggressive (*AAggr1/AAggr2*). If the fish was inside the zone but not moving, or being faced toward the mirror at an angle ≤ 45°, or ≤ 45° away from the mirror, the behavior was scored as passive confrontation (*PAggr1/PAggr2*). For a graphical illustration of the definitions, see Fig. 2c<sub>2</sub>. These behaviors were scored every tenth second between the 5th and the 10th minute after the mirror was inserted into the arena.

In all cases, lines and zones used to score behavior in the trial arenas were drawn on plastic film which was put on the computer LCD-monitor when analyzing the recorded films. Statistical analyses were conducted in SPSS 22 (IMB Corp., USA), if not stated otherwise.

Behavioral scores from each test were analyzed using GLMMs (covariance type: compound symmetry; robust covariance estimates; residual method for degrees of freedom estimation). Factors included in the models were TR, DAY and FL. Initially we also included the interactions TR ×

DAY and TR  $\times$  FL, but these interactions were not significant in any of the analyses (all  $p > 0.2$ ) and therefore removed from the final models. Pairwise contrasts for fixed factors were checked if  $p \leq 0.1$ . From the results of the *A*Aggr-GLMM, a pattern occurred where fish ending on low ration seemed to be more aggressive. As an ad-hoc analysis, we pooled the TR-levels HH and LH, and HL and LL, and ran the model again. In addition, as there was substantial variation in growth rate within treatment groups, we conducted complimentary analyses where we modelled behavioral scores as linear functions of specific growth rate during Period 2, without including treatment group as a factor.

Repeatability of the scored behaviors was analyzed by ICC, using the PSYCH package in R 3.0.3 (R Core Team, 2014). Correlations among different behaviors in the different tests (Table 3) were used to combine data into principal components in a PCA. However, as the novel-object test did not appear to result in any informative behaviors with respect to boldness (see electronic supplement, Section 2), *Boldn1* and *Boldn2* were not included in the PCA. It can be noted that, if included, these variables would load in a separate component, *Boldn1* positively and *Boldn2* negatively (data not shown). Out of the confrontation scores, we chose to include only *A*Aggr1/*A*Aggr2 in the PCA (see Results: Aggression for details). The component obtained from the PCA, including *Act1*, *Act2*, *A*Aggr1 and *A*Aggr2, was analyzed using a GLM (Gaussian distribution, identity link-function), including TR and FL; the interaction was initially included, but removed in the final analysis as it was non-significant ( $p = 0.3$ ).

To investigate whether distinct behavioral groups could be discerned, we used two-step cluster-analysis (distance measure: log-likelihood), set to automatically categorize a number of clusters (maximally five). The cluster analysis was based on the variables *Act1*, *Act2*, *A*Aggr1 and *A*Aggr2. Detected clusters were analyzed using binomial GLM (logit link-function), including TR and FL. Furthermore, to investigate whether detected clusters were set already prior to the experiment, we analyzed the cluster assignment using a binomial GLM with only initial body size (i.e. fork length prior to the onset of the feeding treatments) as a factor.

