

**Behavioural and physiological responses to predators of  
captive-bred Arctic charr: significance of genetics,  
learning and ontogeny**

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Academic dissertation

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# **Behavioural and physiological responses to predators of captive-bred Arctic charr: significance of genetics, learning and ontogeny**

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- I Laakkonen, M.V.M., Roff, D.A. & Hirvonen, H. Genetic variation in antipredator behaviour of Arctic charr: adaptive responses to predators with different tactics. Manuscript.
- II Laakkonen, M.V.M. & Hirvonen, H. (2007) Is boldness towards predators related to growth rate in naïve captive-reared Arctic char (*Salvelinus alpinus*)? *Canadian Journal of Fisheries and Aquatic Sciences* 64(4): 665-671. *Reprinted with kind permission of NRC Research Press.*
- III Vilhunen, S., Hirvonen, H. & Laakkonen, M.V.M. (2005) Less is more: social learning of predator recognition requires a low demonstrator to observer ratio in Arctic charr (*Salvelinus alpinus*). *Behavioral Ecology and Sociobiology* 57: 275-282. *Reprinted with kind permission of Springer Science and Business Media.*
- IV Laakkonen, M.V.M., Vilhunen, S. & Hirvonen, H. Induced and learned responses to predators during fish ontogeny: in search of sensitive periods. Manuscript.
- V Laakkonen, M.V.M. (2006) The effects of long-term predator exposure on body composition and condition of young Arctic charr (*Salvelinus alpinus*). *Annales Zoologici Fennici* 43: 263-270. *Reprinted with kind permission of Finnish Zoological and Botanical Publishing Board.*

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- I Genetic variation in antipredator behaviour of Arctic charr: adaptive responses to predators with different tactics.
- II Is boldness towards predators related to growth rate in naïve captive-reared Arctic char (*Salvelinus alpinus*)?
- III Less is more: social learning of predator recognition requires a low demonstrator to observer ratio in Arctic charr (*Salvelinus alpinus*).
- IV Induced and learned responses to predators during fish ontogeny: in search of sensitive periods.
- V The effects of long-term predator exposure on body composition and condition of young Arctic charr (*Salvelinus alpinus*).

# Summary

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## 1. Introduction

### ***1.1 Antipredator responsiveness: from the population level to the individual level responsiveness***

Predation forms one of the most important selective forces in nature and has significant effects on prey individuals, populations and communities (Lima 1998; Vamosi 2005). Prey species have evolved several different traits to reduce and avoid this predation pressure. These protective adaptations may include morphological structures (e.g. armour), cryptic colourations, chemical repellents and life history adaptations (e.g. delayed hatching) (Godin 1997; Kats & Dill 1998). In a vast number of species, however, behavioural responses form the main way to avoid predation. Behavioural responses towards predators include for example changes in overall activity, reduced foraging activity, escape reactions and spatial predator avoidance (Lima & Dill 1990; Kats & Dill 1998; Vilhunen 2005).

A single encounter with a predator can have an irreversible effect on the fitness of prey: if prey do not innately recognize the predator as dangerous and elicit antipredator responses the prey may be eliminated. Indeed, the predator recognition and avoidance skills of several animal species contain a clear innate component (e.g., snails, Dalesman et al. 2006; crustaceans, Åbjörnsson et al. 2004; fishes, Hawkins et al. 2004b; reptiles, Arnold & Bennett 1984; amphibians, Orizaola & Braña 2003; birds, Wiebe 2004; mammals, Pongrácz & Altbäcker 2000; Monclús et al. 2005), reflecting the significant role of predators in shaping the antipredator traits of prey. Perhaps the clearest examples of antipredator responsiveness with an inherited basis have been reported in various laboratory and field studies comparing the behaviour of naïve prey individuals from different populations. For example, fish populations [e.g. three-spined stickleback (*Gasterosteus aculeatus*, Trinidadian guppy (*Poecilia reticulata*), European minnow (*Phoxinus phoxinus*)] that inhabit high-predation-risk areas have stronger antipredator responses than populations that live in low-risk habitats (see Magurran 1999 for review), which indicates a clear innate background for differences in antipredator behaviour. Correspondingly there can be wide individual differences within populations in antipredator behaviour as well as in other behavioural traits (e.g. boldness, aggressiveness) (Wilson et al. 1994; Coleman & Wilson 1998; Wilson 1998; Brick & Jakobsson 2002; van Oers et al. 2005). A part of the phenotypic behavioural variation detected in wild animals is obviously caused by environmental factors, since experience of predators can also fine-tune and modify the innate predator avoidance skills of prey (e.g. Berejikian 1995; Wiebe 2004; Dalesman et al. 2006), whereas the other part of this behavioural variation is inherited (Wilson 1998). Genetic differences in behaviour can be

defined as the raw material on which natural selection acts, rather than as the end product of natural selection (Wilson 1998).

During recent years, individual differences in suites of inter-correlated behaviours such as antipredator behaviour, aggression, risk-taking and exploratory behaviour have received increased attention (see Sih et al. 2004; van Oers et al. 2005; Dingemans & Réale 2005; Bell 2007 for reviews). Such behavioural correlations may also consist of one behavioural trait in different situations (Sih et al. 2003). For example, some individuals may be more aggressive than others across many situations. Huntingford (1976) demonstrated in her pioneering work that the more aggressive three-spined sticklebacks were also bolder towards predators. These different correlations, termed ‘behavioural syndromes’, ‘coping strategies’ or ‘personalities’ have been identified in various animal taxa, including fish, amphibians, birds and also humans (Wilson et al. 1994; Sih et al. 2004; Quinn & Cresswell 2005; Salonen & Peuhkuri 2006), and studies suggest that these ‘syndromes’ are inherited (Dingemans & Réale 2005; van Oers et al. 2005). Thus, behavioural traits may not evolve independently, but a trait may be correlated with some other behavioural trait(s) resulting in the evolution of multiple traits simultaneously (van Oers et al. 2004, 2005). Genetic correlations between traits are due to linkage disequilibria and/or pleiotropic effects, but it seems that pleiotropy is the main cause of genetic correlations (van Oers et al. 2005).

