Food Competition and its Relation to Aquaculture in Juvenile *Perca fluviatilis*

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Abstract

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In this thesis, explanations for, and predictors of, the large growth heterogeneity, in juvenile perch in aquaculture and natural environments, were studied. A large variation between individuals in competitive ability, estimated as feeding success or growth, was found. Relative feeding success (in aquaria) and growth rates (in tanks) of individuals were consistent over time within environments but not positively correlated between them. It was indicated that individual feeding success was negatively correlated between environments. Individuals may be differently prone to be successful in specific environments due to variations in innate characteristics, but this has not been tested. Predation risk decreased boldness (risk proneness) but did not affect food intake at the individual level. Better competitors were also bolder. Feeding success was positively correlated to growth rate within aquaria, but not between environments (aquaria vs. tanks). Group composition affected individual boldness but not food intake. Strong social hierarchies were not found, but aggressive behaviour was observed in one study. Thus, a large variation in boldness and competitive ability was found, and this variation may be of importance for the large variation in growth. There was a seasonal variation in growth. This knowledge is important for optimising feed management, thereby maximising growth and economics and minimising environmental impact of future perch farms. The consistency in the differences in individual growth rate indicates that perch have a large potential for successful breeding programs. Boldness and competitive success in aquaria experiments can not be used as indicators of individual growth potential. High light intensities were found to stress the perch, indicated by an increased swimming activity. Tank wall colour did not seem to affect behaviour or growth, and no colour was selected over others.

Keywords: Eurasian perch, competition, shyness, social learning, preference, selection, swimming activity

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Till Karin, Emil och Hilding.

Contents

Appendix

Papers I - VI

The present thesis is based on the following papers, which will be referred to by their roman numerals:

I. Staffan, F., Magnhagen, C. & Alanärä, A. 2002. Variation in food intake within groups of juvenile perch. *Journal of Fish Biology*, 60, 771-774.

II. Westerberg, M., Staffan, F. & Magnhagen, C. 2004. Influence of predation risk on individual competitive ability and growth in Eurasian perch, *Perca fluviatilis*. *Animal Behaviour*, 67, 273-279.

III. Magnhagen, C. & Staffan, F. Is boldness affected by group composition in young-of-the-year perch (*Perca fluviatilis*)? *Behavioural Ecology and Sociobiology*, in press.

IV. Staffan, F., Magnhagen, C. & Alanärä, A. Individual feeding success of juvenile Eurasian perch is consistent over time in aquaria and under farming conditions. *Submitted*.

V. Magnhagen, C. & Staffan, F. 2003. Social learning in young-of-the-year perch encountering a novel food type. *Journal of Fish Biology*, 63, 824-829.

VI. Staffan, F., Strand, Å. & Alanärä, A. Self selection of tank colour at different light intensities by juvenile *Perca fluviatilis*. *Manuscript*.

Introduction

As a result of intensive fishing, the catches of the fisheries industry have decreased dramatically world wide over the last decades, and some species may have been driven to the verge of extinction (Myers & Worm, 2003). To compensate for the losses in catches from our oceans, and to meet the increasing need for food by the growing world population, the importance of aquaculture is increasing. Actually, aquaculture is the most rapidly increasing food industry in the world (http:// www.omvarldsbilder.se/2000/001109.htmlTTT; 6-Sept-2004). Today, the Swedish aquaculture production is dominated by rainbow trout *Oncorhynchus mykiss* (Walbaum) and Arctic charr *Salvelinus alpinus* (L.). New species are considered for aquaculture in Sweden and among them is Eurasian perch *Perca fluviatilis* L.

There are several factors that determine whether a fish species is suitable for aquaculture or not. For a species to be economically profitable for intensive farming it must be requested by the consumer, grow relatively fast and heterogeneously, reach market size before maturation, have a high survival rate, be easily bred under captive conditions, accept formulated feed as first feed, or soon after first feeding, and not have unwanted social interactions leading to, for example, cannibalism or strong dominance hierarchies (Pillay, 1990). Research on the domestication of perch has been conducted for about 10 years, mainly in Belgium and France (e.g. Mélard *et al*., 1995, 1996 a, 1996 b; Kestemont *et al*., 1996; Fontaine *et al*., 1997; Jourdan *et al*., 2000; Baras *et al*., 2003; Kestemont *et al*., 2003; Mandiki *et al*., 2004). From these, and other, studies, a number of issues have emerged, that need to be solved for successful farming of perch. Among them are optimising feed composition (Mélard *et al*., 1996 a), lowering levels of cannibalism at young stages (Mélard *et al*., 1996 b) and decreasing growth heterogeneity (Mélard *et al*., 1995). This thesis will focus on inter-individual variation in feeding behaviour of juvenile perch to try to understand why there is large growth heterogeneity in perch and to possibly give some suggestions for how it can be reduced.