### Ethical note

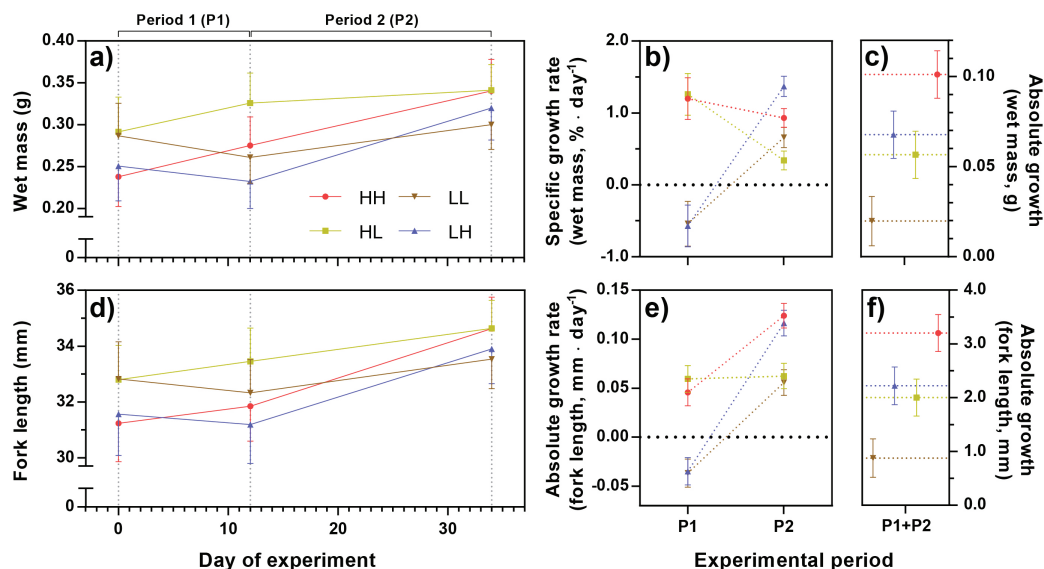
The experimental procedures were approved by the Ethical Committee on Animal Experiments in Gothenburg, Sweden (ethical license number 8-2011). Food rations were continuously assessed for adequacy with respect to fish survival, based on visual inspection of fish condition, behavior and mortality. Although most fish fed on the provided food from the first day in the lab, some fish never started to feed. Such failure of feeding in some young salmonid fry (so called “pin-heads”) is commonly noted in lab and hatchery environments.

## Results

### Growth

The initial mean sizes of HL and LL groups were slightly, but significantly, larger than the HH and LH groups and as a consequence there was no significant differences among groups in size at the end of the treatment (wet mass: Fig. 1a, Table S2, S3; fork length: Fig. 1d, Table S6, S7). During Period 1 the growth rates were faster for fish on high ration; in general high ration fish showed positive growth, while low ration fish showed negative growth ( $SGR_M$ , Fig. 1b, Table S4;  $AGR_L$ : Fig. 1e; Table S8). During Period 2, all treatment groups differed in  $SGR_M$ , with the LH group





**Figure 1:** Growth patterns for the experimental fish: (a) mean wet mass; (b) specific growth rate in mass, adjusted for initial size; (c) absolute growth in mass over the experiment, adjusted for initial size; (d) mean fork length; (e) absolute growth rate in fork length, adjusted for initial size for P2; (f) absolute growth in fork length over the experiment, adjusted for initial size. Error bars show 95% confidence intervals. Detailed statistics are found in the electronic supplement (Section 3). For details on treatment groups (HH, HL, LH and LL) see Table 1.

