



Behaviour and metabolic rates of brown trout and Atlantic salmon

Influence of food, environment and social interactions

Linnea Lans

Faculty of Social and Life Sciences

Biology

DISSERTATION | Karlstad University Studies | 2012:4

Behaviour and metabolic rates of brown trout and Atlantic salmon

Influence of food, environment and social interactions

Linnea Lans

Behaviour and metabolic rates of brown trout and Atlantic salmon - influence of food, environment and social interactions

Linnea Lans

DISSERTATION

Karlstad University Studies | 2012:4

ISSN 1403-8099

ISBN 978-91-7063-408-6

©The author

Distribution:
Karlstad University
Faculty of Social and Life Sciences
Department of Biology
SE-651 88 Karlstad, Sweden
+64 54 700 10 00

Print: Universitetstryckeriet, Karlstad 2012

WWW.KAU.SE

ABSTRACT

For Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*), the decision to migrate or when to migrate is believed to be influenced by the individual's metabolic rate (MR) relative its food intake. As MR was expected to be related to behaviour, the potential links between behaviour and metabolic costs was studied. For both salmon and trout the dominant individual had a higher standard metabolic rate (SMR) than its subordinate counterpart. Also, successful migrants of brown trout had a higher SMR than unsuccessful migrants, whereas no such difference was found for obligate migratory Atlantic salmon. Measures of variation in MR and boldness indicated that Atlantic salmon was more sensitive to stress than brown trout and became passive when stressed. When two trout were interacting, an increase in ventilation rate (VR) was positively correlated to fighting intensity. The first day after an interaction, VR did not differ between small dominant and subordinate trout (mean size 3.7g), whereas for large trout (26.0g) subordinates had higher VR than dominants. However, a combination of low temperature (10°C) and high water velocity (22cm/s) eliminated this difference. This probably reflects the high swimming activity of small dominants and the low motivation for dominants to defend a large territory when temperatures were low and the cost of moving was high. These results show that the relationship between MR and behaviour may differ depending on species, fish size and environmental factors.

CONTENTS

| | |
|------------------------------------|-----------|
| PUBLICATIONS | 3 |
| INTRODUCTION | 4 |
| OBJECTIVES..... | 7 |
| MATERIALS AND METHODS | 8 |
| Study area | 8 |
| Paper I | 8 |
| <i>Metabolic rates</i> | 10 |
| Paper II..... | 10 |
| Paper III | 11 |
| Paper IV..... | 13 |
| RESULTS..... | 14 |
| Paper I | 14 |
| Paper II..... | 15 |
| Paper III | 16 |
| Paper IV..... | 17 |
| DISCUSSION..... | 18 |
| ACKNOWLEDGEMENT..... | 23 |
| REFERENSES | 25 |

PUBLICATIONS

This thesis is based on the following papers which are referred to by their Roman numerals. Paper IV is reprinted with the permission from John Wiley and Sons.

- I. Lans, L., Bergman, E. & Greenberg, L.A. 2012. Individual variation in behaviour and metabolic rates of brown trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*). *Manuscript*.
- II. Lans, L. & Metcalfe, N.B. 2012. The cost of being aggressive: a comparison of winners and losers of territorial contests. *Manuscript*.
- III. Lans, L., Bergman, E. & Greenberg, L.A. 2012. The effect of temperature and current velocity on ventilation rates of dominant and subordinate trout. *Manuscript*.
- IV. Lans, L., Greenberg, L.A., Karlsson, J., Calles, O., Schmitz, M. & Bergman, E. 2011. The effects of ration size on migration by hatchery-raised Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*). *Ecology of Freshwater Fish* 20:548-557.

INTRODUCTION

Migration is believed to occur when the advantage of migrating is higher than the cost of changing environments (Näslund 1990; Bohlin et al. 2001; Solomon 2007). However, the cost and benefit of migrating are not necessarily the same for all individuals in a population, which can result in a situation where some individuals remain in the area whereas others migrate; a phenomenon referred to as partial migration (Terrill & Able 1988). This situation is common among brown trout (*Salmo trutta*) populations (e.g. Forseth et al. 1999; Bohlin et al. 2001), where, especially for females, fitness is positively correlated with body size (Solomon 2007). It is believed that an individual is more inclined to migrate when it cannot allocate enough resources for growth, and several studies have reported that migrants typically have higher metabolic costs than non-migrants (Forseth et al. 1999; Morinville & Rasmussen 2003). The standard metabolic rate (SMR) of an individual may therefore be expected to be higher in migrating than non-migrating individuals. In Atlantic salmon (*Salmo salar*), however, only males have the possibility to reproduce without first performing a smolt migration, whereas all females have to migrate (Klemetsen et al. 2003). For both Atlantic salmon and brown trout the age at migration differs between individuals in the same population, depending on their growth rates when young (Økland et al. 1993). Therefore the net energy gain should influence the migratory behaviour of individuals in both species.

To be able to have a high net energy gain an individual has to maximize food intake and minimize energy consumption (Elliott & Hurley 1999). Therefore the behaviour of young individuals influences their decision to migrate. Before migrating, young individuals, parr, of both Atlantic salmon and brown trout live in running waters where they form dominance hierarchies (Jonsson & Jonsson 2010). The dominant individuals exclude their subordinate counterparts either temporarily or, in the case of territories, more permanently from the most profitable areas (Fausch 1984). One of the advantages of being dominant is therefore the possibility to have more food and thereby a higher growth rate (Höjesjö et al. 2002) and a higher fitness (Mendl et al. 1992; Hahn & Bauer 2008). But to be dominant also involves high costs in the form of more agonistic interactions when defending one's position in the dominance hierarchy (Mendl et al. 1992). Furthermore dominants may have a higher SMR than subordinates (Burton et al. 2011), which means that they need more food to maintain their body weight when inactive. The metabolic demand of an individual is also expected to be correlated with other behavioural traits.

Individuals with high SMR have been found to be bolder (Huntingford et al. 2010) and more aggressive than conspecifics with low SMR (Metcalfe et al. 1995; Cutts et al. 1998; Yamamoto et al. 1998; McCarthy 2001; Lahti et al. 2002). To date, however, no single study has examined multiple behavioural traits together with measures of SMR for Atlantic salmon and brown trout. Furthermore, an individual's total energy consumption is expected to be related to its behaviour. Other measures of MR, such as the maximum value or the first values measured, may therefore be correlated with behaviour (Careau et al. 2008).

The advantage of being dominant is known to be context-dependent, where the nature of the habitat and its physical structure (Hasegawa & Yamamoto 2009) differences in temperature (Elliott & Hurley 1999) and water velocity (Clark & Seymour 2006), as well as the predictability and accessibility of food (Bryant & Grant 1995) are important factors. It is not always the individual that has the possibility to eat most that grows best (Sloman et al. 2000a), as the energy used by individuals in a dominance hierarchy need not be the same. This raises the question as to whether some of the differences in growth rate between dominants and subordinates may be explained by differences in energy consumption. To fight for, and defend, a feeding position is an energy consuming activity, and the metabolic cost of defence may differ according to dominance status. Several studies have revealed that subordinates have an increased metabolic rate (MR) or poorer food conversion efficiency when dominants are present (Abbott & Dill 1989; Eisermann 1992; Sloman et al. 2000b; Millidine et al. 2009), even over a time span of several months (Eisermann 1992). The cause of this greater metabolic rate is not clear, although it has been suggested that it is related to either increased stress or to a greater cost of aggression. Thus it has been found that the physiological costs of aggression may be more prolonged for lower ranked individuals, as the long term energy depletion for the subordinate fish after a fight has been found to be more severe than for the dominant individual (Neat et al. 1998). Moreover, Peters et al. (1988) showed that metabolic rates tended to be higher for subordinate steelhead trout than for dominant steelheads for some 11 hours after a fight, although the difference was not significant, probably because of low statistical power due to small sample sizes.