Competition

An important key to understand the feeding behaviour of a specific fish species is knowledge on how individuals compete with each other for a common resource. Intraspecific competition in fish ranges from exploitative competition, where individuals interact indirectly by lowering the level of the resource, to interference competition, where one or a few individuals actively prevent others from utilising the resource (Wootton, 1998). One form of interference competition occurs in social hierarchies, where individuals decrease the potential fitness of conspecifics by defending and monopolizing feeding or breeding sites. Individuals within social hierarchies possess different competitive abilities and the most aggressive ones are often more successful in exploiting a shared resource (Metcalfe, 1986;

Alanärä *et al*., 2001). In Arctic charr and rainbow trout, held under an aquaculture husbandry routine, individuals of high status have been found to suppress the growth of low status individuals (Alanärä & Brännäs, 1996, Alanärä *et al*., 2001). Other negative effects of aggressive behaviour on salmonids in aquaculture are fin damage (Moutou *et al*., 1998) and stress (reviewed in Brännäs *et al*., 2001). It is therefore important to know whether a species, that is intended for farming, displays aggressive behaviour and social hierarchies. Furthermore, in Atlantic salmon *Salmo salar* L., competitive success in aquarium experiments was found to be correlated with growth under an aquaculture husbandry routine (Metcalfe *et al*., 1989, 1990; Metcalfe, 1991). Possibly, a variation in competitive success could explain the large variation in growth also of perch in farming environments (Mélard *et al*., 1995, 1996 a). In perch, social interactions and competitive success during feeding have hitherto not been studied to a large extent on the individual level. It is important to study variation in individual competitive success and possible occurrence of aggression in juvenile perch in order to be able to minimise inter-individual variation in growth by designing suitable farming environments and routines.

Shyness/boldness

Fish behaviour is often considered to be general for individuals of the same species, but it has been found that individuals of similar age and size can respond in different ways to a specific situation. For example, the ability to learn new tasks has been found to vary between individuals of the same species and of similar size (Wilson *et al*., 1993; Sneddon, 2003). Also, the propensity to take risks differs between individuals. In a number of species of fish, such variation has been ascribed to innate variations in behaviour and has been referred to as the shy-bold continuum (Huntingford, 1976; Wilson *et al*., 1993; Sneddon, 2003; Sundström *et al*., 2004; Ward *et al*., 2004). Boldness has been found to be positively connected to dominance in brown trout *Salmo trutta* L. (Sundström *et al*., 2004) and it has been suggested, for a number of taxa, that a high stress tolerance makes an animal more risk prone, or "bold" (Koolhaas *et al*., 1999). The aquaculture environment can be very stressful for the fish, since factors such as density, light intensity, sound level and frequency of vibrations in the water are very different from those in their natural environment. For example, vibrations in the water, which is a way for prey fish to locate threats from predators (Hawkins, 1993), are occurring on a daily basis in fish farms, caused by splashes at the surface or by vibrations from slamming doors or steps. In a study at a Norwegian fish farm, fish were found to increase their oxygen consumption, which is a stress response, when a person walked by the tanks (Gjedrem, 1993). Even so, in Atlantic salmon cultured strains can have growth rates more than twice as fast as those of wild strains (Thodesen *et al*., 1999). It is possible that this increase in growth rate in farmed Atlantic salmon is partly due to that less stress sensitive, and thus probably bolder, fish have automatically been selected in breeding programs. In accordance, a number of studies are consistently showing that domestication selection reduces anti-predator responses (reviewed by Einum & Fleming, 2001). Similarly, there may be a correlation between boldness and growth rate in a farming environment in perch, which then could be used in future breeding programs.