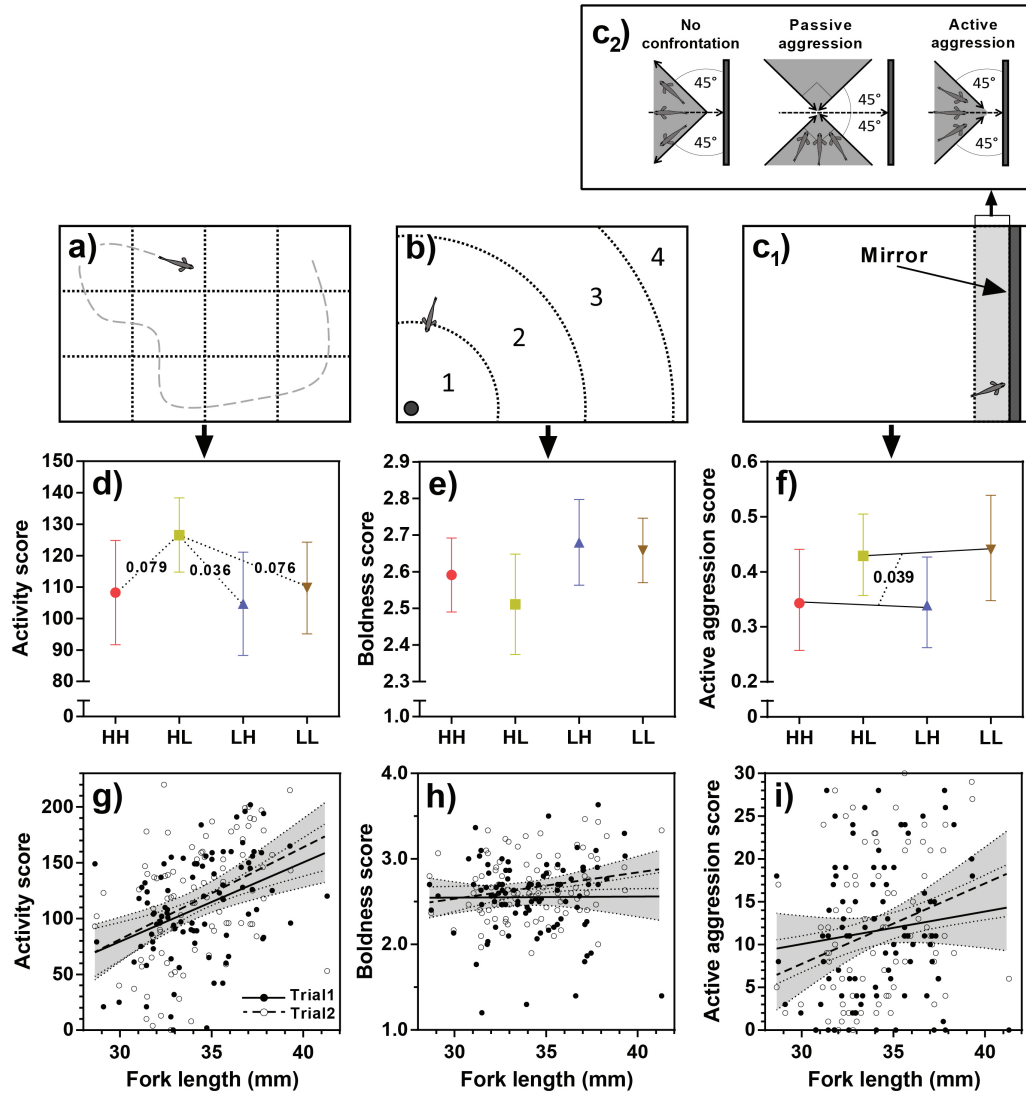
growing at the fastest rate:  $LH > HH > LL > HL$  (Fig. 1b, Table S4). For  $AGR_L$  in Period 2, the high ration groups grew faster than low ration fish:  $HH \approx LH > HL \approx LL$  (Fig. 1e, Table S8). Looking at the absolute growth over the whole experiment (Period 1 + Period 2), HH grew most rapidly, followed by LH and HL, and LL grew slowest (wet mass: Fig. 1c, Table S5; fork length: Fig. 1f, Table S9).

Confidence intervals are presented for evaluation of treatment effects (Fig. 1); for detailed results of GLMs and GLMMs, along with contrast estimates and their  $p$ -values, see electronic supplement (Section 3, Table S2-S9).

### Open-field activity

Body size had a significant effect on swimming activity, where larger fish were more active (FL:  $F_{1,172} = 28.879$ ;  $p < 0.001$ ) (Fig. 2g). In the GLMM, treatment was not a significant factor (TR:  $F_{3,172} = 2.115$ ;  $p = 0.100$ ), but pairwise contrasts suggested that the HL group tended to be more active (HL vs. LH [21% higher]:  $p = 0.036$ ; HL vs. HH [17% higher]:  $p = 0.079$ ; HL vs. LL [15% higher]:  $p = 0.076$ ) (Fig. 2d). Trial day had no significant effect (DAY:  $F_{1,175} = 1.205$ ;  $p = 0.274$ ). Regression analyses indicated that there were negative effects of specific growth rate on activity during Period 2 (see electronic supplement, Fig. S2).