The energy consumption for dominants and subordinates may not be the same in different environments since environmental conditions may influence dominants and subordinates differently. Temperature (Grøttum & Sigholt 1998) and water current (Enders et al. 2005) are two environmental

factors that differ between habitats and with seasons. An increase in temperature increases MR (Elliot & Hurley 1999), speed and stamina of ectotherms (Chen et al. 2003) and an increase in water velocity will increase MR of the fish that swim against the water current (Clark & Seymour 2006). The more actively swimming dominants (Winberg et al. 1992; Yamamoto & Reinhardt 2003) are expected to increase their MR more when water flow increases than the less active subordinates as subordinate individuals typically hide or rest on the bottom, experiencing low current velocities. An increase in temperature, on the other hand, may change the behaviours of subordinates more since they may be forced to be more active in search of food when their MR increases, thereby further increasing their MR.

Not all parr grow up in a natural environment, where they learn to capture live food and conserve energy. In many regulated rivers hatchery-raised smolts are stocked into rivers as compensation for reduced natural smolt production (Brown & Laland 2001). The reported tag recoveries of these smolts have declined in Sweden during the last decades (Fiskeriverket unpubl. data; McKinnell & Karlström 1999). During the same time period the size of smolts stocked in rivers has increased (Eriksson et al. 2008). An increased size might be expected to result in a higher survival because large individuals are less vulnerable to predators. However, the stocked smolts have attained such a large size that recapture rates might be expected to decline (Kallio-Nyberg et al. 2007; Sers et al. 2007). The hatchery-raised smolts are not only large in size but they are also fed large, highly nutritious rations, and this may influence migratory behaviour (Serrano et al. 2009). Previous studies have shown that brown trout and Arctic charr (*Salvelinus alpinus*) fed large rations are less likely to migrate than when fed reduced rations (Nordeng 1983; Wysujack et al. 2009). Furthermore, mortality of stocked salmonids has been shown to be highest during the first few days after they have been released (Aarestrup et al. 2005) and the time spent in the river is negatively correlated with survival rate (Salminen et al. 2007). Therefore any factor that delays migration should lead to a higher mortality, and presumably a lower recapture rate (Tipping et al. 1995). The reason for the reduced recapture rate of hatchery-raised smolts might therefore be that they have not successfully migrated, either because they have chosen not to migrate or because they have stayed in the river for a long time and therefore have suffered from high mortality. It may therefore be possible to increase the recapture rate of released hatchery-raised smolts by giving them less food and thereby increase their motivation to migrate to an area where there is more food.

OBJECTIVES

Metabolic rates are expected to be related to an individual's dominance status (Abbott & Dill 1989; Millidine et al. 2009; Burton et al. 2011), aggressiveness (e.g. Mendl et al. 1992; Lahti et al. 2002), boldness (Huntingford et al. 2010) and inclination to migrate (Forseth et al. 1999; Morinville & Rasmussen 2003). The main aim of this thesis was to investigate if these behavioural variables were related to MR in young Atlantic salmon and brown trout. Furthermore, the influence of food availability on the migratory success of smolts was investigated. In paper I, metabolic rates and behaviour were studied in young-of-the-year brown trout and Atlantic salmon. The purpose was to determine whether or not there were any relationships between an individual's MR and its behaviour, and if the dominance status of an individual was related to its MR. Furthermore, it was tested if the different behaviours studied, i.e. boldness, aggressiveness and dominance, were correlated with each other. The aim of paper II was to study the change in energetic costs for young-of-the-year trout when they interacted with each other compared to when they were alone. Furthermore, the activity and feeding of dominant and subordinate trout were studied. The investigation in paper II was performed in a constant environment with the same water current and temperature for all trout studied. In nature, physical conditions of the environment differ between streams and with season. Therefore, it was of interest to repeat the investigation done in paper II in different environments. Thus, in paper III two different flow conditions and two temperatures were used in a study of how different environmental conditions influenced the change in energetic costs, activity and feeding for paired young-of-the-year trout. The first three papers studied the relationships between MR and behaviour in parr. In paper IV, the migratory behaviour of brown trout and Atlantic salmon smolts were studied. In this investigation SMR of successful and non-successful migrants were compared. Furthermore, the effect of ration size on the proportion of fish that became migrants and the migration speed of stocked hatchery-reared smolts was examined.

MATERIALS AND METHODS

Study area

The field experiment of paper IV was performed in the lowest part of Klarälven, central Sweden in 2006 and 2007. This river originates in Norway and flows southwards into Sweden where it enters this country's largest lake, Lake Vänern. In the lower part of Klarälven there are eight hydropower stations, which have reduced the area of spawning grounds by around one third (Fiskeriverket 1998). The river has also been extensively used for timber floating and today the bottom of the river is mainly covered by sand and silt.

The feeding experiment in paper IV was performed in Gammelkroppa fish hatchery during the first year and in Brattfors fish hatchery the second year. The laboratory experiments in papers I and III were performed at the aquarium facility at Karlstad University from winter 2007 to autumn 2008 and during the spring of 2011. The investigation in paper II was performed at the University of Glasgow during the spring of 2010.

Paper I

In paper I hatchery-reared lake migrating 0+ brown trout (mean size: 9.9 ± 0.5 g) and Atlantic salmon (6.1 ± 0.5 g) were taken from Gammelkroppa fish farm, southwestern Sweden, to Karlstad University. The fish were individually marked with PIT-tags to be able to compare responses of single individuals subjected to multiple experimental situations. The temperature was held at a constant 10°C and the light regime was 10L:14D.

For the behavioural experiments, twelve 200-L aquariums were divided into two sections; a smaller section, the home section, (37 cm of the aquarium's length and around 44 L) with gravel, a flower pot and an artificial plant and a larger section, the barren section, without gravel or structures (61 cm long and 73 L). In the home section, by aerating the water, the water was circulated to simulate a stream environment. Three sides of the aquariums were covered with opaque plastic and the front side of the home section with sunfilm plastic (allows one to view fish with minimal disturbance) and throughout the investigation the fish were fed chironomid larvae at two percent wet weight as a daily ration.

The boldness of the fish was measured in two different contexts: 1. during a feeding acclimation experiment and 2. during a shyness-boldness test. The term boldness is here used to describe the exploratory behaviour of an animal in a new environment. Aggressiveness was measured when a fish met its own mirror image.

For the feeding acclimation experiment, the fish were placed in the home section of the aquariums to settle for 30 min. Then the fish were fed ten chironomid larvae and their behaviour was graded according to Øverli et al. (2006), where 0 means that the fish did not feed, 1 = the fish took only food that was close to the fish's mouth, 2 = the fish always returned to its original position after catching the food; distance moved was more than one body length and 3 = the fish were actively feeding. The feeding was repeated four times a day until the fish ate actively.

A shyness-boldness test followed the feeding acclimation experiment. The water flow was turned off and ten chironomid larvae were placed at the far end of the barren section. The partition between the two sections was removed and the time it took the fish to move to the food and start to eat was measured.

After this experiment, the aggressiveness of the fish, measured as the number of attacks performed towards a mirror during three minutes, was performed. To motivate the fish to be aggressive they were fed just prior to initiating the measurements. This experiment was followed by measurements of metabolic rates (see below).

