

Environmental influences on
the behavioural ecology of
juvenile salmonids
the importance of rearing density

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List of papers

Paper I

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Paper II

Brockmark S and Johnsson JI, in press. Reduced hatchery rearing density increases social dominance, post-release growth and survival in brown trout (*Salmo trutta*). *Canadian Journal of Fisheries and Aquatic Sciences*.

Paper III

Brockmark S, Adriaenssens B and Johnsson JI. Less is more: density influences the development of behavioural life skills in trout. *Manuscript*.

Paper IV

Brockmark S, Neregård L, Bohlin T, Björnsson B Th and Johnsson JI 2007. Effects of rearing density and structural complexity on the pre- and post-release performance of Atlantic salmon. *Transactions of the American Fisheries Society* 136:1453-1462.

Dissertation Abstract

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Background and aims: Early environmental conditions are known to influence the phenotypic development of animals, including behavioural alterations. The overall aim of this thesis is to investigate the effects of density, social stability and structural complexity on growth, behaviour, and survival in the wild, using juvenile brown trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*) as model species. The result can add to the basic knowledge in this research area and can also be used to enhance the welfare and fitness of released hatchery-reared fish.

Methods: In papers II-IV sea-ranched trout and salmon were reared from early life stage in conventional hatchery tanks with modified physical structure and/or density. Hatchery fish were measured for growth, studied for individual and social behaviours, and analysed for fin-erosions and smolt-status. In paper I wild-caught juvenile trout were used for behavioural studies. In papers II-IV fish from different treatment groups were also released in natural streams to investigate treatment effects on survival and growth in the wild.

Results and conclusions: My results collectively show clear positive effects of reduced rearing density, whereas the effects of structure were unclear and harder to interpret. In papers II-IV reduction of conventional hatchery densities generally increased growth rate in the hatchery and post-release survival. Salmonids reared at reduced densities were more dominant in competition for food, consumed more novel prey, escaped faster to refuges after a predator attack and located more food in a maze, compared to fish from higher densities. At time of parr-smolt transformation, salmon reared at reduced densities had less fin erosions and were more fully smolted than salmon reared at higher densities. Taken together, the results presented in this thesis clearly show that reduced rearing densities facilitate the development of adaptive individual and social behaviour in salmonids, resulting in increased growth and survival after release in nature. In paper I wild trout in familiar groups were more vigilant, responded faster to a simulated predator attack and consumed more food compared to trout in unfamiliar groups. These novel results suggest that social stability confer immediate fitness benefits, i.e. higher probability of survival under conditions of high predation risk.

In summary, my results show that conventional rearing methods in supplementary hatcheries do not prepare fish adequately for life in the wild and could be improved considerably, with density reduction as one key factor. Incorporating behavioural aspects in supplementary rearing methods is also important from an ethical point of view. However, there is a limit to what can be accomplished with improving supplementary hatchery rearing methods. Hatchery rearing should therefore be viewed as a complement rather than an alternative to habitat restoration.

Keywords: rearing density, structural complexity, familiarity, antipredator response, limited attention, social status, growth rate, smolt status, fin erosion, post-release performance, hatchery supplementation, Brown trout, Atlantic salmon

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INTRODUCTION

In this thesis I investigate the importance of early environmental conditions for the phenotypic development of salmonid fish. I mainly focus on the effects of density, social stability and structural complexity on growth, behaviour, and survival in the wild. My results add to the basic knowledge in this research area. The findings can be used to modify captive-rearing environments in order to increase fish welfare and to enhance the fitness of released hatchery fish.

The importance of the environment for the phenotypic expression

The phenotype is the product of interactions between the individual's genome and the environment in which it develops. 'The environment' is the catchall term that encompasses what is external to an organism, such as the interactions between abiotic and biotic factors. The abiotic environment is non-living and includes all the physical elements of an organism's existence. The biotic environment is, compared to the abiotic, more complex as it embraces the living environment, including the relation among organisms and what is caused and produced by them. Thus, *how* the interaction between the genome and the environment occurs is neither simple nor clear (Pigliucci 2001).

Environmental conditions can change considerably over an individual's lifetime which may induce a variety of phenotypic responses (West-Eberhard 2003). Some phenotypic traits are plastic in response to environmental variation, whereas others are more fixed genetically and therefore relatively insensitive to environmental conditions (*i.e.* canalisation). Even though plastic responses are adaptive solutions for dealing with environmental change, the ability to express alternative phenotypes may incur fitness costs (Schlichting and Pigliucci 1998). Natural selection will thus favour those phenotypes that yield the highest average fitness over the various environmental conditions encountered over the life span (*i.e.* adaptive plasticity; Falconer and

Mackay 1996). Hence, variation in the environment tends to preserve genetic variation among populations through spatially varying selection and/or reduced gene-flow (*i.e.* local adaptation; Endler 1986).