Swimming activity was generally repeatable (Table 4). However, repeatability seemed to be higher for HL and LH fish than for HH and LL, albeit with overlapping confidence intervals for ICC.



**Figure 2:** Results from the behavioral trials. First panel-row (a-c): top-view schematic illustrations of the behavioral arenas for (a) forced open-field test, (b) novel object test (numbers indicate distance-zones, as described in Materials and Methods), and (c1) mirror aggression test (dark grey zone: mirror; light grey zone: “confrontation zone”). Definitions of aggression based on fish position relative to the mirror within the confrontation zone are shown in c2. Second panel-row (d-f): estimated means, with 95% confidence intervals, based on the GLMMs (i.e. combining both behavioral trials) for (d) activity score (significant and trend contrasts connected with dotted lines and  $p$ -values), (e) boldness score, and (f) active aggression score (dotted line indicate significant difference in ad hoc analysis combining HH and LH, and LH and LL, along with  $p$ -value). Third panel-row (e-i): body size effects on (g) activity score, (h) boldness score, and (i) active aggression score. Gray areas show 95% confidence limits. For details on treatment groups (HH, HL, LH and LL) see Table 1.

### Novel-object boldness

No significant treatment effect was detected (TR:  $F_{3,172} = 1.446$ ;  $p = 0.231$ ) (Fig. 2e), neither was there any effect of body size (FL:  $F_{1,172} = 2.236$ ;  $p = 0.137$ ) (Fig. 2h). Fish tended to be slightly

further away from the novel object on the second trial day compared to the first trial day (DAY:  $F_{1,172} = 3.092$ ;  $p = 0.080$ ). Regression analyses did not indicate any effects of specific growth rate during Period 2 of the feeding period ( $R^2 \leq 0.02$ ,  $p > 0.18$ ).

Individual boldness scoring was not found to be repeatable between the two trial days (Table 4).

In general, boldness scoring was found to be largely reflecting a random swimming pattern for most individuals; i.e. for the majority of the individuals, the number of times a fish was found in each zone did not deviate from what was expected based on the size of each zone (for analyses and further discussion see electronic supplement, Section 2).

### Mirror aggression

Total confrontation levels towards the mirror (i.e.  $AAggr + PAggr$ ) were generally very high and close to the maximum score (electronic supplement Fig. S3), leading to the  $PAggr1$  and  $PAggr2$  being largely complementarily, negatively correlated, to  $AAggr1$  and  $AAggr2$  respectively (this is the reason why we only included  $AAggr$  in the PCA and why we only report results on  $AAggr$ ; for illustration of  $PAggr$  scores see electronic supplement, Fig S3). For active aggression scores, no significant effects were detected for treatment (TR:  $F_{3,172} = 1.464$ ;  $p = 0.226$ ) or trial day (DAY:  $F_{1,172} = 0.001$ ;  $p = 0.974$ ) (Fig. 2f). Larger fish were more aggressive (FL:  $F_{1,175} = 5.913$ ;  $p = 0.016$ ) (Fig. 2i). Pooling fish with respect to the ration given during the second feeding period (i.e. HH+LH, and HL+LL) revealed that fish reared on low ration during the second experimental period were more aggressive (TR<sub>Pooled</sub>:  $F_{1,174} = 4.345$ ;  $p = 0.039$ ) (Fig. 2f). Regression analyses indicated that there negative effects of specific growth rate on aggression during Period 2 of the feeding period (see electronic supplement, Fig. S2).

Active aggression was repeatable overall (Table 4). However, repeatability seemed to be higher for HH and LL fish than for HL and LH, albeit with overlapping confidence intervals for ICC.