### ***1.2 Threat-sensitive and predator-specific predator avoidance***

Antipredator behaviours may trade-off with other fitness related behaviours such as mating and foraging (Lima & Dill 1990; Lima 1998; Kavaliers & Choleris 2001). Therefore, to maximize their fitness prey individuals should reliably assess the degree of predation risk and adjust their behavioural responses accordingly (i.e. form and intensity of responses) (Lima & Dill 1990; Lima & Bednekoff 1999; Kavaliers & Choleris 2001). Otherwise, the responses of prey may underestimate or overestimate the predation threat, which can lead to potentially maladaptive behaviour (Peacor 2006). The hypothesis that prey should behave flexibly in response to different degrees of predation risk is termed the ‘threat-sensitive predation avoidance hypothesis’ (Helfman 1989; Chivers et al. 2001). For example, pike (*Esox lucius*) larvae showed reduced swimming activity and foraging with an increasing degree of threat, i.e. when the size of the potential predators (*Perca fluviatilis*) increased (Engström-Öst & Lehtiniemi 2004). In addition to fish species (Chivers et al. 2001; Kusch et al. 2004; Ferrari et al. 2005, 2006), threat-sensitivity has been reported in amphibians (see Mirza et al. 2006 and references therein), mayflies (McIntosh et al. 1999) and spiders (Persons & Rypstra 2001). The ‘risk allocation hypothesis’ that was presented by Lima & Bednekoff (1999) predicts that prey should be expected to exhibit the highest intensity of antipredator responses in high-risk periods that are infrequent and brief. Conversely, when these risk periods are frequent or prolonged, prey are expected to respond less intensely to the predation threat and thereby reduce the costs associated with antipredator behaviour (Lima & Bednekoff 1999). For example, constant ‘freezing’ behaviour when the predator threat is prolonged will most definitely be highly costly for prey, since it naturally reduces foraging opportunities.

In the wild, prey individuals typically encounter more than one predator species and these predators may use different hunting tactics and also different senses to locate the prey (Hart 1997). Therefore, prey should not only adjust the intensity of their antipredator responses to match the degree of predation risk but also accord the way they respond to the predation risk. Thus, an adaptive antipredator response towards one predator species may be maladaptive towards other predator species. Prey should be able to use predator-specific antipredator responses to effectively avoid predation (Edmunds 1974; Sih et al. 1998; Turner et al. 1999). For example, Kats & Dill (1998) pointed out that a decrease in activity and immobility may be the best antipredator responses of a prey individual against the predators that use vision when hunting. Indeed, there is now growing evidence that prey species can discriminate among predator species and exhibit predator-specific responses (see Relyea 2003 and references therein; Petersson & Järvi 2006; Wohlfahrt et al. 2006; Botham et al. 2006). Blumstein (2006) recently presented the ‘multipredator hypothesis’, which predicts that the genetic basis of antipredator behaviour has, by pleiotropy or linkage, become a functional package (i.e. ‘personality’). According to this hypothesis, prey species living with multiple predators may have evolved predator-specific traits to avoid predation in response to each predator, but their expression is not predicted to vary independently. Thus, the presence of a single predator species should maintain antipredator adaptations for predators that no longer exist. However, as Blumstein (2006) highlighted, the precise genetic evidence to support this logical hypothesis is still lacking.

Studying responses to single predator species may not give an accurate picture of the true costs and benefits of predator-induced responses (Storfer & White 2004). Especially the ability of fish species to show plasticity in their behavioural antipredator responses towards different predator species has been rather poorly studied. Magurran (1999) emphasized that comparisons of this kind could also increase our understanding of behavioural variation. In my thesis I have investigated the antipredator responses of young Arctic charr (*Salvelinus alpinus*) to two natural predators differing in predatory tactics, the actively- and widely-searching pikeperch (*Sander lucioperca*) and the burbot (*Lota lota*), which hunts more from ambush, and recorded four antipredator responses of Arctic charr towards these predator species (I). Furthermore, I tested whether there is family-based constancy in the responses of charr to these two predators with different tactics according to the multipredator hypothesis (Blumstein 2006).

### ***1.3 Learning about predators***

Experience is necessary for some prey species to accurately recognise their predators, since they appear to have no innate ability (see Chivers & Smith 1998 for review; Wisenden & Millard 2001). Experience of predators (chemical, visual, tactile) can, however, also enhance and modify innate avoidance responses through learning (Dalesman et al. 2006). In aquatic environments, chemical cues have proven particularly effective in predator recognition and predator avoidance learning (Chivers & Smith 1998; Kats & Dill 1998; Wisenden 2000). Chemical recognition of predators is especially advantageous in environments where the



water is turbid, that are structured, and at night or for species with poor visual senses (Wisenden 2000).