Objectives and aims

The objective of this thesis was to find explanations for, and predictors of, the large variation in growth that has been found in juvenile perch of the same age in farming environments (Mélard *et al.*, 1995, 1996 a). Understanding the mechanisms behind the large growth heterogeneity is of importance to enable a reduction of the variation in growth that occurs in aquaculture of perch. General scientific studies on individual behaviour were performed to find the mechanisms behind the large growth heterogeneity (I - III). These studies are of importance also for understanding the role of individual behaviour in an ecological context. For example, the results from these studies may indicate some of the mechanisms behind the large variation in size of juvenile perch of the same age that is found also in natural environments (Spanovskaya & Grygorash, 1977; Thorpe, 1977; Radke & Eckmann, 1999). In addition, applied studies were performed to try to find ways to reduce the growth heterogeneity of juvenile perch in aquaculture environments and to promote the development of perch farming (IV - VI). In the six articles, I have investigated whether:

- individuals vary in competitive ability, and whether there is occurrence of aggressive behaviour (**I**).
- the differences in growth are connected to differences in competitive ability and if those, in turn, are connected to differences in ”shyness/boldness” (**II**).
- individual ”shyness/boldness” and competitive ability are affected by these behaviours of other group members (**III**).
- the variation in competitive ability is consistent over time within two different environments, and if competitive ability in the two different environments are positively correlated (**IV**).
- the ability of juvenile perch to learn to feed on a novel food type is affected by the presence of demonstrators and by differences in ”shyness/boldness” (**V**).
- juvenile perch prefer certain tank colours when given the choice and whether light intensities and differences in competitive ability affect this choice (**VI**).

Materials and methods

Eurasian perch

Perch is one of the most widely distributed fish species in Sweden (Svärdson, 1976). The perch start their lives as zooplanktivores, become benthivores as they grow larger and, eventually they become piscivores (Persson, 1988). As perch switch feeding behaviour, their social behaviour change accordingly from shoaling as zooplanktivores (Craig, 2000) towards feeding in small groups (Eklöv, 1992) or solitary (Bruylants *et al.*, 1986) as piscivores.

Fish and rearing

Wild caught young-of-the-year perch were used in all studies. They were caught in lakes close to the city of Umeå (63°47’N; 20°17’E) by beach seining or electro fishing. Prior to experiments, the perch were either weaned to formulated feed or fed thawed red chironomid larvae. All experiments were conducted at the Umeå Marine Research Centre. Before and between (IV) aquarium experiments, perch were held in 1 m^3 tanks under aquaculture husbandry routines (constant temperature, fed in excess, high densities).

Experimental procedures

Small groups of individually marked juvenile perch were studied in aquarium experiments (I-VI). Marking techniques used were Alcian blue dye (I-VI), Visible Implant Elastomer (IV) and Passive Integrated Transponders (PIT-tags, VI). Aquaria of either 170 l (I-V) or 660 l (VI) were used. Water was constantly renewed and held at temperatures of approximately 10ºC (I) or 17ºC (II-VI). Food items used were thawed red chironomids (I - IV) and/or formulated feed (IV, V, VI). Feeding with chironomids in aquarium experiments was performed by delivering single food items from the top of the aquaria (I, IV) or by presenting all food items on the bottom of the aquaria (II, III). When food was presented at the bottom of the aquaria, we used the term “prey attacks” instead of “prey consumed” as a quantification of food intake, as it was impossible to see if an attack was successful or not. However, the difference between the number of prey items added and the number of prey attacks (II) was always small. Fish were fed chironomids by hand (I - IV) and formulated feed was fed by hand (VI) and/or by automatic point source feeders (IV, V, VI). We estimated the individual degree of boldness as the proportion of time that an individual spent out in open water as opposed to in plastic vegetation (II, III, IV). By visual observations we recorded the position of each individual once every 60 s (II, III) or 120 s (IV). Competitive ability or feeding success was estimated as individual mean share of the group meal in aquarium experiments and as growth in tanks. Growth was calculated as the Specific Growth Rate, SGR (Ricker, 1979, II, III) or as the Thermal Growth Coefficient, TGC (Iwama & Tautz, 1981, IV- VI).

$$SGR = [(\ln W_2 - \ln W_1)/D]*100,$$

$$TGC = [(W_2^{1/3} - W_1^{1/3})/ (D * T)]*1000,$$

where W_1 is initial weight (g), W_2 is final weight, D is the number of days and T is temperature (ºC). SGR is affected more by fish size than is TGC (Cho 1992), but also, SGR is more widely used whereas TGC, so far, is used mainly in aquacultural studies. Therefore, SGR was used to calculate growth in studies that were of a general scientific character, were of short duration and included fish of similar sizes (II, III). In studies that had clear aquaculture approaches, were run over longer time periods and included fish with relatively large size differences, TGC was used (IV - VI).