### Principal component analysis

In the PCA we extracted one single component (PC1), as judged from both Cattell's scree test and the Kaiser–Guttman criterion (eigenvalue > 1). All included variables loaded positively on PC1 (see correlation matrix, communalities and factor loadings in Table 3). Thus, higher values of swimming activity and active aggression were represented by higher values of PC1. PC1 explained 48.9% of the variation in the included data and the eigenvalue was 1.96. Sampling adequacy as indicated

**Table 3:** Relationships among behavioral variables. Pearson correlation coefficient  $r$  (left table, below diagonal); significance  $p$  (left table, above diagonal); principle component analysis summary (right table). *Act*: swimming activity; *AAggr*: active aggression; *PAggr*: passive confrontation; *Boldn*: boldness; 1: first trial; 2: second trial. Significant correlations are marked bold.

N=90	Correlation matrix								Principal component analysis	
	<i>Act1</i>	<i>Act2</i>	<i>AAggr1</i>	<i>AAggr2</i>	<i>PAggr1</i>	<i>PAggr2</i>	<i>Boldn1</i>	<i>Boldn2</i>	Communalities	Factor loadings
<i>Act1</i>	—	***	**	NS	□	NS	NS	□	0.499	0.706
<i>Act2</i>	<b>0.439</b>	—	**	**	*	NS	NS	NS	0.594	0.771
<i>AAggr1</i>	<b>0.335</b>	<b>0.290</b>	—	**	***	□	NS	NS	0.462	0.680
<i>AAggr2</i>	0.172	<b>0.363</b>	<b>0.300</b>	—	□	***	NS	NS	0.401	0.633
<i>PAggr1</i>	-0.180	<b>-0.224</b>	<b>-0.507</b>	-0.187	—	*	NS	NS	—	—
<i>PAggr2</i>	-0.077	-0.131	-0.187	<b>-0.464</b>	<b>0.233</b>	—	NS	NS	—	—
<i>Boldn1</i>	-0.043	0.173	0.038	-0.030	-0.074	0.072	—	NS	—	—
<i>Boldn2</i>	0.192	-0.003	0.151	-0.003	-0.023	0.140	-0.058	—	—	—

□ =  $p < 0.1$ ; \* =  $p < 0.05$ ; \*\* =  $p < 0.01$ ; \*\*\* =  $p < 0.001$ ; NS = not significant,  $p > 0.1$ .

by the KMO-test (0.649) and Bartlett's sphericity-test ( $p < 0.001$ ) was regarded as acceptable, but results should be treated with some caution due to the KMO-value being  $< 0.7$  (following Budaev 2010).

Given the factor loadings from the PCA (Table 3), PC1 is indicating the presence of a behavioral syndrome between swimming activity and active aggression in the subject fish. The PC1 scores were not significantly different among treatments (TR: Wald  $\chi^2 = 5.9$ ;  $df = 3$ ;  $p = 0.117$ ), but higher scores were associated with longer bodies (FL: Wald  $\chi^2 = 20.235$ ;  $df = 1$ ;  $p < 0.001$ ) (Fig 3b), indicating that larger fish were more active and aggressive.

### Cluster analysis

Two behavioral groups were detected in the cluster analysis. In general, lower activity and lower aggression were associated with one cluster (Cluster A, 44.9% of individuals, Fig. 3a), and higher activity and higher aggression were associated with the other cluster (Cluster B, 55.1% of individuals, Fig. 3a). In concordance with the other results on activity and aggression, larger body size increased the probability of being assigned to Cluster B (Fig. 3b) (FL: Wald  $\chi^2 = 10.685$ ;  $df = 1$ ;  $p = 0.001$ ). Treatment group did not affect the probability of being assigned to a particular cluster (TR: Wald  $\chi^2 = 3.552$ ;  $df = 3$ ;  $p = 0.314$ ). Behavioral clusters were defined already prior to the onset of the experiment, as initial fork length alone was a significant predictor of cluster assignment (Wald  $\chi^2 = 11.520$ ;  $df = 1$ ;  $p = 0.001$ , see Fig. S4).