Social learning has also been shown to play an important role in the development of antipredator behaviour in fish and other animal taxa (Brown & Laland 2001, 2003; Griffin 2004). This means that naïve prey individuals modify their antipredator behaviour as a result of observing the responses of experienced conspecifics (demonstrators) to a predator stimulus. For example, Mathis et al. (1996) demonstrated that cultural transmission of the recognition of pike odour occurred between experienced and naïve fathead minnows. In their study a shoal of predator-experienced and naïve minnows were first introduced to pike odour and as a result both experienced and naïve fish showed antipredator responses. In a second trial these previously naïve minnows continued to show antipredator responses to pike odour in the absence of experienced conspecifics. In a minnow shoal that was comprised of purely naïve individuals no learning was recorded.

Prey may also habituate (i.e. stop responding) to the originally threatening stimulus. Habituation due to repeated presentation of a predatory stimulus has been reported in many fish studies (e.g. Magurran & Girling 1986; Jachner 1997; Berejikian et al. 2003). In addition to the repeatedly presented stimuli, potential habituation seems to depend on the authenticity of predator stimuli, i.e. habituation to predator models is especially rapid (Magurran & Girling 1986; Curio 1993). Furthermore, prolonged exposure to predatory stimuli has been shown to lead to habituation in isopods (Holomuzki & Hatchett 1994). Habituation may be adaptive if the risk of being captured by predators is low and/or it is more valuable for prey to allocate energy and time to other actions (e.g. foraging) than to antipredator responses (e.g. according to the risk-allocation hypothesis under frequent predation threat).

#### ***1.4 Captive rearing: salvation or doom?***

Captive breeding programs are widely used to produce fish and other animal species for conservational reintroductions or other population enhancement purposes (Philippard 1995; Frantzen et al. 2001; Brown & Day 2002). These programs are sometimes the only ways to maintain endangered populations. However, rearing animals in the absence of predators in captivity has been shown to weaken their predator avoidance skills and lead to substantial behavioural divergence between wild and captive-bred populations (McPhee 2003; Huntingford 2004; Blumstein et al. 2004; Brokordt et al. 2006; Håkansson et al. 2006). These behavioural deficiencies can evidently explain part of the low success of reintroduction programs, since in many cases predation shortly after release forms the main cause of mortality (Short et al. 1992; Snyder et al. 1996; Wolf et al. 1996; Olla et al. 1998). In general, the success rate of reintroduction programs is very low (Beck 1994). This is especially true for fishes, and a major reason is the lowered ability of captive-bred fish to survive after release into the wild (Brown & Day 2002). Several studies have also reported that post-release survival of hatchery-reared Atlantic salmon (*Salmo salar* L.) smolts is much lower than that of wild smolts (Jonsson et al. 1991; Saloniemi et al. 2004; Jokikokko et al. 2006).

Behavioural divergence due to captive breeding can arise in at least three interlinked ways (Huntingford 2004): (1) different experience, (2) different mortality of behavioural phenotypes over one generation, and (3) genetic changes due to different selection over generations. The aspects of predator recognition and avoidance skills that are based on specific experience of predators are easily ‘lost’ in a predator-free environment (Huntingford 2004; Murray et al. 2004). Consequently, the inter-individual variation in these learned responses should be low, since animals are reared in a stable and inflexible environment (Kieffer & Colgan 1992). On the contrary, ‘hard-wired’ innate behaviours are thought to change at a slower rate over several generations in captivity (Huntingford 2004). The selection resulting from predation is relaxed in captivity, which can lead to increased phenotypic variation in animals’ innate responsiveness, since individuals possessing low innate predator avoidance skills can also survive and be used to form new brood stocks (Kohane & Parsons 1988; Price 1999; McPhee 2003). Furthermore, natural selection and intentional or unintentional artificial selection could result in directed genetic changes, causing weakened behavioural responses (Price 1984; Price 1999; McPhee 2003). Some studies have also suggested that increased risk-taking behaviour detected in captive-bred salmonid fish populations could be linked with directed selection for an increased growth rate (e.g. Johnsson et al. 1996; Yamamoto & Reinhardt 2003). Thus, the growth rate of fish and risk-taking behaviour could be highly linked. However, this hypothesis has not been thoroughly tested.

In this thesis I investigated whether fast growth within hatchery-reared Arctic charr population is linked with weakened antipredator responsiveness (**II**), which could partly explain wide inter-individual differences in antipredator responsiveness earlier detected in this charr population (see Vilhunen & Hirvonen 2003). In addition, I tested whether behavioural variation could be associated with the full-sib family background of individuals (**I**). Answers to these two major questions (**I**, **II**) would help us to understand the causes and extent of antipredator behavioural variation within hatchery-bred charr populations.

### ***1.5 Antipredator training***

One way to enhance the probability of captive-reared fish surviving in the wild is to train the fish to avoid their natural predators prior to release. In recent years, several promising ‘life-skills training’ techniques have been presented to improve these important predator avoidance skills. Techniques have varied from, for example, social learning to exposures to chemical alarm cues combined with predator stimuli (e.g. Brown & Laland 2001, 2003; Kelley & Magurran 2003). The chemical cues from predators have proved especially effective in predator avoidance learning (Brown 2003; Kelley & Magurran 2003), also improving the subsequent predation survival probability of these trained fish compared to their naïve conspecifics (e.g. Mirza & Chivers 2000; Mirza & Chivers 2003; Darwish et al. 2005; Vilhunen 2006). For example, Vilhunen (2006) reported that short conditioning (once or repeated four times, 6 min at a time) of hatchery-reared Arctic charr fry to chemical cues from charr-fed predators enhanced the antipredator responsiveness of charr young. In addition,

these conditioned fish survived better in later real predation trials than their predator-naïve conspecifics.