During the next behavioural experiment, the dominance test, two individuals were released together and allowed to settle for two hours in the home section of an aquarium. Both fish were of the same species and of similar size. Ten larvae were given one at a time, and the number of larvae each individual consumed was noted. Thereafter the number of aggressive acts during three minutes was counted. After that the fish were fed several chironomid larvae at the same time. When these had been consumed the number of antagonistic acts was counted again for three minutes. The most frequently observed antagonistic behaviour was attacking and was the only behaviour considered when evaluating social status. This test was repeated three times the first day and four times the following days until it was possible to tell which fish was dominant. The most aggressive fish that consumed most of the food and held position swimming in the water column was considered as dominant.

Metabolic rates

The fish were held without food for around 43 h before being placed in the respirometer chambers. The metabolic rates were measured as oxygen consumption in an intermittent flow respirometry system with a LDAQ-4 instrument (Loligo Systems ApS, Hobro, Denmark). Oxygen consumption was measured during five minutes every ten minutes for 20-24 h at a temperature of 10°C and in complete darkness. For estimating standard metabolic rate a period of three hours, eighteen consecutive measurements, towards the end of the test period was used. The median value for this period was used as the fish's SMR. For 9 of 56 trout it was not possible to use this period because they were not calm. For these trout earlier periods with stable values were used.

To compare the stress response of the fish, the maximum value, the average value during the first hour and the CV for the whole test period were used. The maximum value was divided by the measured SMR to produce a ratio that shows the stress response relative to the metabolic rate when the individual is resting.

Paper II

Young-of-the-year brown trout from Almondbank hatchery (mean weight $3.7 \pm \text{SE } 0.1$ g) were transported to the University of Glasgow where they were held in 1 x 1 m holding tanks. The light regime throughout the experiment was 9L:15D and the water temperature was 13°C. The experiment used two sets of three interconnected glass stream tanks, each stream tank divided into eight compartments of equal size (40:13:20 cm, with a water depth of 16 cm and a water velocity of 2 cm/s). Adjacent compartments in each row were treated as pairs during the experiment. A shelter was provided in each compartment and the bottom was covered with gravel.

The trout in a pair were separated for five days (the settling period) and allowed to interact for four days (the interaction period). Twice a day during the settling period the trout's spatial position within the compartment, their eye and body colour and opercular ventilation rate (VR) were measured. Possible spatial positions were: resting in the shelter, resting on the substrate out of the shelter, swimming in the water column or swimming within 2 cm of the water surface. As darkening of the body end eye colour signal a subordinate status in trout (O'Connor et al. 1999; McCarthy 2001; Suter & Huntingford 2002) the colour

of the eye sclera were graded according to Suter & Huntingford (2002) on a five point scale where a pale eye scores one and a completely black eye scores five. The body colour was scored from one (pale) to three (dark) following O'Connor et al. (1999). VR was measured as the number of opercular beats during 20s. Three measurements, at least five minutes apart, were taken on each trout during each observation. At 16:00 the fish were fed with bloodworms administered in three groups of three and the number of larvae eaten was counted.

On the morning of the first day of the interaction period the partition dividing each pair of compartments was removed. When an interaction started, the position of each fish (i.e., whether or not they were in the half that was their own original compartment) and the identity of the initiator was noted. The number of attacks, chases and displays were noted during three minutes every ten minutes for 50 minutes. Displays were scored as 1, chases 2, and attacks 3. Then the same measurements (position, VR, eye and body colour) as during the settling period were taken once an hour for three hours. During the second to fourth day of the interaction period the position, eye and body colour and VR were measured twice a day as during the settling period. To have a relative measure of the change in VR the average value for VR during each observation period, except for the first hour where the highest value was used in aggressive pairs, was divided by the median value of VR for day 2-4 of the settling period. The fish were fed in the evenings with five bloodworms one after the other and thereafter thirteen bloodworms were administered simultaneously.

Paper III

Ventilation rates of hatchery-raised young-of-the-year brown trout from Gammelkroppa fish farm were studied under different flow and temperature conditions in three 7m long stream channels. In each stream channel an inner channel was built to standardize the environment. These inner channels were divided into four equally sized (70:30:37 cm) compartments, with a water depth of 16 cm. The bottom of each compartment was covered with gravel. There were two overhead shelters, consisting of a roof made of thick cloth and a combined overhead and velocity shelter consisting of a glass jar and a cloth that functioned as a roof behind the jar (Fig. 1). Initially, the trout were separated from each other with a removable transparent plastic partition that divided the compartments down the middle into two halves.

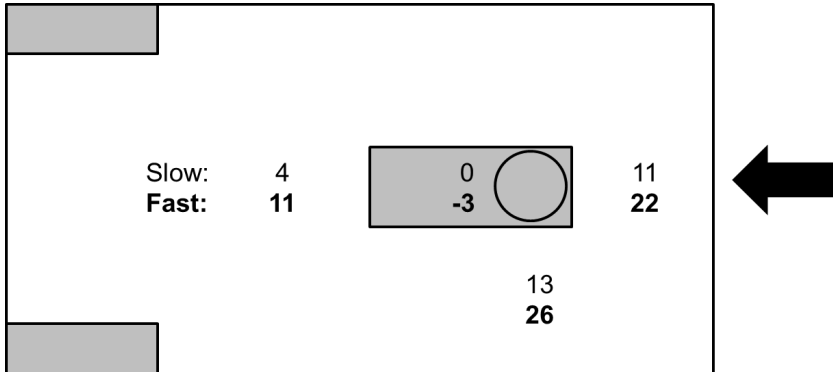


Figure 1: One of the compartments in the stream channel. The grey areas depict roofs made of thick cloth that served as cover for the trout. The circle represents a glass jar and the arrow shows the direction of the water flow. The numbers in boldface show the water velocity (cm/s) in fast flowing conditions and the other numbers show the water velocity in slow flowing conditions.

The water velocity in the free flowing section in front of the glass jar was on average 22cm/s (fast) or 11cm/s (slow) and the temperature was either 10°C or 16°C. The light intensity was on average 47 lux with a light regime of 12L:12D. The experiment was first performed at 10°C and then at 16°C.

One trout (mean weight 22.6 ± 0.7 g) was released into each compartment. The fish were separated for three days (the settling period) before they were allowed to interact with each other for two days (the interaction period). The trout were fed at 18:00 h on the second day of the settling period. They were fed three pellets three times and the number of times they ate was noted. This gave a maximum of three feeding bouts for each trout during one feeding occasion. Four times a day during the third day of the settling period the trout's spatial position within its compartment was noted as well as its eye and body colour and opercular ventilation rate (VR). The vertical position was one of four possible: resting in a shelter, resting on the bottom out of a shelter, swimming in the water column or staying in the upper part of the water column (a combination of resting on the roof of a shelter and swimming within two centimetres of the water surface). The darkening of the eye sclera and body colour was graded as in paper II. The number of opercular beats per 20s was counted three times (at least four minutes apart) for each fish during each observation period.

On the morning of the first day of the interaction period the partitions separating the trout in each pair were removed. Once every hour, for eight to ten hours, the VR, eye and body colour and position was noted. Furthermore, the time when the first interaction was initiated was noted. In the evening the trout were given five pellets one by one and three pellets three times as done in the settling period. The second day of the interaction period the same measurements were taken as in the settling period.

After the experiments were finished at 10°C the temperature was slowly increased to 16°C and the trout were allowed to acclimate to the new temperature for at least 14 days. The experiment at 16°C was performed in the same way as at 10°C. Even though the trout had grown (weight 29.3 ± 0.9 g) the size difference between two individuals in a pair did not differ between treatments.