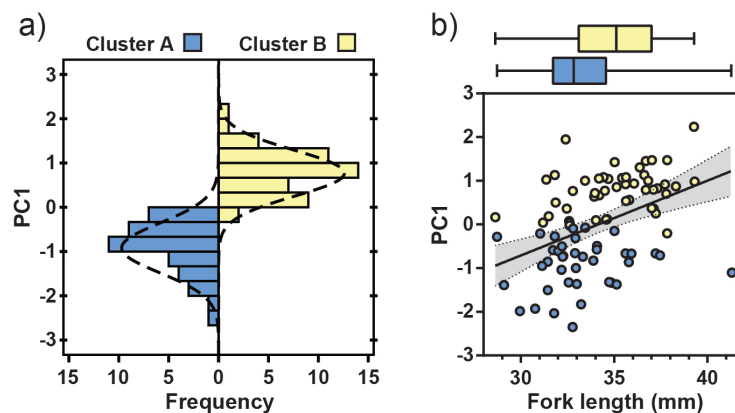
## Discussion

The results presented here provide some evidence for state-dependent behavior in brown trout fry, but not following the pattern we predicted. We predicted that the LH group (initially starved and subsequently re-fed at high rations), which was assumed to have entered a compensatory growth phase, would be more active due to being in a hyperphagic state, but this effect could not be confirmed. Instead we found that the treatment group with a negative change in food ration in Period 2 (HL) tended to be more active in the open-field test than the other groups. We also found that food restricted fish in Period 2 (i.e. HL + LL pooled) showed higher levels of active aggression than fish fed high rations. This is in contradiction to Hoogenboom et al. (2012), who detected no effects among trout of similar age. However, the fish in their study were scored in groups which may have affected aggression levels of subordinate fish. Nicieza and Metcalfe (1997)

**Table 4:** Repeatability of behaviors as indicated by the intraclass correlation coefficient (ICC).  $N$ : sample size;  $F$ :  $F$ -statistic. Numbers within brackets denote 95% confidence interval of ICC. Significant ICC are bold. For details on treatment groups (HH, HL, LH and LL) see Table 1.

	$N$	Activity		Boldness		Active aggression	
		ICC	$F$	ICC	$F$	ICC	$F$
Overall	90	<b>0.43***</b>	2.5	-0.066	0.88	<b>0.30**</b>	1.9
		(0.25 – 0.58)		(-0.27 – 0.14)		(0.11 – 0.48)	
HH	23	0.25	1.7	-0.31	0.53	<b>0.48**</b>	2.9
		(-0.16 – 0.60)		(-0.63 – 0.11)		(0.11 – 0.74)	
HL	23	<b>0.59***</b>	3.9	0.062	1.1	0.048	1.1
		(0.25 – 0.80)		(-0.35 – 0.45)		(-0.36 – 0.44)	
LH	22	<b>0.68***</b>	5.3	0.033	1.1	0.23	1.6
		(0.38 – 0.85)		(-0.38 – 0.44)		(-0.20 – 0.59)	
LL	21	0.22	1.5	-0.078	0.86	<b>0.47*</b>	2.8
		(-0.22 – 0.59)		(-0.48 – 0.35)		(0.072 – 0.75)	

\* =  $p \leq 0.05$ ; \*\* =  $p \leq 0.01$ ; \*\*\* =  $p \leq 0.001$ .



**Figure 3:** Clustering of behavioral types: (a) distribution of individuals into the two clusters in relation to their score of the extracted principal component, PC1 (Cluster A = less active and less aggressive; Cluster B = more active and more aggressive); (b) relationship between PC1 and body size (fork length). Box-plots on top of the graph show the fork length of the two clusters; box hinges show the first and third quartile, the line inside the box shows the second quartile (median), and the whiskers show minimum and maximum values. Regression line with 95% confidence interval is shown for both clusters combined. Blue = Cluster A; Yellow = Cluster B.

showed that older juveniles of Atlantic salmon increased aggression after being food restricted, in line with our findings. The prediction that initially starved and subsequently re-fed fish should be more aggressive than all other groups was not realized. Both activity and aggression were negatively correlated with growth rate during Period 2, albeit with relatively low  $R^2$  values, indicating large inter-individual variation (see Fig S2, electronic supplement). Smaller trout in general have faster growth rate (Jonsson and Jonsson 2011), as long as they are not being suppressed by dominant individuals (e.g. Brown 1957). Here, smaller fish were indeed growing faster, as expected by the fact that the fish were reared without competition for food. The finding that larger individuals were generally more active and more aggressive indicates that larger fish are more likely to belong to a more territorial behavioral type (i.e. Cluster 2 in this study, see further discussion below).