I examined the role of learning in the development of antipredator responsiveness in hatchery-reared Arctic charr. Firstly, we tested the role of social learning in acquired predator recognition in charr shoals and, moreover, whether the demonstrator-to-observer ratio in these shoals affects the intensity of learning (III). Secondly, we examined the ability of Arctic charr to learn about chemical cues from predators in different stages of early ontogeny from embryo to fry (IV). To date, the possible ‘sensitive periods’ in chemical predator avoidance learning have remained practically unexplored, although fish have been shown to respond to the chemical cues from predators soon after hatching (Mirza et al. 2001; Jones et al. 2003). These results provide valuable information for the life-skills training of hatchery fish.

## ***1.6 Predators as stressors***

In addition to behavioural antipredator responses, the presence of predators can provoke physiological stress responses in fishes (e.g. Breves & Specker 2005; Sundström et al. 2005). The general patterns of stress responses in teleost fish are very similar to the responses in other vertebrates. However, fish are typically more sensitive in their detection of and response to many stressors, especially chemicals, than other vertebrates (Wendelaar Bonga 1997).

### *1.6.1 An overview of stress responses in fish*

Stress can be defined as a ‘condition in which the dynamic equilibrium of animal organisms called homeostasis is threatened or disturbed as a result of the actions of intrinsic or extrinsic stimuli, commonly defined as stressors’ (Chrousos & Gold 1992, according to Wendelaar Bonga 1997). In addition to predators, stressor stimuli can include acute changes in the physical environment (water temperature, salinity, turbidity, pH, oxygen levels), aquatic pollution (heavy metals and chemicals), human interference in hatcheries (handling, transport, disease treatments) and other animal interactions (dominance hierarchies, parasites, competition) (Järvi 1990; Wedemeyer et al. 1990; Wendelaar Bonga 1997; Wingfield et al. 1998).

The two principle routes by which animals respond to the stressor are: (1) the hypothalamic-sympathetic-chromaffin cell axis and (2) the hypothalamic-pituitary-interrenal axis (Wingfield et al. 1998; Barton 2002). These routes lead to the release of stress hormones, namely catecholamines (CAs) and corticosteroid hormones. In an acute threat, CAs in particular prepare an animal for the ‘fight or flight’ response (Kilpelä 1995; Wendelaar & Bonga 1997; Wingfield et al. 1998). The stress hormones cause many physiological effects that help an animal to cope with the stressor, including an increase in oxygen uptake, ventilation rate and heart rate, overall mobilization of energy substrates and reallocation of energy away from growth and breeding (Wedemeyer et al. 1990; Wendelaar Bonga 1997). The integrated stress responses of fish can be divided into primary, secondary and tertiary stress responses (Wedemeyer et al. 1990).

### *1.6.2 Primary stress responses*

Firstly, after detection of a stressor (e.g. predation threat) the central nervous system is activated and as a result large amounts of CAs (e.g. epinephrine) and corticosteroids (e.g. cortisol) are released into the blood stream. Epinephrine (adrenalin) is mainly released from the chromaffin tissue of the head kidneys (Wedemeyer et al. 1990; Kilpelä 1995). The release of CAs is very rapid and happens within a few seconds after a stressful stimulus is presented (Johnson et al. 1992; Wendelaar Bonga 1997). The main corticosteroid stress hormone in teleost fish is cortisol, and the hypothalamus and pituitary gland control the release of cortisol from the interrenal cells of the head kidneys (Wendelaar Bonga 1997). Plasma cortisol levels rise within a few minutes after the stressful stimulus is presented. If the stressor is chronic the cortisol level may remain high, although below the highest peak levels (Wendelaar Bonga 1997).

### *1.6.3 Secondary stress responses*

Secondary stress responses can be defined as the actions and effects of stress hormones (CAs and corticosteroids) on the blood and tissue levels. The major effects include an increase in the ventilation rate, oxygen uptake, heart rate and blood pressure as well as the mobilization of energy (e.g. depletion of liver glycogen) and disturbances in osmoregulation (hydromineral balance) (Wedemeyer et al. 1990; Wendelaar Bonga 1997). In the presence of predators we may expect changes in the cardio-ventilatory system of fish, since one of the main functions of this system is to supply enough oxygen for various behavioural tasks, such as escape reactions (Höjesjö et al. 1999; Barreto et al. 2003). Not surprisingly many studies have reported secondary stress responses in fish in the presence of predator stimuli (e.g. Holopainen et al. 1997; Huuskonen & Karjalainen 1997; Johnsson et al. 2001; Barreto et al. 2003; Woodley & Peterson 2003; Hawkins 2004a,b; Brown et al. 2005).

### *1.6.4 Tertiary stress responses*

Tertiary stress responses can be seen at the whole individual or population level (Shuter 1990; Wedemeyer et al. 1990), and are typically responses to chronic (prolonged) or repeatedly presented stressors. The observed tertiary stress responses include reduced growth and survival, poor condition (measured as condition factor), reduced resistance to fish diseases, reduced reproductive success, and also a reduced capacity to tolerate additional stressors (see Donaldson 1990; Goebe & Barton 1990; Wedemeyer et al. 1990; Wendelaar Bonga 1997).