The hour when the trout started to interact on the first day of the interaction period was defined as hour one. When calculating the relative VR the average value of the three measurements taken during each observation period was divided by the median value on the third day of the settling period.

Paper IV

During two consecutive seasons a food ration experiment was performed from December and until the smolts were released in late spring. During the first year (2005-2006) two groups of 1+ Atlantic salmon with 500 individuals in each group were held in separate holding tanks at Gammelkroppa fish farm. During the second year (2006-2007) two groups of 1+ Atlantic salmon and two groups of 1+ brown trout, with 250 individuals in each group, were held at the Brattfors fish farm. During both years and species one group was fed according to the recommendations given by the fish-farming industry, hereafter called the normal ration group, and the other group, the reduced ration group, was given around 15% of this amount. In late spring, just prior to the release of the smolts, the size of the fish was measured and their smolt status was determined visually using a four grade scale, modified after Tanguy et al. (1994) for trout and according to Staurnes et al. (1993) for salmon.

During the first season, 45 salmon from each group were marked with surgically implanted radio-transmitters. In the second year the number of marked individuals from each group was 30. These were released downstream of the southernmost power plant station and were tracked during their migration to Lake Vänern, a distance of around 25 km.

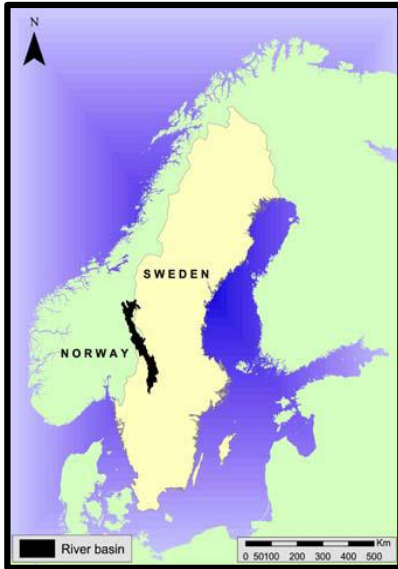


Figure 2: The drainage basin of River Klarälven (SMHI 2009).

During the first year 21 wild salmon were caught in the river. They were anesthetized with MS-222 and measured (total length in mm, Ricker 1979) and weighed (0.1 g). Seven individuals were retained and their fat content was measured. This was also done for fifteen hatchery-raised salmon in the normal and reduced ration groups, respectively.

In the second year, 31 trout and salmon were randomly-selected and their standard metabolic rate was measured with an intermittent flow respirometry system (Loligo Systems ApS, Hobro, Denmark). The fish

were starved for 24 h before placed in the respirometry chambers, where they were held for around 22 hours. The median value for a period of two hours (12 measurement periods) was used as a measurement of the fish's SMR.

RESULTS

Paper I

There was a negative correlation between SMR and the total feeding score assigned to an individual trout in the feeding acclimation experiment. At the same time there was an inverse correlation between feeding score and condition factor (CF). For salmon there was a positive correlation between boldness and “maximum MR / SMR” and boldness and the CV for MR. No other

correlations between MR and behaviour were found, nor were there any correlations between the different behaviours studied.

In general trout were more aggressive than salmon during the aggression test and a pair of trout established a dominance relationship faster than a pair of salmon. For both salmon and trout the dominant individual in a pair had a higher SMR than the subordinate counterpart (Fig. 3), although the difference was not significant for salmon, perhaps related to small sample sizes. Also, MR during the first hour was higher in dominant than subordinate salmon. The dominant salmon were more aggressive towards their own mirror image than the subordinates were, but there was no difference in boldness between dominant and subordinate salmon. For trout no differences between dominants and subordinates were observed in the different behavioural tests.

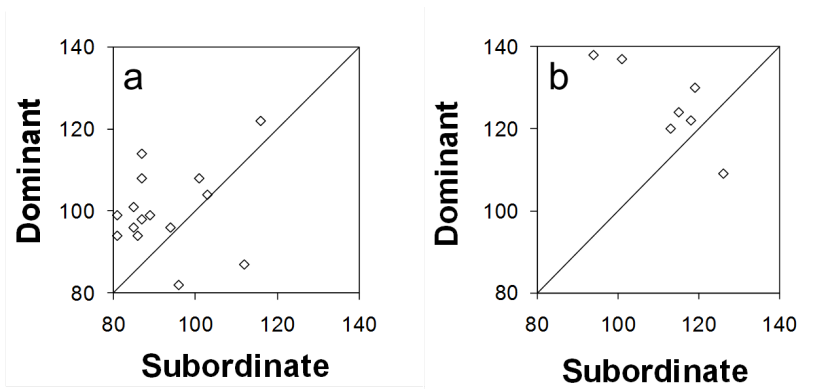


Figure 3: Comparison between standard metabolic rate ($\text{mg O}_2/\text{kg, h}$) for the dominant and the subordinate trout (a) and salmon (b). A point above the diagonal indicates that the dominant individual has a higher SMR than the subordinates.

Dominant trout were significantly longer (1.8%) than their subordinate counterparts, a difference that could not be seen in salmon. Moreover, SMR, CV, and the maximum value divided by SMR was higher for salmon than trout, whereas no differences could be seen between the species for the average value of MR during the first hour.

Paper II

It was possible to distinguish the dominance relationship for 48 of the pairs studied. In 32 of these at least one of the trout showed aggressive behaviour

and these will later be referred to as “aggressive pairs”. In the remaining “non-aggressive” pairs no aggression was noted. The probability for the larger trout to become dominant increased with increasing size difference and for the aggressive pairs the majority of the fights were initiated in the compartment half that had originally been inhabited by the dominant individual.

When the trout were fighting the increase in VR was positively correlated with the intensity of the fight and the more intense a fight the longer time it took for the VR to decrease to the same level as before the interaction. On the first day of the interaction period, there was an effect of time and aggressiveness on the relative VR, where aggressive pairs had higher relative VR the first hour than non-aggressive pairs, a difference that decreased with time. There was no effect of dominance status on the relative VR during the first day, whereas the values were higher in dominants than subordinates later on during the interaction period.

During the interaction period the dominant individuals ate more than their subordinate counterparts. Furthermore, dominants spent more time actively swimming throughout the experiment, something that was pronounced during the interaction period.

Paper III

The VR increased when the trout interacted with each other, an increase that persisted during the whole interaction period for subordinates, whereas the VR eventually returned to the same level as when alone for dominants. During the first day of the interaction period the relative VR of dominants decreased over time, whereas the relative VR of subordinates remained relatively constant over time. The difference in relative VR between dominants and subordinates was the same, independent of water temperature in slow-flowing water, whereas the difference increased with temperature in fast-flowing water. During the second day of the interaction period there was only an effect of dominance status on the relative VR, where dominants had lower values than subordinates.

The activity level of the dominant trout at 10°C was higher the first day than second day of the interaction period, whereas at 16°C the activity level of dominants did not change over time. In general the dominant individuals had a higher swimming activity than the subordinates during the interaction period. The subordinates, on the other hand, spent time in the upper part of the water column during the interaction period, something that they did not do during

the settling period. The proportion of time spent in the upper part of the water column was lowest at 10°C in fast-flowing water during the first day of the settling period.

The number of feeding bouts was the same over time for dominants, independent of water current and temperature. For subordinates, feeding activity was affected by temperature but not water current so that at 10°C the number of feeding bouts was the same relatively constant over time, whereas at 16°C the number of feeding bouts was lower during the interaction period than the settling period. This resulted in a higher feeding activity for dominants than subordinates during the interaction period at 16°C, something that was not generally seen at 10°C.