Results - Summary of papers

Paper I

Individual food intake varied between 4-68 % of the total number of chironomids fed to the group. We assigned fish within each group a rank number (1-4) based on their relative food intake within their group. Thereafter we sorted fish into new groups where they were placed with fish of their own rank, and the competitive tests were performed again. The CV decreased after sorting individuals into the new groups. The CV of body size within groups was not correlated to the CV of food intake. No aggressive interactions were detected during feeding. Thus, there was a large variation in competitive success between individuals and this variation did not seem to be affected by differences in social status of group members.

Paper II

Individual competitive ability and degree of boldness were estimated in the presence and the absence of a predator (first part). Thereafter a growth study was performed with groups in the presence and absence of a predator (second part). Individual competitive ability, estimated as the proportion of individual prey attacks out of the total number of prey attacks in the group, was consistent over time. The individual number of prey attacks was also correlated between the two treatments, with and without predator (Fig. 1). The relative size was correlated with the number of prey attacks, so that the largest individual within a group made more prey attacks than the smaller, even though size differences within groups were very small (± 1 mm). However, no correlation between absolute body length and the number of prey attacks was found when pooled across tanks. Competitive ability was correlated to the degree of boldness. The presence of a predator increased the differences in boldness between good and poor competitors so that poor competitors (feeding ranks 2-4) decreased their time in the open, whereas good competitors (feeding rank 1) did not change their habitat use compared to in the absence of a predator (Fig. 2). Body length and boldness were negatively correlated, both with and without a predator present. Growth rate was positively correlated with total number of prey attacks during the first part of the study, and in the second part, they tended to be positively correlated in the absence ($p = 0.06$), but not in the presence of a predator. There was no difference in growth of juveniles between the predator treatments. Aggressive acts, in the form of charges towards the other fish, were observed but not quantified. Four of the six individuals that were aggressive also had the highest number of prey attacks in their group. Thus, there were clear differences between individuals in competitive ability and in boldness, and the differences in boldness were increased by the presence of a predator. Growth seemed to be connected to competitive ability but not to risk behaviour. The observed aggressive acts may be connected to the differences in competitive success.

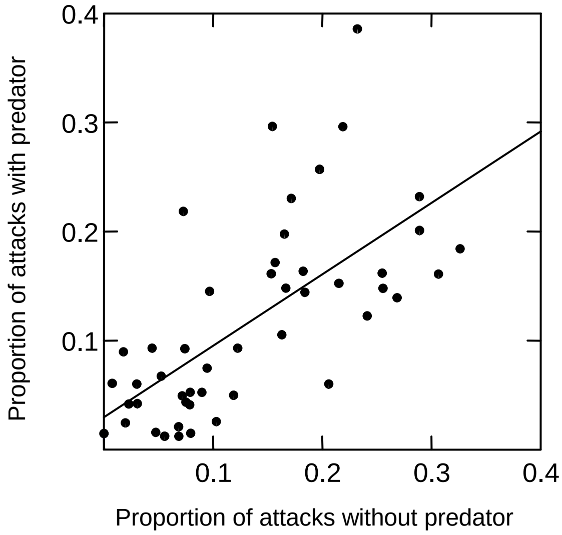

Fig. 1. The relation between the proportion of prey attacks made by the individuals in the presence and the absence of a predator.

Paper III

The number of prey attacks was again positively correlated to the degree of boldness in visual contact with a predator. Perch were categorised into "personality types" (shy, bold and intermediate) according to these differences in habitat utilisation and feeding activity (first part). Thereafter they were sorted into new groups, containing only one personality type and the same experimental procedure was repeated (second part). Shy individuals increased both their time in the open water and the number of prey attacks in the second part, probably due to habituation to the environment and the experimental procedure. Also, the feeding activity of shy individuals in the second part was affected by group composition in the first part, so that individuals with only shy companions in the first part fed more in the second part than did shy fish which had previous experience of bold or intermediate companions. Bold individuals decreased their time in the open in the second compared to the first period whereas there was no change in behaviour after regrouping of intermediate individuals. During the first part, the individual degree of boldness was influenced by the behaviour of the other group members whereas the number of prey attacks was not. Thus, group composition was found to be important for individual degree of shyness/boldness.