Reduced growth due to long term stress is typically associated with an increased metabolic rate, energy demand and stimulated catabolism (Pickering 1998). However, reduced growth could also be a result of an impaired feeding rate under stress (e.g. social stress in Arctic charr; Alanärä et al. 1998). Similarly, reduced feeding rates under risk of predation have been recorded in several fish studies (e.g. Johnsson 1993; Johnsson et al. 1996; Jönsson et al. 1996; Abrahams & Pratt 2000). Because stress is energetically highly demanding, it can have wide effects on an animal's body composition. The catabolism of body protein and lipid deposits is

typically linked with stress hormones, primarily cortisol (Sheridan 1988; Vijayan et al. 1991; Sheridan 1994).

Although the possible effects of long term stressors on animal physiology and body composition are now quite well known, the long term effects of predators as stressors have still been rather poorly studied. In particular, effects on the body composition level (protein and lipid content, condition) have so far remained practically unknown, and my study **V** was one of the first to focus on this area. This knowledge is also highly valuable in life-skills training programs where long term predator exposure is one potential method to improve the antipredator skills of captive-reared individuals.

## 2. Outline of the thesis

In this thesis, I have investigated antipredator responsiveness in salmonid fish species, measuring behavioural (**I-IV**) and physiological responses (**V**) to predation threat. I used captive-reared Arctic charr from the Lake Saimaa population as a model species. This charr population is the most endangered fish population in Finland and its existence is highly dependent on captive rearing (Piironen 2003). Furthermore, Primmer et al. (1999) reported that this population has a low level of genetic variability. During recent years, the antipredator behaviour of this population has been quite extensively studied and a good amount of background information has been gathered (e.g. Hirvonen et al. 2000; Vilhunen 2005). Especially the study by Vilhunen & Hirvonen (2003), demonstrating wide within-population differences in antipredator responsiveness in this Arctic charr population, provided a valuable starting point for my own studies (**I, II**). My thesis deepens our understanding of behavioural and physiological responses to predators in captive-bred Arctic charr and will assist in the development of life-skills training techniques.

The main aims of my thesis were to examine whether:

1. captive-bred Arctic charr are able to recognise the chemical cues from two predator species [burbot (*Lota lota*) and pikeperch (*Sander lucioperca*)] with different hunting tactics and show predator-specific antipredator responses towards these predator species (**I**);
2. growth rate (**II**) or genetic background (**I**) are associated with antipredator responsiveness in a captive-reared Arctic charr population;
3. there is family-based constancy in the antipredator responses of Arctic charr to chemical cues from pikeperch and burbot, (i.e. if those full-sib families that respond strongly to pikeperch also do so to burbot), and whether there exists genetic correlations among behavioural traits within predator treatments (**I**);

4. social learning plays a role in the development of antipredator behaviour in charr fry (**III**);
5. possible ‘sensitive periods’ exist in the early ontogeny of Arctic charr allowing them to learn about the chemical cues from their natural predators (**IV**);
6. long-term predator odour exposure affects the physiology (i.e. body condition, whole-body lipid and water content) of young Arctic charr (**V**).

### **3. Material and methods**

The main material and methods used in the original papers of my thesis are briefly summarised below. More detailed descriptions can be found in the original papers.

#### ***3.1 Predator species***

The predator species that I focused on in my thesis were burbot and pikeperch, which are potential predators of young charr in the wild and have a long history of co-evolution with Arctic charr in Lake Saimaa. Moreover, pikeperch and burbot are very different predator species, particularly in terms of their hunting tactics. The pikeperch is mainly an actively moving and pelagic predator species (Rundberg 1977; Bradrand & Faafeng 1993; Vehanen & Lahti 2001; Wysujack et al. 2002), whereas the burbot is a more local and bottom-dwelling ‘ambush’ predator (Carl 1995).

#### ***3.2 General behavioural study design***

All my experiments were carried out over the years 2001 and 2003-2005, and all behavioural observations were performed during summer (June-September). Full-sib charr families were used in two of my studies (**I**, **V**), while in the remaining studies (**II**, **III**, **IV**) the parental background of individual fish was unknown. In studies **I** and **II** fish were reared in a hatchery without any prior experience of predators before the behavioural studies (i.e. under standard hatchery conditions). In study **IV** the young charr were exposed to chemical cues from charr-fed pikeperch in different developmental stages prior to behavioural trials, and in study **V** charr were exposed to chemical cues from charr-fed pikeperch for 72 days prior to physiological measurements. The methods used in the social learning study are described in detail in the original paper (**III**).

All behavioural trials (**I-IV**) were conducted in a Y-maze fluvium (Fig. 1) and one fish was always used at a time in a behavioural trial. We used fluvium in our antipredator behavioural studies since earlier studies have demonstrated that this experimental setup provides very sophisticated results of antipredator behaviour in Arctic charr (see Hirvonen et al. 2000; Vilhunen & Hirvonen 2003). The fluvium contained two channels (length 74 cm, width 17 cm) that were divided by a waterproof wall. During the trials water flowed into each channel at a rate of 5 L min<sup>-1</sup> from one of two identical 80 L containers. In the predator

treatments one container held the predators, either pikeperch (**I-IV**) or burbot (**I, II**). The other container held only odourless control water. In the control trials both channels received odourless control water.



**Figure 1.** The Y-maze fluvium that was used in the behavioural trials. Note the young charr in the middle of the left channel (picture by Mika Laakkonen).

During the behavioural trial we recorded the following behavioural traits: *time spent in the predator odour channel* (except in paper **IV** *the percentage of time spent in non-scented channel*), *direct approaches to the predator odour channel*, *relative swimming activity* and *freezing behaviour*. These different traits were chosen because they indicate different aspects of antipredator behaviour. For example reduced activity and freezing are probably the best antipredator responses against visually hunting predators (Kats & Dill 1998).