No effects were detected for the behavior in the novel-object test. In fact, this test seemed to be largely uninformative in the way it was carried out here (see electronic supplement, section 2). It should be noted here, that other designs of novel-object tests for recently emerged brown trout fry have proved to be useful (e.g. Sundström et al. 2004). Overall the effects of treatment appeared to be relatively small, compared to the general behavioral expression, in agreement with another recent study on the same life-stage of brown trout from the same population (Näslund et al. 2015b).

The overall pattern of our results suggest that the scope for adjustments of behavior is limited in brown trout fry, which further suggests that fry are under general pressure to attain a larger size, to avoid predation and increase competitive ability. Similar results have been obtained for juvenile stages of other fish species (e.g. Peck et al. 2014), as well as for larval insects (Brodin and Drotz 2011). Early survival of brown trout is largely dependent on whether the fish can attain a territory or not during a critical period, which corresponds to the experimental period for this study, and is negatively influenced by increased population density (Elliott 1990). It should be noted, that the fish were not stimulated by any predator models during trials, and thus the conclusion that state-dependent safety is of large importance for the trout fry behavior may be less valid when individuals perceive direct predation risk. Other studies have shown that salmonid juveniles (slightly larger

than our trout) rely on asset protection, i.e. larger fish take fewer risks, when directly attacked by model predators (Reinhardt and Healey 1999).

The brown trout fry showed individual consistencies in swimming activity and aggression at similar levels as previously reported for this species (Hoogenboom et al. 2012; Adriaenssens and Johnsson 2013; Kortet et al. 2014). Interestingly, the treatment groups tended to differ in repeatability of these traits. Regarding activity, the groups which experienced a switch in their food ration (HL and LH) showed relatively stronger repeatability than the stable ration groups (HH and LL). Repeatability in the latter two groups was not statistically significant, although showing similar patterns as the former two groups. Previous studies have shown that environmental factors can affect the strength of personality traits (e.g. behavioural syndromes being stronger in the presence of a predator; Bell and Sih 2007) and cognitive abilities (e.g. higher ability when food rations have changed during the juvenile stage; Kotrschal and Taborsky 2010). Possibly, stability of food ration may affect the consistency of behavioural traits. Further investigation into the strength of repeatability in different environments is warranted.

Activity and aggression were generally positively correlated in the brown trout fry, forming a behavioral syndrome. This behavioral syndrome has also been observed in juveniles of European eel (Geffroy et al. 2015), and in adults of several fish species (reviewed in Conrad et al. 2011). When adding the same behavioral variables into a cluster analysis, two general clusters could be discerned – one with lower activity and aggression (Cluster A), and one with higher activity and aggression (Cluster B). The clustering of two general behavioral types is in line with much of the previous literature describing the biology of early brown trout stages. In general, two behavioral groups are discerned when fry emerges from the spawning gravel. One group takes station close to the nest, and the other, having delayed formation of static swimming behavior, drift downstream away from the nest (Cuinat and Héland 1979; Héland 1999). The downstream drifters have been suggested to constitute a group of individuals with the strategy of forming territories in areas where there are less competition (Héland 1999; Skoglund and Barlaup 2006). Trout fry show these different behaviors even if reared in isolation (Héland 1999), a finding which is supported by our results. In general for salmonids, the early emerging fry are the ones taking station close to the nests and become dominant over later emerging fry (Mason and Chapman 1965; Chandler and Bjornn 1988; Metcalfe and Thorpe 1992). This dominance could potentially lead to a size advantage during the rest of the juvenile stage and thereby earlier smoltification (preadaptation for seaward migration), as shown in hatchery studies (Metcalfe and Thorpe 1992). Dominant fish can choose the best foraging grounds, and also have precedence in choosing when to forage, and can thereby optimize food intake in relation to risk (Alanärä et al. 2001). Some evidence suggests that early emergers have basal higher metabolic rate, which could lead to higher activity levels (Metcalfe et al. 1995). This, in turn, would further support the inference that the active group is constituted of early emergers. Similar strategies are also found in wild brook char *Salvelinus fontinalis* fry, but in this species the strategies appear to be associated with stress reactivity (i.e. cortisol expression) (Farwell and McLaughlin 2009; Farwell et al. 2014).