Paper IV

Differences in competitive ability (feeding success) were consistent over time in both aquarium experiments and in tanks. No connection between food intake in aquaria and growth in tanks during the following growth period was found in the last two of the three aquarium experiments, whereas in the first, food intake and subsequent growth were negatively correlated. Condition factor right before the

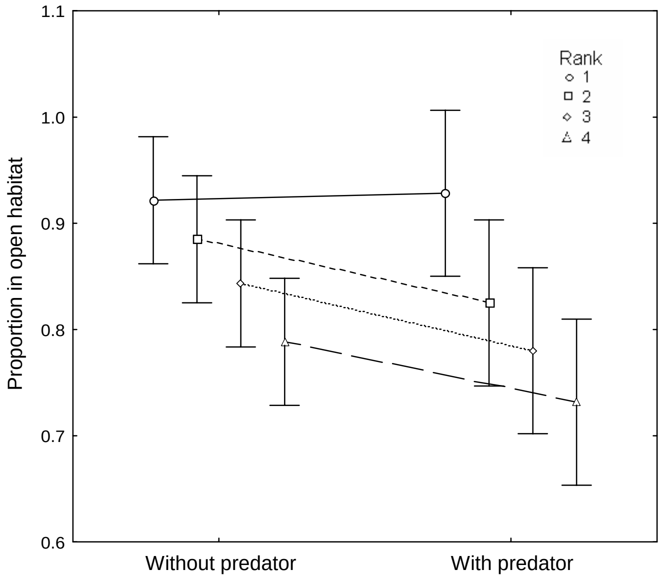

Fig. 2. The proportion of time (X ± 95 % C.I.) that individuals with different feeding ranks spent in the open water in the presence and the absence of a predator.

start of the aquarium experiments and feeding success in aquaria were negatively correlated in the last aquarium experiment and tended to be so also in the middle one (p = 0.07). Boldness in aquaria was negatively correlated to growth in tanks but not connected to the condition factor at the start of the aquarium experiment. Hence, a fish that was successful in one of the environments tended to be less successful in the other. Thus, differences in competitive ability are consistent over time in different environments, but competitive ability is not positively correlated between environments. A seasonal variation in growth, with an increase in April and July was found, despite constant temperature and day length. This growth variation indicates that juvenile perch have an endogenous rhythm that can act without external cues.

Paper V

Groups of young-of-the-year perch, with or without previous experience of the environment, were presented with a novel food type, dry feed, in the presence or absence of experienced demonstrators, which were habituated to the feed. Individuals that were together with experienced demonstrators and had no previous experience of the environment, seemed to learn how to feed on formulated feed faster than individuals that also were inexperienced of the environment but not placed with demonstrators and than fish that had previous experience of the environment and were placed with or without demonstrators. The body mass change was positively correlated to boldness. This indicates that social environment, previous experience and individual characteristics (boldness) affect learning in perch.

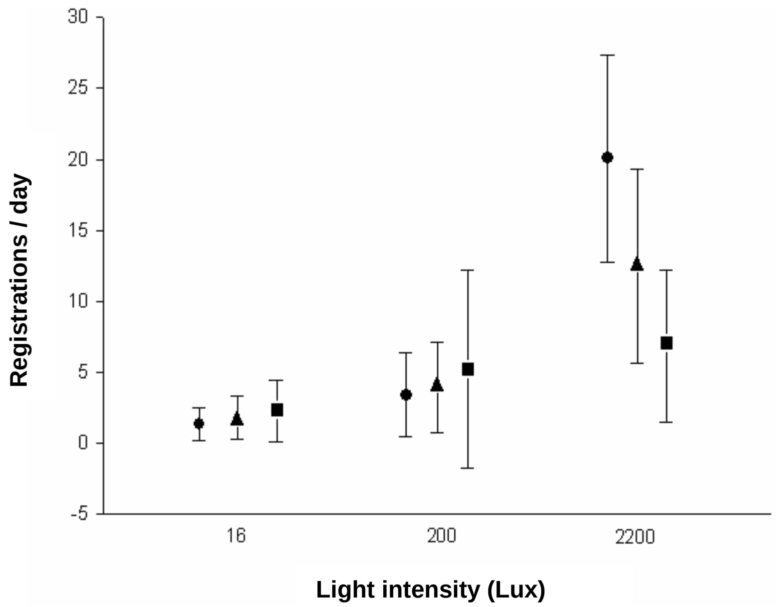

Fig. 3. Means (± S.D.) of the mean per aquarium of number of registrations per individual during daytime (7.00-19.00) per colour combination and light intensity. Circles: grey/white, triangles: black/grey, squares: black/white.