Less *time spent in the odour channel* indicated spatial odour avoidance of Arctic charr and *direct approach to the predator channel* indicated boldness to approach the predator odour

source. A direct approach was recorded when a charr swam directly to the last section of the odour channel, across the last marker line (Fig. 1), without stopping or turning back during this approach. *Relative swimming activity* and occurrence of *freezing* behaviour measured possible changes in overall activity of charr young in the presence of predator odour. *Relative swimming activity* was the total number of times a charr crossed the marker lines on the bottom of the fluvium divided by the time that the charr was moving (not freezing) (Fig. 1). A line cross was recorded when the fish crossed the line with its full body length.

### ***3.3 Physiological measurements***

In study V, captive-reared Arctic charr were exposed to chemical cues from charr-fed pikeperch for 72 days and after this period the body condition, whole-body lipid and whole-body water content of each fish were measured. Lipid and water content were determined using standard laboratory techniques (V). Body condition was measured as the residuals of the wet weight to length regression. Similarly, the residuals of the lipid to weight and water to weight regressions were used in the statistical analysis.

## **4. Main results and discussion**

### ***4.1 Predator-specific antipredator responses (I)***

In this study we demonstrated that the captive-bred charr recognised and responded to chemical cues from both pikeperch and burbot, but the magnitude of different responses was highly linked to the predator species. The burbot odour increased the spatial odour avoidance of the charr young and they were less prone to approach the predator channel than the fish in the pikeperch treatment. On the other hand, in the pikeperch treatment charr reduced their relative swimming activity and tended to show more freezing behaviour relative to the burbot treatment. The charr young adjusted their antipredator behaviour in a threat sensitive way (Helfman 1989). ‘Threat-sensitive predator avoidance hypothesis’ predicts that prey should match the intensity of their antipredator behaviour to the degree of threat posed by the predator (Brown et al. 2006). In our study in the presence of both burbot and pikeperch chemical cues charr young increased spatial predator avoidance, reduced swimming activity and direct approaches towards predator, but the intensity of responsiveness in these traits was clearly associated to the predator species. This finding highlights that when threat-sensitivity of prey is estimated more than just one behavioural trait should be measured. Otherwise we could easily underestimate the responsiveness of a prey. To conclude, the naïve charr young evidently possess sophisticated ability to respond towards different predator species and these responses seem to be related to the hunting tactics of predator species (Rundberg 1977; Carl 1995; Vehanen & Lahti 2001). Further, it seems evident that predator-specific responses of Arctic charr are linked with long co-evolutionary history in the Lake Saimaa with the predator species.



#### ***4.2 Within-population behavioural variation (I, II)***

Study **II** clearly showed that growth rate was not associated with antipredator responsiveness in this captive-reared Arctic charr population and factors other than growth rate must therefore evidently explain inter-individual differences in antipredator responsiveness in this population. Earlier studies have indicated that a high growth rate in domesticated salmonids is linked to higher growth hormone levels that especially stimulate the appetite of fish (Johnsson et al. 1996; Fleming et al. 2002). The high heritability of the salmonid growth rate provides wide potential for artificial growth manipulation in hatcheries (Gjerde & Schaeffer 1989; Nilsson 1990; Martyniuk et al. 2003). Recently, Biro et al. (2006) suggested that hormonal motivation to feed may drive the elevated activity and lower antipredator behaviour observed in domesticated and growth-manipulated salmonids. Indeed, in whole-lake studies Biro et al. (2006) demonstrated that domesticated trout (artificially selected for maximum growth rate) used risky habitats more than wild trout. As a result, the domesticated fish grew better in all situations but had a significantly lower survival rate (40% survival disadvantage) compared to wild fish when the predators were present. Thus, domesticated fish evidently accepted a greater risk while foraging to achieve a high growth rate, most likely reflecting the significant role of growth hormones in stimulating appetite (Biro et al. 2006).

On the contrary, when intentional selection for fast growth is avoided in a hatchery it is likely that the growth performance of individuals is more dependent on environmental conditions, especially social interactions (i.e. dominance hierarchies, Jobling 1995), than on inherited physiological growth properties. In other words, even if there are genetic individual differences in growth rate, they may be easily masked from selection because they are strongly influenced by behavioural processes (Björklund et al. 2003). Thus, reduced antipredator responses possibly linked with more active endocrine growth regulatory components of fast growth are also easily hidden. I hypothesize that this might be the main reason why no interaction was detected between growth rate and antipredator behaviour in this study.

Interestingly, in my other study (**I**) we detected wide between-family differences in antipredator responsiveness (i.e. inherited variation in antipredator behaviours) in this captive stock. Detected differences were greater in the response towards burbot than towards pikeperch. In the burbot treatment, families differed from each other in three antipredator traits (direct approaches, relative swimming activity and freezing), whereas in the pikeperch treatment between-family differences were only detected in freezing. These results suggest that there is a clear inherited component in antipredator responsiveness in this charr population and that the detected inherited differences could explain a part of the behavioural phenotypic variation in this population (Vilhunen & Hirvonen 2003). As the behavioural responses of Arctic charr measured in the Y-maze fluvium clearly predict their survival in subsequent live predation trials (Vilhunen 2005), my results suggest that wide behavioural differences between families could even lead to family-specific mortality rates in the wild.

Thus, detected inherited variation in antipredator responsiveness provides evolutionary potential for natural selection to act in wild (Wilson 1998).