Paper IV

In both years and for both species the groups given a reduced food ration were smaller and had a lower condition factor. Body fat content was greater for salmon fed normal rations (9.1 %) than reduced rations (5.9 %) in the first year. Moreover, individuals in both groups had a higher fat content than wild smolts (1.2 %).

For salmon during the first year there was no difference in smolt status between the normal ration and reduced ration groups, whereas there was a statistically significant difference in smolt development during the second year. Salmon fed a reduced ration were more developed as smolts than those fed a normal ration. For trout, no difference in smolt development between the two feeding regimes could be seen. This difference in smolt status is reflected by the proportion of migrants, where salmon during the second year had more than twice as many migrating fish in the reduced ration group than in the normal ration group, whereas no such difference could be seen for salmon the first year or for trout (Fig. 4).

Fish fed reduced rations migrated faster than fish fed normal rations. This difference, however, was not significant for salmon during the second year. Time of release also influenced migration speed. In 2006 salmon released 30 May migrated faster (median = 0.32 days/25km) than those released 25 April (1.8 days) and 9 May (1.6 days). During the same time the water temperature increased from 2.6 to 10.5°C. No relationship between date of release and migration speed could be found in 2007, when the water temperature was between 12 and 21°C.

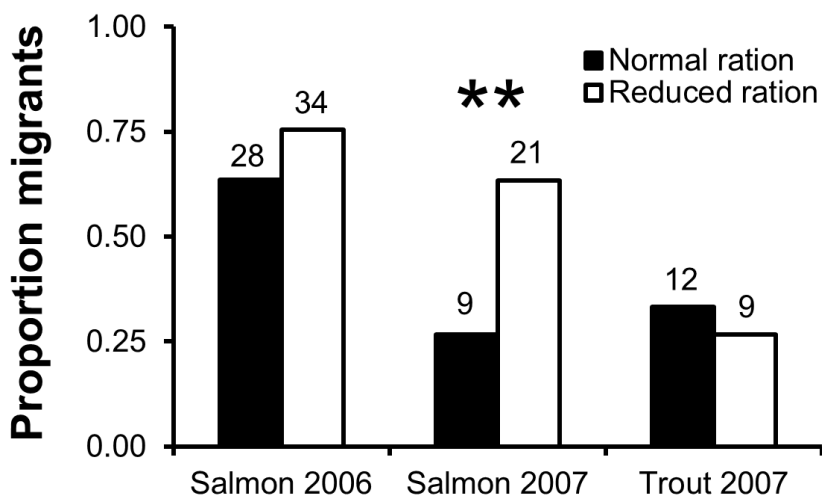


Figure 4: The proportion of smolt migrants for Atlantic salmon in 2006 and for Atlantic salmon and brown trout in 2007 fed a normal and reduced ration. Note that the number of migrating smolts is shown above the bars.

The SMR for migrating versus non-migrating trout in the group fed a normal ration was higher for the migrants; a difference that was not seen for salmon.

DISCUSSION

Relationships between MR and behaviour were observed for both Atlantic salmon and brown trout. However, these relationships differed between species. Parr of Atlantic salmon seemed to be less adaptable to a new environment as measures of variation in MR and boldness indicated that they were sensitive to stress and became passive when stressed, whereas no correlations between individual behaviour and MR were found for brown trout (paper I). Furthermore, SMR seems to influence the decision to migrate in brown trout since migrants had higher SMR than non-migrants, a difference that was not present in Atlantic salmon (paper IV). These between-species differences are probably an effect of the species' different life histories. Young

individuals of brown trout have the possibility to choose whether they should stay in their natal stream or migrate to the sea or a lake where they may find more food, whereas Atlantic salmon seem to be programmed to migrate (Klemetsen et al. 2003). Therefore, differences in SMR may be more important for the decision to migrate in brown trout than Atlantic salmon. Furthermore, the plastic brown trout may find it easier to adapt to a new situation than the more rigid Atlantic salmon.

There was also a difference between species in the time it took before a dominance relationship had been established (paper I). This probably reflects that brown trout are more aggressive than Atlantic salmon (paper I; Harwood et al. 2002) and that the high level of aggression forced one of the individuals in a pair to give up rapidly and thereby reduce the risk of injury. When two individuals of either young-of-the-year Atlantic salmon or brown trout form a dominance relationship, the individual with the highest SMR is most likely to win an aggressive encounter (paper I; Metcalfe et al. 1995). Furthermore, the probability of becoming dominant is higher for the larger individual in a pair (paper I; paper II) and increases with increasing size difference (paper II; Gowan & Fausch 2002). However, if an individual already has established a territory, the competing conspecific is less likely to out-compete the territory holder (paper II) unless the size difference is large (Johnsson et al. 1999). It is possible that prior residence (paper II; Metcalfe et al. 2003; Rhodes & Quinn 1998; Johnsson et al. 1999) and the size difference between individuals may interact (paper II) and reduce or eliminate the difference in SMR for dominants and subordinates, but this requires further study.

For salmon the MR measured during the first hour was higher for dominants than for subordinates, and the dominant salmon were more aggressive than their subordinate counterparts in the aggression test (paper I). This is consistent with an earlier study of sticklebacks, where individuals that had higher VR during the first minute in confinement were also more aggressive towards conspecifics (Bell et al. 2010). However, no such relationships were found for brown trout (paper I).

Interestingly, for some pairs of brown trout, dominance was established without fighting (paper II): These pairs were less active and ate less, both in isolation and when together, than trout in aggressive pairs. Since low ranked individuals are more inactive and less aggressive than their higher ranked counterparts (Mendl et al. 1992), one possibility could therefore be that the non-aggressive trout were from the lower end of the dominance hierarchy spectrum in the population. Another possibility is that the difference in

dominance rank between the two fish was large (Nakano 1994), resulting in a quick resolution of the territorial conflict with no aggression (Jaeger et al. 1983). In paper II one third of the pairs that decided their dominance relationship did so without fighting, whereas in paper I and paper III trout in all pairs fought to some degree. Furthermore, subordinates spent a larger proportion of time in the upper part of the water column in paper III than in paper II. This position is occupied by individuals that want to avoid attracting the attention of a dominant conspecific (Winberg et al. 1992; Yamamoto & Reinhardt 2003) and the low proportion of time spent by subordinate trout in the upper part of the water column in paper II may indicate that they were less stressed by the dominant conspecific than the subordinates in paper III. The trout used in paper II were smaller than the trout in paper I and paper III. One explanation to the different proportion of non-aggressive pairs in paper II compared to paper I and paper III could therefore be that small trout are less aggressive toward conspecifics than large trout. Another possibility is that the relatively larger size of the compartments in paper II compared to paper I and paper III made it easier for a dominant individual to accept a subordinate conspecific without physically attacking it.

To fight is energy consuming, where the increase in relative VR is positively correlated with fighting intensity (paper II). After a fight the effect of dominance status on the relative VR was context-dependent, influenced by fish size (paper II; paper III), temperature and water velocity (paper III). As small fish actively swim more than large fish, (Grøttum & Sigholt 1998, Petrie & Ryer 2006; paper II, paper III), the high activity level of dominant trout may have masked any effects of stress experienced by the subordinates during the first day of the interaction period, thereby resulting in no difference in VR between dominants and subordinates in paper II (Abbott & Dill 1989; Eisermann 1992; Sloman et al. 2000b; Millidine et al. 2009), whereas subordinate trout in paper III had higher relative VR than dominant individuals due to a higher stress level. When the dominance relationship had been established the relative VR for dominants was higher than for subordinates in paper II, whereas the opposite was the case in paper III. The trout in paper II had a different activity level when the dominance relationship had been established than when alone, something that was not seen in paper III. Therefore the higher relative VR for dominant than subordinate trout in paper II corresponds to a higher activity level in dominants than subordinates, whereas the effect of dominance on the second day of the interaction period in paper III probably was an effect of the stress induced in subordinate trout (Abbott & Dill 1989; Millidine et al. 2009).