Paper VI

Juvenile perch were tested for preference of three different tank wall colours (white, grey and black), combined pair-wise, in three different light intensities (16, 200 and 2200 lux). A self-selection system was used and individuals were monitored with PIT-tags. The fish had no preference for any of the tank wall colours tested. They were, however, more active (were registered by the antenna between the compartments more often) during daytime (7 am -7 pm) in the highest light intensity than in the two lower (Fig. 3). This indicates increased stress in higher light intensities. Growth did not differ between the three different combinations of tank wall colour. Neither colour preference nor growth differed between individuals of different competitive abilities, which were estimated in a second aquarium experiment. In conclusion, this study indicates that white, grey and black tank wall colour are equally suitable for farming of juvenile perch and that light intensities lower than 2200 lux should be used in aquaculture of perch, due to that this light intensity seemed to stress the fish. Also, the social behaviour of perch does not seem to be an obstacle for perch farming.

Discussion

This thesis aimed to study the mechanisms behind the large size heterogeneity that is often found in perch of the same age, both in aquacultural (Mélard *et al.*, 1995, 1996 a) and natural environments (Spanovskaya & Grygorash, 1977; Thorpe, 1977; Radke & Eckmann, 1999) and to possibly present suggestions to how this variation in growth rate can be reduced in aquacultural environments.

Competitive ability

We found a large variation in competitive ability, measured as individual mean share of group meal in aquaria and as growth in tanks, in all experiments where it was studied (I - IV and VI). This variation was consistent over both short (II) and long (IV) time periods and in both aquaria (II, IV) and tanks (IV). When individual share of group meal and growth was measured in the same environment, positive correlations were found (II), whereas when measured in different environments, no correlation was found (IV, VI). In accordance with these results, the competitive success of individual Arctic charr in aquaria, estimated as relative food intake, relative size and relative aggressiveness, was found to be uncorrelated with their performance under aquacultural conditions, measured as growth, age at maturation and reproductive investment (Adams & Huntingford, 1996). In perch, negative correlations were found between feeding success in aquaria and growth in tanks (in one of the three months where aquarium experiments were performed) and between condition factor and feeding success (in two of the months), respectively (IV). This indicates that individuals that were less successful in tanks, and thereby developed a poor condition, were prone to be more successful in aquarium experiments.

Furthermore, in this thesis, the results on the effect of the relative body size (within groups) on the relative competitive success were not uniform. In one of the studies no connection was found (I). In another, absolute body length was not correlated to competitive success (II). The fact that only a restricted amount of food was offered to each of the groups, and that there was a slight size difference between groups, explains the lack or correlation between absolute body size and competitive success (II). In the same study, relative size was of importance for the relative competitive success within groups, with the largest individual being more successful than the smallest (II). Larger perch are more efficient foragers than smaller ones, because of increased searching ability and handling efficiency with increasing size (Byström & Garcia-Berthou, 1999). Due to very small size differences in our study, this explanation seems less likely. Instead the larger size of the most successful individuals may be a consequence rather than a cause of them being better competitors as has been found in Atlantic salmon parr (Huntingford *et al*., 1990). Possibly, a combination of, for example, behavioural (shyness/boldness; Wilson *et al*., 1993; Sneddon, 2003), physiological (standard metabolic rate or stress tolerance; Metcalfe *et al*., 1995; Koolhaas *et al*., 1999; Pottinger & Carrick, 2001; Øverli *et al*., 2002) and morphological (body shape; Schluter, 1995; Hjelm *et al*., 2000) traits in specific individuals of juvenile perch make them successful in some environments but not in others.

Shyness/Boldness

A large variation in boldness was found between individuals (II, III, IV) and this variation increased in the presence of a predator (II). Boldness was negatively correlated to body length (II), which means that risk behaviour is not necessarily dependent on vulnerability to predation related to body size. Metabolic rate is negatively correlated to body size. Thus, smaller individuals may need to be more bold in order to meet their energy requirements. Smaller fish also need to grow out of a size-range where they are more vulnerable to predators, so the optimal behaviour may be a trade off between several components of risk. It has been argued that the relative benefits of growing quickly, and hence taking risks while foraging, should decrease with increasing body size (Grant & Noakes, 1987). Furthermore, boldness was found to be positively correlated to the competitive ability of juvenile perch (II, III, IV). On the other hand, individuals that were more successful feeding in aquaria were less successful in tanks (IV). This may have been due to that they had developed a poor condition in tanks and were therefore more motivated to feed than fish in good condition. Hunger level and time exposed to predators (i.e. boldness) have previously been found to be correlated in several species of fish (Dill & Fraser, 1984; Milinski, 1985; Magnhagen, 1988). However, it seems unlikely that hunger level alone affected boldness in our study (IV), since condition factor before the aquarium experiment with vegetation was not correlated to time in the open. Instead, since condition factor was negatively correlated to feed intake (VI), differences in foraging strategies (risk-proneness) may influence time spent in the open and seemingly more risky habitat as in rainbow trout (Sneddon, 2003). The occurrence of different foraging strategies is also indicated by the fact that the time that the juveniles spent in open water, but not their relative number of attacks, was decreased in the presence of a predator, compared to in the absence (II). Furthermore, group composition influenced individual boldness, but not individual food intake (III). This foraging success under farming conditions may, however, not be influence by these different foraging strategies.