#### ***4.3 Family-based differences in antipredator behavioural types (I)***

In addition to the above-presented between-family differences and predator-specific antipredator responses, we detected significant genetic correlations among behavioural traits within the predator treatments, and most interestingly family-based constancy in antipredator responses to the two predator species, i.e. charr fry from families that responded relatively strongly to burbot by spatial odour avoidance also increased their spatial odour avoidance in the presence of pikeperch cues in relation to other families. These findings indicate differences in family-based behavioural types in responses to the two predators. I must emphasize that antipredator responses of individual fish were tested only against one predator species and therefore behavioural types were not measured at the individual level but at the family level. However, our finding raises an interesting hypothesis that hatchery selection causing changes in an inherited antipredator trait against one predator species may actually be linked to inherited responsiveness to other predator species. Thus, there could be co-selection in antipredator responsiveness, which would support the multipredator hypothesis presented by Blumstein (2006).

#### ***4.4 Role of social learning in acquired predator recognition (III)***

In this study we demonstrated that social learning does occur in Arctic charr shoals and naïve individuals learn to recognize predators as dangerous in the presence of experienced conspecifics (demonstrators). Interestingly, however, learning only occurred in the shoal where the demonstrator (d) to observer (o) ratio was the lowest (i.e. 4d/16o). Altogether, the behavioural responses of these fish were as strong as in fish with direct experience of predators. Learning was not observed in other shoals that had ratios of 10d/10o or 16d/4o. This finding is very interesting as, for example, several authors have suggested that social learning would be more effective when there are more demonstrators than observers (Giraldeau 1997; Lachlan et al. 1998). It seems evident that the different behaviour of demonstrators in different shoal structures during the exposure phase explains our finding. Interestingly, recent studies suggest that the intensity of the demonstrators' behaviour is associated with the subsequent behaviour of the observer, i.e. the intensity of antipredator responses is culturally transmitted (Ferrari et al. 2005; Shier & Owings 2007). This could also explain the findings of the present study, i.e. demonstrator behaviour could depend on the shoal structure. It is possible, for example, that when the predator-experienced charr were a minority they could have performed more startle responses and naïve fish were therefore also more alerted. On the other hand, when the proportion of predator-experienced charr increased the shoal cohesion could have been a more specific response as more fish (i.e. demonstrators) were originally aware of the predation risk. Future studies, however, are needed test these hypotheses in more detail and the next logical step would be to observe the behaviour of fish during the social learning phase. Our results are highly valuable in the light of life-skills

training programs. Thus, both direct exposure to live predators and social learning evidently enhance the antipredator responsiveness of naïve charr young.

#### ***4.5 Sensitive periods in the development of antipredator responsiveness (IV)***

This study tested the sensitivity of naïve hatchery-reared Arctic charr to induced behavioural prey defences or learned responses in different ontogenetic stages. The present work is to my knowledge the first antipredator behavioural fish study examining ‘sensitive periods’.

In study **IV**, naïve hatchery-reared Arctic charr were exposed to chemical cues from charr-fed pikeperch in different developmental stages (embryo, alevin, fry, and in all possible combinations of these). The behaviour of charr and possible existence of enhanced antipredator responsiveness was tested later in the fry stage. The results demonstrated that predator exposures in alevin and fry stages seemed to develop the strongest responses towards predators. These results are in accordance with previous studies showing that fry (Brown & Smith 1998; Berejikian et al. 1999; Mirza & Chivers 2003; Vilhunen 2005) as well as alevins (Mirza et al. 2001; Jones 2003) of salmonids react behaviourally to the chemical cues of predators. However, we did not detect significant differences in behaviour between the naïve charr and any of the predator-exposed fish, which suggests that early experiences simply fine-tuned the innate antipredator responsiveness of Arctic charr. A potential reason for this might be that the antipredator responses of naïve charr in the present study were already innately near adaptive level and earlier experience therefore only moderately affected their responsiveness. It is also possible that the diet of the predators may have affected results, as one-year-old Arctic charr were used as food for the predators. Previous studies have demonstrated that fish young respond to the chemical alarm cues from different sized and aged conspecifics, but the responses may be more intense towards chemical cues from same sized/aged conspecifics (Jachner 2001; Mirza & Chivers 2002). Therefore, the chemical alarm cues from consumed one-year-old charr conspecifics may also be weaker as conditioning stimuli.

Interestingly, fish conditioned to the predator cues in all three developmental stages (total 48 exposure bouts) did not habituate to the presented stimulus. I suggest that the lack of habituation might be explained by two main factors: Arctic charr have a long history of co-evolution with pikeperch in Lake Saimaa and the chemical cues from eaten conspecifics combined with predator cues may provide such a reliable indication of a predation threat that habituation is slower (**V**, Vilhunen 2006).

#### ***4.6 Physiological responses under severe predation risk (V)***

Study **V** evaluated the physiological and energetic costs of severe predation risk in Arctic charr. The charr young were exposed to chemical cues from charr-fed pikeperch for 72 days, after which the body condition and body composition (whole-body lipid and water content) of the exposed fish were measured. The results showed that the long-term presence of predators

causes severe physiological changes in young fish, since the exposed charr had a lower body condition and water content but higher lipid content than the non-exposed fish. These most likely maladaptive responses (see Biro et al. 2005) may be a result of severe physiological stress responses (chronic predator-induced stress) and/or predator-induced behavioural responses (reduced feed intake due to exposure or reduced overall swimming activity). These results are also consistent with study (IV) suggesting that possible habituation of charr young towards chemical cues from charr-fed pikeperch is slow. The study also provides important new information for the development of life-skills training techniques and it highlights that in future studies it would be valuable to measure not only behavioural but also physiological effects of life-skills training.