The effect of dominance on relative VR the first day of the interaction period in paper III was present in all treatments except at 10°C in fast flowing water. This lack of an effect was reflected by the low proportion of time that subordinates spent in the upper part of the water column at 10°C in fast-flowing water, which may indicate that the dominant trout were more tolerant of their conspecifics. Thus, a combination of cold temperatures and fast currents may not make it worthwhile for the dominant fish to restrict the subordinate fish to the upper part of the water column, since high swimming costs associated with high water velocities reduce the distance travelled to capture a prey (Godin & Rangeley 1989), resulting in small territories (Kemp et al. 2006). Furthermore, speed and stamina decrease with decreasing temperature (Chen X.-J. et al. 2003), which makes it more costly for ectotherms to move, further restricting the space occupied by an individual. As temperature, and thereby MR, decreases (Elliott & Hurley 1999) the dominant trout should also be less inclined to defend a feeding territory. Dominants had a higher food intake than subordinates at 13°C (paper II) and at 16°C (paper III), whereas there was no consistent difference between dominant and subordinate fish at 10°C (paper III). These results indicate that the advantage of being dominant differs depending on the environmental conditions and the size of the competing individuals. Furthermore, food availability in a stream is expected to affect a parr's growth rate and thereby its migratory behaviour.

The availability of food could be used in hatcheries to increase the migratory success of hatchery-raised smolts. A reduced food ration increased the migratory speed for both Atlantic salmon and brown trout (paper IV), confirming an earlier study on steelhead smolts (Tipping & Byrne 1996). In salmon the number of successful migrants was higher for the group fed a reduced than a normal ration during the second but not first year (paper IV). This probably reflects the importance of release time on the migratory success of smolts. Smolts released late migrated faster than those released early in 2006, probably because the smolts released early were not fully developed as smolts. Smolt development was important for the difference in the proportion of successful migrants, where the more developed smolts in the group fed a reduced ration in 2007 had a larger proportion of successful migrants than smolts in the group fed a normal ration. For salmon in 2006 and for trout, there was no difference in smolt development, nor was there any difference in the proportion of successful migrants.

The study in paper IV indicates that even if the migratory behaviour of a smolt is influenced by its SMR, it is possible to change this behaviour by giving

the hatchery-raised Atlantic salmon and brown trout less food. Furthermore, it has previously been found that fish that have experienced a lack of food are more active than individuals that have been fed to satiation (Petrie & Ryer 2006). The fish used in all four papers in this dissertation were hatchery-raised individuals that had been fed a high ration during their entire lives. It is possible that the results would have been different if wild individuals had been used. Furthermore the predator-free environment in a hatchery, with its lack of natural selection, may have resulted in individuals of Atlantic salmon and brown trout showing other behaviours than wild fish. A number of studies have suggested that correlations between behaviours have evolved in environments with high predation pressure (Bell & Stamps 2004; Bell 2005; Brydges et al. 2008). Further studies are needed to examine the relationship between MR and behaviour of wild fish.

ACKNOWLEDGEMENT

To begin with I would like to thank my supervisors, Larry Greenberg and Eva Bergman, for guiding me during the creation of this thesis, and all colleagues at the Department of Biology at Karlstad University for valuable discussions about the studies included in this thesis. A special thanks goes to Björn Arvidsson for help with the statistical calculations.

When tracking the smolts in Klarälven, it was necessary to work long days, often late at night and sometimes even without taking a break to sleep. Anders Glad worked hard during the whole field season and made it possible to follow the smolts out to Lake Vänern. Also Jonas Andersson, Jonas Bergqvist and Pär Gustafsson were of valuable help during the field work, and Johanna Bengtson worked hard during the laboratory experiment in paper I.

The help in tracking smolts in Lake Vänern by Joakim Eriksson at Sportfiskeakademin was invaluable, and I thank the staff at Forshaga fiscecamp for letting us use their boat and marina. The staff at Brattfors and Gammelkroppa fish-farms took care of the fish during the feeding experiments and kindly provided us with fish for the laboratory experiments. I also thank the County Administration Board in Värmland for financial support.

Jörgen Johnsson, University of Gothenburg and two anonymous referees have given valuable comments on earlier drafts of paper IV.

During the spring of 2010 I had the possibility to visit the University of Glasgow and perform a laboratory study. I am grateful to Neil Metcalfe, who made this possible, and to the Department of Biology at Karlstad University for financially support the trip and my stay in Glasgow. Mike Miles and the team at Marine Scotland's Almondbank Hatchery provided the fish used in that experiment and Graham Law, John Laurie and Graham Adam helped to maintain them in Glasgow. Thank you for a good job.

The most important individuals, without whose participation this thesis would not have been possible, are all the brown trout and Atlantic salmon who, without complaining, took part in the investigations.

Last, but not least, I would like to give my heartfelt appreciation to the great man who invited me to the field of science. Already as young I learned to “never guess (Sign)”, but to “observe and to draw inferences from [the] observations (Stud)”. During the investigations for this PhD-thesis “the scientific use of imagination (Houn; Tyndall 2008)” had to be applied when planning and when interpreting the results of the studies. When there were never any “trout in the milk (Nobl; Thoreau)” I remembered that “there is

nothing more deceptive than an obvious fact (Bosc)” and I tried to convince myself that “there is nothing more stimulating than a case where everything goes against you (Houn)”. The words “You can, for example, never foretell what any one man will do, but you can say with precision what an average number will be up to. Individuals vary, but percentages remain constant (Sign; Reade 2003)” was a good guide when the results were summarized and the statistical calculations done. Unfortunately, I never managed to compete with his working hours when he “never worked less than fifteen hours a day and had more than once [...] kept to his task for five days at a stretch (Reig)”. Therefore there is still lot of work to do before the mystery concerning the migratory behaviour of brown trout smolts is solved. However, a work of science can never be finished. There is always something new to learn; “education never ends (RedC)”.

Karlstad, January 2012

Linnea Lans

REFERENCES

- Aarestrup, K; Jepsen, N; Koed, A. & Pedersen, S. 2005. Movement and mortality of stocked brown trout in a stream. *Journal of Fish Biology* 66:721-728.
- Abbott, J.C. & Dill, L.M. 1989. The relative growth of dominant and subordinate juvenile steelhead trout (*Salmo gairdneri*) fed equal rations. *Behaviour* 108:104-113.
- Bell, A.M. 2005. Behavioural differences between individuals and two populations of stickleback (*Gasterosteus aculeatus*). *Journal of Evolutionary Biology* 18:464-473.
- Bell, A.M. & Stamps, J.A. 2004. Development of behavioural differences between individuals and populations of sticklebacks, *Gasterosteus aculeatus*. *Animal Behaviour* 68:1339-1348.
- Bell, A.M., Henderson, L. & Huntingford, F.A. 2010. Behavioral and respiratory responses to stressors in multiple populations of three-spined sticklebacks that differ in predation pressure. *Journal of comparative physiology, B*, 180, 211-220.
- Bohlin, T; Pettersson, J. & Degerman, E. 2001. Population density of migratory and resident brown trout (*Salmo trutta*) in relation to altitude: evidence for a migration cost. *Journal of Animal Ecology* 70:112-121.
- Brown, C. & Laland, K. 2001. Social learning and life skills training for hatchery reared fish. *Journal of Fish Biology* 59:471-493.
- Bryant, M.J. & Grant, J.W.A. 1995. Resource defence, monopolization and variation of fitness in groups of female Japanese medaka depend on the synchrony of food arrival. *Animal Behaviour* 49:1469-1479.
- Brydges, N.M; Colegrave, N; Heathcote, R.J.P. & Braithwaite, V.A. 2008. Habitat stability and predation pressure affect temperament behaviours in populations of three-spined sticklebacks. *Journal of Animal Ecology* 77:229-235.
- Burton, T., Killen, S.S., Armstrong, J.D. & Metcalfe, N.B. 2011. What causes intraspecific variation in resting metabolic rate and what are its ecological consequences? *Proceedings of the Royal Society B-Biological Sciences* 278:3465-3473.
- Careau, V; Thomas, D; Humphries, M. & Réale, D. 2008. Energy metabolism and animal personality. *Oikos* 117:641-653.
- Chen, X.-J., Xu, X.-F. & Ji, X. 2003. Influence of body temperature on food assimilation and locomotor performance in white-striped grass lizards, *Takydromus wolteri* (Lacertidae). *Journal of Thermal Biology* 28:385-391.