The observed behavioural differences between individuals in shyness/boldness in this thesis may be explained by differences in innate characteristics, for example in physiological traits. Connections between physiology and behaviour have previously been found in several species, namely connections between standard metabolic rate and dominant behaviour (Metcalfe *et al*., 1995) and between stress tolerance (cortisol levels) and boldness (Koolhaas *et al*., 1999), dominance (Pottinger & Carrick, 2001) and locomotor activity (Øverli *et al*., 2002), respectively. Variation in physiological traits, such as standard metabolic rate or stress tolerance, might also in perch explain the variation in boldness that was observed in several of the articles in this thesis (II, III, IV).

Implications for aquaculture

Growth

A seasonal variation in growth, with an increase in April and June was found in juvenile perch (IV, Fig. 4). Karås (1990) found a seasonal variation in growth in perch at a constant temperature of 15ºC, and natural day length (Fig. 4). Considering perch, no studies have hitherto reported seasonal fluctuations in growth in constant temperature and day length, which could be due to that aquacultural studies on perch are often conducted over time periods that may be too short to discover such variations (Mélard *et al*., 1995; Fontaine *et al*., 1997; Jourdan *et al*., 2000; Juell & Lekang, 2001). However, Mélard *et al*., (1996 a) conducted an aquacultural study on perch over 14 months, where growth tended to increase in January and not in April-May as in our study. The appetite of several fish species is known to fluctuate over the season, triggered by fluctuations in temperature and/or in day length (Karås, 1990; Smith *et al*., 1993; Saether *et al*., 1996; Simpson *et al*., 1996). In accordance with our results, some species, such as Arctic charr, show seasonal variation in growth in constant temperature and day length (Saether *et al*., 1996). Knowledge of seasonal variation in appetite is of major importance in aquaculture as feed alone stands for the largest expense of fish farms. Optimisation of feeding management is therefore of great importance to maximise the economic gain and also to minimise the environmental impact of specific farms.

The growth rate of selected lines of Atlantic salmon can be doubled after five generations, compared to the wild strain (Thodesen *et al*., 1999). A large potential for successful breeding programs also in perch is indicated in this thesis by the large variation in growth, and the consistency in relative growth of individual perch over longer time periods in aquaculture environments (IV). Competitive success in aquarium experiments can, however, not be used in perch as an indicator of growth potential under aquaculture husbandry routines, as these factors were found not to be correlated (IV, VI).

Since boldness was either positively (V), negatively (IV) or un-correlated to growth, it is, consequently, not useful as an indicator of growth performance under aquaculture conditions. Thus, there were no clear indications of whether boldness is correlated to a high tolerance of stress or not in this thesis. If such a connection existed, growth would be expected to be positively correlated to boldness as in three-spined stickleback *Gasterosteus aculeatus* L. (Ward *et al*., 2004).

Aggression

Strong social hierarchies, often mediated by aggressive interactions, can in farmed fish have negative effects of subordinate individuals as, for example, fin damage and stress (Moutou *et al*., 1998; reviewed in Brännäs *et al*., 2001) and can also cause large variations in growth (Alanärä & Brännäs, 1996). It is therefore important to be aware of whether a species that is intended for farming display aggressive behaviour and social hierarchies. Different studies gave counteracting results regarding whether aggressive behaviour occurs in juvenile perch or not (I, II). Possibly, the water temperature could have affected the occurrence of aggression, as the water was warmer in the study where charges were observed (II), than in the study where no aggressive acts where seen (I). Another difference between these studies was that food was delivered as single food items from above (I), or with all food items presented at once, at the bottom of the tank (II).