In some cases, a passive strategy may not be viable during the early critical period, as indicated by high mortalities in non-territorial fry in their first months of life in the Black Brows Beck, Britain (Elliott 1990). In other cases, like in the tributaries to the Norwegian river Daleelva, non-territorial drifting fry do not seem to starve and may thus not be outcompeted; instead this appears to be a specific dispersal strategy (Skoglund and Barlaup 2006). The possibility of coexistence of different behavioral types is likely positively influenced by territory availability and environmental complexity (Höjesjö et al. 2004; Hoogenboom et al. 2012; Reid et al. 2012), which likely differ among study

sites and over time. The different clusters of behavioral types could be a result of frequency dependent selection based on underlying physiological mechanisms (e.g. metabolic rate or stress reactivity) as modelled by Wolf and McNamara (2012). However, studies on young hatchery reared salmonids have indicated that agonistic behavior, which is part of the behavioral syndrome in our study, show virtually no heritability (Vøllestad and Quinn 2003; Kortet et al. 2014). Still, salmonid selection programs seem to be able to create genetic strains with altered aggression levels compared to wild populations, indicating that there actually is a genetic component for the behavioural expression (Huntingford and Adams 2005). Substantial among-sibling variation in behavior has previously been found in brown trout, attributed to the location of the eggs in the egg sac and possibly pre-natal hormone exposure (Burton et al. 2011, 2013). Thus, behavioral strategies of individual fry may be depending on embryonal environment, which can vary within females (Jonsson and Jonsson 2014). For instance, within-egg size variation in female fish (southern pygmy perch *Nannoperca australis*) can be influenced by e.g. environmental predictability, with more variation in unpredictable environments (Morrongiello et al. 2012). If within-female differences in investment into eggs affect behavior, e.g. through effects on metabolic rate (Régner et al. 2012), this may be an indication of bet-hedging with different behavioral types performing well in different situations, utilizing different niches, or different competitive strategies (e.g. Grant and Noakes 1987; Skoglund and Barlaup 2006; Závorka et al. 2015). In this way the offspring from a single female may have a wider total niche breadth. Given the many non-genetic factors which can affect offspring behavior, the frequency of behavioral types in a population may be an effect of selection for intra-female variation in offspring phenotypes and fine-tuned each generation through environmental effects, rather than being an effect of direct genetic inheritance of specific behavioral traits.

It is not yet known whether brown trout retain their behavioral strategy, or personality, over longer time-periods (for similar issues see e.g. Groothuis and Trillmich 2011). Possibly, if the low-activity fish would retain their passive behavior over time, they may in fact perform equally well, or even better, than active individuals at later life-stages (e.g. Adriaenssens and Johnsson 2010; Závorka et al. 2015).

In summary, we argue that behavior in brown trout fry is influenced by recent food availability after experimentally controlling for acute hunger effects, albeit with effects being relatively weak due to inter-individual variation. Size was associated with behavior, with larger fish being more active and more actively aggressive on average. We found evidence for both consistent individual differences in activity and active aggression, and a behavioral syndrome where activity and active aggression were positively correlated. Finally, two distinct behavioral groups could be discerned, after removing effects of social environment for a month prior to behavioral trials, suggesting two behavioral strategies in brown trout fry.

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