- Clark, T.D. & Seymour, R.S. 2006. Cardiorespiratory physiology and swimming energetics of a high-energy-demand teleost, the yellowtail kingfish (*Seriola lalandi*). *The Journal of Experimental Biology* 209:3940-3951.
- Cutts, C.J., Metcalfe, N.B. & Taylor, A.C. 1998. Aggression and growth depression in juvenile Atlantic salmon: the consequences of individual variation in standard metabolic rate. *Journal of Fish Biology*, 52, 1026-1037.
- Doyle, A.C. 1989. *Sherlock Holmes: The complete illustrated short stories*. Chancellor Press, London.
- Doyle, A.C. 1992. *Sherlock Holmes: The complete illustrated novels*. Chancellor Press, London.
- Eisermann, K. 1992. Long-term heartrate responses to social stress in wild European rabbits: predominant effect of rank position. *Physiology & Behavior* 52:33-36.
- Elliott, J.M. & Hurley, M.A. 1999. A new energetics model for brown trout, *Salmo trutta*. *Freshwater Biology* 42:235-246.
- Enders, E.C., Boisclair, D. & Roy, A.G. 2005. A model of total swimming costs in turbulent flow for juvenile Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* 62:1079-1089.
- Eriksson, L-O; Rivinoja, P; Östergren, J; Serrano, I. & Larsson, S. 2008. Smolt quality and survival of compensatory stocked Atlantic salmon and brown trout in the Baltic sea. Report 62. Department of Wildlife, Fish, and Environmental studies, Umeå.
- Fausch, K.D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. *Canadian Journal of Zoology* 62:441-451.
- Fiskeriverket. 1998. Lax och öringfisket i Vänern. Fiskeriverket Information 8 (In Swedish).
- Forseth, T; Næsje, T.F; Jonsson, B. & Hårsaker, K. 1999. Juvenile migration in brown trout: a consequence of energetic state. *Journal of Animal Ecology* 68: 783-793.
- Godin, J-G. J. & Rangeley, R.W. 1989. Living in the fast lane: effects of cost of locomotion on foraging behaviour in juvenile Atlantic salmon. *Animal Behaviour* 37:943-954.
- Gowan, C. & Fausch, K.D. 2002. Why do foraging stream salmonids move during summer? *Environmental Biology of Fishes* 64:139-153.
- Grøttum & Sigholt 1998. A model for oxygen consumption of Atlantic salmon (*Salmo salar*) based on measurements of individual fish in a tunnel respirometer. *Aquacultural Engineering* 17:241-251.

- Hahn, S. & Bauer, S. 2008. Dominance in feeding territories relates to foraging success and offspring growth in brown skuas *Catharacta antarctica lonnbergi*. *Behavioural Ecology and Sociobiology* 62:1149-1157.
- Harwood, A.J; Armstrong, J.D; Griffiths, S.W. & Metcalfe, N.B. 2002. Sympatric association influences within-species dominance relations among juvenile Atlantic salmon and brown trout. *Animal Behaviour* 64:85-95.
- Hasegawa, H. & Yamamoto, S. 2009. Effects of competitor density and physical habitat structure on the competitive intensity of territorial white spotted charr *Salvelinus leucomaenis*. *Journal of Fish Biology* 74:213-219.
- Huntingford, F.A., Andrew, G., MacKenzie, S., Morera, D., Coyle, S.M., Pilarczyk, M. & Kadri, S. 2010. Coping strategies in a strongly schooling fish, the common carp *Cyprinus carpio*. *Journal of Fish Biology* 76:1576-1591.
- Höjesjö, J; Johnsson, J.I. & Bohlin, T. 2002. Can laboratory studies on dominance predict fitness of young brown trout in the wild? *Behavioral ecology and sociobiology* 52:102-108.
- Jaeger, R.G., Nishikawa, K.C.B. & Barnard, D.E. 1983. Foraging tactics of a terrestrial salamander: costs of territorial defence. *Animal Behaviour* 31:191-198.
- Johnsson, J.I., Nobbelin, F. & Bohlin, T. 1999. Territorial competition among wild brown trout fry: effects of ownership and body size. *Journal of Fish Biology* 54(2):469-472.
- Jonsson, B. & Jonsson, N. 2010. *Ecology of Atlantic salmon and brown trout: Habitat as template for life histories*. Springer, Dordrecht.
- Kallio-Nyberg, I., Saloniemi, I., Jutila, E. & Saura, A. 2007. Effects of marine conditions, fishing, and smolt traits on the survival of tagged, hatchery-reared sea trout (*Salmo trutta trutta*) in the Baltic sea. *Canadian Journal of Fisheries and Aquatic Sciences* 64: 1183-1198.
- Kemp, P.S., Gilvear, D.J. & Armstrong, J.D. 2006. Variation in performance reveals discharge-related energy costs for foraging Atlantic salmon (*Salmo salar*). *Ecology of Freshwater Fish* 15:565-571.
- Klemetsen, A; Amundsen, P-A; Dempson, J.B; Jonsson, B; Jonsson, N; O'Connell, M.F. & Mortensen, E. 2003. Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. *Ecology of Freshwater Fish* 12:1-59.
- Lahti, K., Huuskonen, H., Laurila, A. & Piironen, J. 2002. Metabolic rate and aggressiveness between brown trout populations. *Functional Ecology* 16:167-174.
- McCarthy, I.D. 2001. Competitive ability is related to metabolic asymmetry in juvenile rainbow trout. *Journal of Fish Biology* 59:1002-1014.