Thus, juvenile perch do not seem to have strong social hierarchies (I), even though aggressive acts, mostly performed by competitively superior individuals, were observed in one of the studies (II). Perch can therefore be considered as suitable

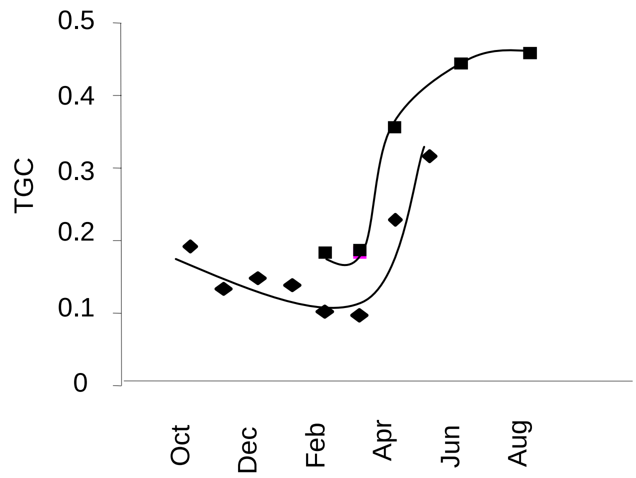

Fig. 4. Growth of perch over the season in 15ºC and natural day lengths (diamonds, calculated from Karås 1990) and in 17 ºC and constant day lengths (squares, calculated from IV).

for farming environments in this aspect, as fin damage and stress of subordinates are unlikely. However, more studies need to be performed on the connection between social interactions and variation in growth in perch (II).

Farming environment

The light intensity for juvenile perch in aquaculture should be lower than 2200 lux, as this light intensity increased the activity of the fish, probably due to increased stress levels. Regarding tank wall colour, neither preference nor growth of the perch differed between the colours tested (white, grey and black), which indicates that all of these colours are equally suitable for farming perch of the studied size class (VI).

Feed training

Boldness was found to be positively connected to learning (V), which is in accordance with previous studies on guppy *Poecilia reticulata* (Peters) (Dugatkin & Alfieri, 2003) and rainbow trout (Sneddon, 2003). It is difficult to get wild caught perch to accept formulated feed. Results from this thesis indicate that it may be possible to use social learning to teach wild-caught juvenile perch to feed on formulated feed (V), which could be useful in the development of farming of perch.

Conclusions

In this thesis, it has been found that the ability to compete for food differs greatly between individuals, whereas strong social hierarchies have not been observed. Thus, competitive ability may be an underlying mechanism for the large variation in growth that has been reported both in aquaculture and in natural environments. The large variation and individual consistency in growth, found in this thesis, indicates that perch has a large potential for successful breeding programs, which, by selecting for fast growing individuals, may decrease the growth heterogeneity which has been observed in perch in aquaculture. Boldness and competitive success in aquarium experiments can not be used as an indicator of growth capacity in an aquaculture environment.

Outcome of hypothesis testing:

Paper I) YES, there is a difference between individuals in competitive ability. NO, there is no occurrence of aggressive behaviour.
Paper II) YES, differences in growth are connected to differences in competitive ability, and these are, in turn, connected to differences in “shyness/boldness”.
Paper III) YES, group composition affects individual ”shyness/boldness”, NO group composition does not affect individual competitive ability.
Paper IV) YES, the difference in competitive ability is consistent over time and in different environments. NO, competitive ability is not correlated between environments.
Paper V) YES, the company of demonstrators improves the ability to learn to feed on a novel food type. YES, differences in ”shyness/boldness” seem to affect learning.
Paper VI) NO, juvenile perch do not prefer any of the presented tank wall colours over the others. NO, neither light intensity nor differences in competitive ability affects the preference for tank colour.

Future prospects

Breeding programs could be one way to reduce the growth heterogeneity of perch in aquaculture. Still, further research on how to diminish the large variation in growth in perch in aquaculture is needed. Other possible keys to reduce this problem could lay in finding suitable densities at different sizes, proper feeding regimes, suitable frequency of sorting of perch and enriched farming environments. The variation in boldness in perch, observed in several of the articles in this thesis (II, III, IV), might be explained by variation in physiological traits, such as standard metabolic rate (SMR) or stress tolerance. Finding such connections would give physiological explanations to observed behavioural differences. In natural environments, a variation in SMR may lead to different trade-offs between spending time in refuges and feeding under the risk of predation. Individuals with a relatively high SMR might be forced to expose themselves more to the risk of predation in order to avoid starvation (as suggested in Cutts et al. 2002) and thereby be classified as bold, whereas individuals with a relatively low SMR can spend a larger proportion of time in shelter, as the risk of starvation for them is lower, and be classified as shy. A possible benefit of having a high SMR might be a potential for a higher growth rate. Regarding the consequences of social and aggressive interactions on growth heterogeneity in perch, more research is needed.

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