## 5. Conclusions

In this chapter I evaluate the significance of my findings, especially from the perspective of conservation and life-skills training of Arctic charr and also other salmonids. I demonstrated in my thesis that on the population level (i.e. over all full-sib families), hatchery-reared Arctic charr were highly sensitive to the chemical cues from different predator species and displayed sophisticated predator-specific antipredator responses (I). However, within the population (i.e. between full-sib families) there was wide variation in antipredator responsiveness. Both of these above-presented findings are encouraging from the conservational perspective. The ability to recognize and respond to different predator species and ample genetic variation in this antipredator responsiveness indicates that there is evolutionary potential in this captive-bred population. After fish are released into the wild, natural selection will favour those individuals that have the 'best' ability to avoid predators and thus potentially be founders of a new viable population. Behavioural variation was more pronounced in responses towards burbot than towards pikeperch which probably indicates that the predation selection of pikeperch rather than burbot could have been stronger on Arctic charr in the Lake Saimaa. The detected genetic variation in antipredator responsiveness, however, also includes a negative aspect that could be especially meaningful in future generations in captivity. Namely, there is a potential for selection processes occurring in captivity to cause changes in antipredator traits in this population (Price 1999). For example McPhee (2003) demonstrated in their study that the more generations the oldfield mice (*Peromyscus polionotus subgriseus*) population was reared in captivity, the less likely the individuals were to show antipredator responses. In addition, the variance in antipredator responses increased. Thus, these effects accumulated with generations in captivity (McPhee 2003). Eventually, the antipredator traits of the captive population could become very different from those in the wild population, making captive-bred animals increasingly vulnerable to predation in the wild (McPhee & Silverman 2004).

The above situation becomes even more complex when we take into account family-based differences in behavioural types consisting of antipredator traits in this population. Study I indicated that correlations between the same antipredator traits in different situations exist

(measured in a family-level responsiveness), supporting the multipredator hypothesis presented by Blumstein (2006). Thus, there could be co-selection of antipredator responsiveness towards multiple predators. However, relaxed predation selection of all predators in captivity could have unwanted effects on this responsiveness, simultaneously changing antipredator responsiveness towards multiple predator species. Further studies (i.e. individual level studies on behavioural types), however, are needed to test the multipredator hypothesis in more detail. In addition, if antipredator traits are correlated with some other behavioural trait (e.g. aggressiveness, boldness), then the selection of a trait in one context could have consequences for the evolution of another trait (van Oers et al. 2004). Several studies have already shown that antipredator traits are linked with other personality traits (e.g. aggressiveness) in fish (Huntingford 1976) and birds (Quinn & Cresswell 2005). Hypothetically, selection acting in captivity could therefore easily lead to the co-selection of several traits, changing not only the antipredator skills of individuals but also other fitness-related traits and making phenotypes of captive-bred animals very different from their wild conspecifics. From the conservation perspective this would naturally be a highly unwanted outcome.

In future studies it would be extremely valuable to explore in more detail the possible existence of ‘personalities’ in the Lake Saimaa Arctic charr as well as in other captive-bred salmonids. This knowledge would help us to predict how multiple behavioural traits are altered in captivity and to develop hatchery practices that could maintain the viability of captive-bred populations. However, the primary goal in all conservational attempts should be that the viability of natural fish populations is protected, for example, with fishing restrictions, habitat protection and the restoration of spawning areas and that no supportive captive-breeding would be needed. Captive-breeding should always be the last resort in species conservation because of the unwanted genetic and phenotypic changes that may occur in captivity (Snyder et al. 1996; Lynch & O’Hely 2001; Ford 2002).

Finally, in the light of life-skills training programs the findings of studies **III-V** are extremely valuable. We demonstrated that both social learning and direct exposure to live predators enhance the antipredator responsiveness of charr young (**III**). In addition, there were indications that predator odour exposures (i.e. life-skills training) in alevin and fry stages fine-tune the innate antipredator responsiveness of charr (**IV**). Thus, these methods have the potential to enhance the innate antipredator responsiveness of naïve charr young, possibly also improving the post-release survival of these ‘trained’ individuals in the wild. However, large scale survival studies in the wild would be necessary to test this hypothesis. Results from my final study emphasize that possible long-term training methods should take into account not only the behavioural but also the physiological effects of training (**V**). In addition, it would be important in future studies to measure both behavioural and physiological responses of prey in long-term as well as short-term exposures to predation threat. For example, Holopainen et al. (1997) tested in a very sophisticated study how chemical cues of pike affect oxygen consumption, heart rate and behaviour in crucian carp

(*Carassius carassius*). The acute responses of carp towards chemical cues were an increase in heart rate and oxygen consumption. However, after 115 days of exposure the opposite responses were recorded: a reduced heart rate, lowered oxygen consumption and reduced activity. In addition, the growth rate was higher in the predator-exposed fish than in the non-exposed fish. These results clearly demonstrate that the short term (acute) behavioural and physiological responses towards predators can differ greatly from the long-term responses. In this case, energy saved due to reduced behavioural and physiological activity in the treated fish seems to be allocated to somatic growth, and an interesting connection between physiological and behavioural responses exists. A similar combination of behavioural and physiological data both in short- and long-term antipredator studies in the future would deepen our knowledge of predator – prey interactions and also help us in the development of the life-skills training methods.

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