- McKinnell, S.M. & Karlström, Ö. 1999. Spatial and temporal covariation in the recruitment and abundance of Atlantic salmon populations in the Baltic sea. *ICES Journal of Marine Science* 56:433-443.
- Mendl, M., Zanella, A.J. & Broom, D.M. 1992. Physiological and reproductive correlates of behavioural strategies in female domestic pigs. *Animal Behaviour* 44:1107-1121.
- 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.
- Metcalfe, N.B; Valdimarsson, S.K. & Morgan, I.J. 2003. The relative roles of domestication, rearing environment, prior residence and body size in deciding territorial contests between hatchery and wild juvenile salmon. *Journal of Applied Ecology* 40:535-544.
- Millidine, K.J., Armstrong, J.D. & Metcalfe, N.B. 2009. Juvenile salmon with high standard metabolic rates have higher energy costs but can process meals faster. *Proceedings of the royal society B* 276:2103-2108.
- Morinville, G.R. & Rasmussen, J.B. 2003. Early juvenile bioenergetic differences between anadromous and resident brook trout (*Salvelinus fontinalis*). *Canadian Journal of Fisheries and Aquatic Sciences* 60: 401-410.
- Nakano, S. 1994. Variation in agonistic encounters in a dominance hierarchy of freely interacting red-spotted masu salmon (*Oncorhynchus masou isibikawai*). *Ecology of Freshwater Fish* 3:153-158.
- Neat, F.C; Taylor, A.C. & Huntingford, F.A. 1998. Proximate costs of fighting in male cichlid fish: the role of injuries and energy metabolism. *Animal Behaviour* 55:875-882.
- Nordeng, H. 1983. Solution to the “char problem” based on Arctic char (*Salvelinus alpinus*) in Norway. *Canadian Journal of Fisheries and Aquatic Sciences* 40:1372-1387.
- Näslund, I. 1990. The development of regular seasonal habitat shifts in a landlocked Arctic charr, *Salvelinus alpinus* L., population. *Journal of Fish Biology* 36:401-414.
- O'Connor, K.I; Metcalfe, N.B. & Taylor, A.C. 1999. Does darkening signal submission in territorial contests between juvenile Atlantic salmon, *Salmo salar*? *Animal Behaviour* 58:1269-1276.
- Peters, G; Faisal, M; Lang, T. & Ahmed, I. 1988. Stress caused by social interaction and its effect on susceptibility to *Aeromonas hydrophila* infection in rainbow trout *Salmo gairdneri*. *Diseases and Aquatic Organisms* 4:83-89.
- Petrie, M.E. & Ryer, C.H. 2006. Hunger, light level and body size affect refuge use by post-settlement lingcod *Ophiodon elongatus*. *Journal of Fish Biology* 69:957-969.

- Reade, W. 2003. *The martyrdom of man*. Kessinger Publishing, Whitefish.
- Ricker, W.E. 1979. Growth rates and models. In: Hoar, W.S; Randall, D.J. & Brett, J.R. (eds.) *Fish physiology*. Academic Press, New York, pp. 677-743.
- Rhodes, J.S. & Quinn, T.P. 1998. Factors affecting the outcome of territorial contests between hatchery and naturally reared coho salmon parr in the laboratory. *Journal of Fish Biology* 53:1220-1230.
- Salminen, M; Alapassi, T. & Ikonen, E. 2007. The importance of stocking age in the enhancement of River Kymijoki salmon (*Salmo salar*). *Journal of applied ichthyology* 23:46-52.
- Serrano, I., Larsson, S. & Eriksson, L.-O. 2009. Migration performance of wild and hatchery sea trout (*Salmo trutta* L.) smolts - implications for compensatory hatchery programs. *Fisheries Research* 99: 210-215.
- Sers, B., Degerman, E. & Nyberg, P. 2007. Utvärdering av märkningar av Gullspångslax i Vättern. Fiskeriverket PM 2007-01-02 (In Swedish).
- Sloman, K.A; Gilmour, K.M; Taylor, A.C. & Metcalfe, N.B. 2000a. Physiological effects of dominance hierarchies within groups of brown trout, *Salmo trutta*, held under simulated natural conditions. *Fish Physiology and Biochemistry* 22:11-20.
- Sloman, K.A; Motherwell, G; O'Connor, K.I. & Taylor, A.C. 2000b. The effect of social stress on the standard metabolic rate (SMR) of brown trout, *Salmo trutta*. *Fish Physiology and Biochemistry* 23:49-53.
- Solomon, D.J. 2007. Migration as a life-history strategy for the sea trout. In: Harris, G. & Milner, N. (ed.) *Sea-trout – Biology, conservation and management*. Blackwell Publishing, Oxford.
- Staurnes, M; Lysfjord, G; Hansen, L.P. & Heggberget, T.G. 1993. Recapture rates of hatchery-reared Atlantic salmon (*Salmo salar*) related to smolt development and time of release. *Aquaculture* 118:327-337.
- Suter, H.C. & Huntingford, F.A. 2002. Eye colour in juvenile Atlantic salmon: effects of social status, aggression and foraging success. *Journal of Fish Biology* 61:606-614.
- Tanguy, J.M; Ombredane, D; Baglinière, J.L. & Prunet, P. 1994. Aspects of parr-smolt transformation in anadromous and resident forms of brown trout (*Salmo trutta*) in comparison with Atlantic salmon (*Salmo salar*). *Aquaculture* 121:51-63.
- Terrill, S.B. & Able, K.P. 1988. Bird migration terminology. *Auk* 105(1):205-206.
- Tipping, J.M; Cooper, R.V; Byrne, J.B. & Johnson, T.H. 1995. Length and condition factor of migrating and nonmigrating hatchery-reared winter steelhead smolts. *The Progressive Fish-Culturist* 57:120-123.

- Tipping, J.M. & Byrne, J.B. 1996. Reducing feed levels during the last month of rearing enhances emigration rates of hatchery-reared steelhead smolts. *The Progressive Fish-Culturist* 58:128-130.
- Tyndall, J. 2008. *Scientific use of imagination and other essays*. Kessinger Publishing, Whitefish.
- Winberg, S., Nilsson, G. E. & Olsén, H. 1992. Changes in brain serotonergic activity during hierarchic behavior in Arctic charr (*Salvelinus alpinus* L.) are socially induced. *Journal of Comparative Physiology A*, 170, 93-99.
- Wysujack, K; Greenberg, LA; Bergman, E. & Olsson, IC. 2009. The role of the environment in partial migration: food availability affects the adoption of a migratory tactic in brown trout *Salmo trutta*. *Ecology of Freshwater Fish* 18(1):52-59.
- Yamamoto, T. & Reinhardt, U.G. 2003. Dominance and predator avoidance in domesticated and wild masu salmon *Oncorhynchus masou*. *Fisberies science* 69:88-94.
- 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.
- Økland, F., Jonsson, B., Jensen, A.J. & Hansen, L.P. 1993. Is there a threshold size regulating seaward migration in brown trout and Atlantic salmon? *Journal of Fish Biology* 42:541-550.
- Øverli, Ø; Sørensen, C. & Nilsson, G.E. 2006. Behavioral indicators of stress-coping style in rainbow trout: Do males and females react differently to novelty? *Physiology & Behavior* 87:506-512.



Behaviour and metabolic rates of brown trout and Atlantic salmon

For Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*), the decision to migrate or when to migrate is believed to be influenced by the individual's metabolic rate (MR) relative its food intake. As MR was expected to be related to behaviour, the potential links between behaviour and metabolic costs was studied. For both salmon and trout the dominant individual had a higher standard metabolic rate (SMR) than its subordinate counterpart. Also, successful migrants of brown trout had a higher SMR than unsuccessful migrants, whereas no such difference was found for obligate migratory Atlantic salmon. Measures of variation in MR and boldness indicated that Atlantic salmon was more sensitive to stress than brown trout and became passive when stressed. When two trout were interacting, an increase in ventilation rate (VR) was positively correlated to fighting intensity. The first day after an interaction, VR did not differ between small dominant and subordinate trout (mean size 3.7g), whereas for large trout (26.0g) subordinates had higher VR than dominants. However, a combination of low temperature (10°C) and high water velocity (22cm/s) eliminated this difference. This probably reflects the high swimming activity of small dominants and the low motivation for dominants to defend a large territory when temperatures were low and the cost of moving was high. These results show that the relationship between MR and behaviour may differ depending on species, fish size and environmental factors.

ISBN 978-91-7063-408-6

ISSN 1403-8099

DISSERTATION | Karlstad University Studies | 2012:4