Under certain conditions, a single genotype can produce two or more distinct phenotypes, each with a unique ecological and social role, such as alternative mating strategies (Calsbeek et al. 2002). However, plasticity more commonly varies as a function of the environmental variation (*i.e.* reaction norm). A striking example of this is found in ectothermic organisms, where growth in body traits exhibits a convex response curve to temperature (David et al. 1990). Behavioural traits are often plastic, as learning allows animals to modify their behaviour in response to changes in their environment. An animal may either learn by own experience (*e.g.* trial and error), and/or by watching and/or interacting with others (*i.e.* social learning) (Heyes 1994; Hoppitt and Laland 2008). Learning may also vary during ontogeny, where certain periods may be more sensitive (*i.e.* windows of plasticity), as the learning ability depends on an individual's neural and sensory developmental state (Hawkins et al. 2008) and ecological conditions (Shettleworth 1998). Phenotypic plasticity is known to be particularly pronounced early in ontogeny when organs and their nervous control are under the process of differentiation. Exposure to appropriate cues during sensitive periods have shown to be essential for ensuring appropriate behavioural response (Alcock 2009), but little is still known about the significance of such periods in fish.

Physical structure

Structural complexity in the natural environment is an important determinant of species richness (McArthur and McArthur 1961; Bell et al. 1991). Animals prefer structurally enriched habitats for many reasons. A structurally complex habitat may provide shelter for prey to escape predators (Jarman 1974). Also, interactions between competitors generally decrease with increasing habitat complexity (Eason and Stamps 1992),

which in turn may reduce intraspecific competition (Basquill and Grant 1998; Höjesjö et al. 2004; Einum and Nislow 2005; Baird et al. 2006) and defendable territory size (Kalleberg 1958; Imre et al. 2002). In general, resource defence is more beneficial in structured habitats like streams and coral reefs, compared to pelagic zones in lakes or oceans (*reviewed by* Grant 1997), since structured habitats are patchier and therefore easier to defend. Structural complexity *per se* increases habitat dimensionality, resulting in higher carrying capacity (Harmon et al. 1986).

Structural complexity may also affect behavioural variation. For example, song birds are known to vary their repertoire depending on the habitat complexity, where songs containing longer and more highly diverse elements are more common in dense forests relative to open landscapes (Slabberkoorn 2004). Complexity may also affect the relative advantage of using different behavioural strategies. For example, the relative fitness advantage of aggressive dominant behaviour is lower in complex habitats, as it is more difficult to monopolize space and more refuges are available for subordinates (Höjesjö et al. 2004).

The ability to use spatial information to find cover (Markel 1994) or food (Noda 2004) is directly fitness related in animals. In general, species that actively search for food have greater spatial memory compared to passive foragers. Similarly, food-storing birds have a greater capacity for spatial memory and a larger hippocampus (*i.e.* brain region involved processing spatial information) relative to non-storing species (Brodin and Bolhuis 2008; Roth and Pravosudov 2009). Evidence show that experience of structural complexity stimulates neurogenesis in a number of taxa (Nilsson et al. 1998; Freire and Cheng 2004) including fish (Kihlsinger and Nevitt 2006). For example, development of cognitive skills (*i.e.* perception, learning and memory) in fish appears to be associated with visual orientation and well-structured habitats (*reviewed by* Kotrschal et al. 1998, and Braithwaite 2006).

Density and the social environment

Density-dependent processes are thought to have a stabilising effect on population dynamics, especially in demographically closed populations and among organisms with restricted mobility. In general, in species where individuals produce large quantities of offspring density-dependent regulation is strong due to mortality and emigration in early life stages (Murdoch 1994). Understanding density-dependent mechanisms in animal populations can be crucial for predicting the consequences of habitat fragmentation, as individuals are forced together in smaller habitats (*reviewed by* Gross-Custard and Sutherland 2001).

Density conditions (*i.e.* the number of individuals per square unit) and group size (*i.e.* the number of individuals in a group) can influence the development of behaviour in various ways (Fig. 1).

First, the possibility to develop recognition-based social systems depends on the size and density of a group. Individual recognition can be used to reduce levels of aggression in encounters with neighbouring individuals (*i.e.* the dear enemy effect, *sensu* Fisher 1954; Senar et al. 1990). The decision to preferentially associate with familiar conspecifics may thus confer advantages associated with reduced aggression and stabilised social hierarchies (Höjesjö et al. 1998). However, as group size increases, the ability to recognise specific individuals decreases due to cognitive constraints (*i.e.* limited attention, *reviewed by* Dukas 2002).

Second, resource defence theory predicts that individuals should defend a resource if the benefit of defence exceeds the costs, where the economical dependability varies with the density of competitors and the density and distribution of the resource (*reviewed by* Grant 1997). Resources that are unpredictable in time and space are often more difficult to defend. When resource defence becomes too costly, territorial animals often form social hierarchies and the competition mode changes from interference to exploitation competition (*reviewed by* Keddy 2001).

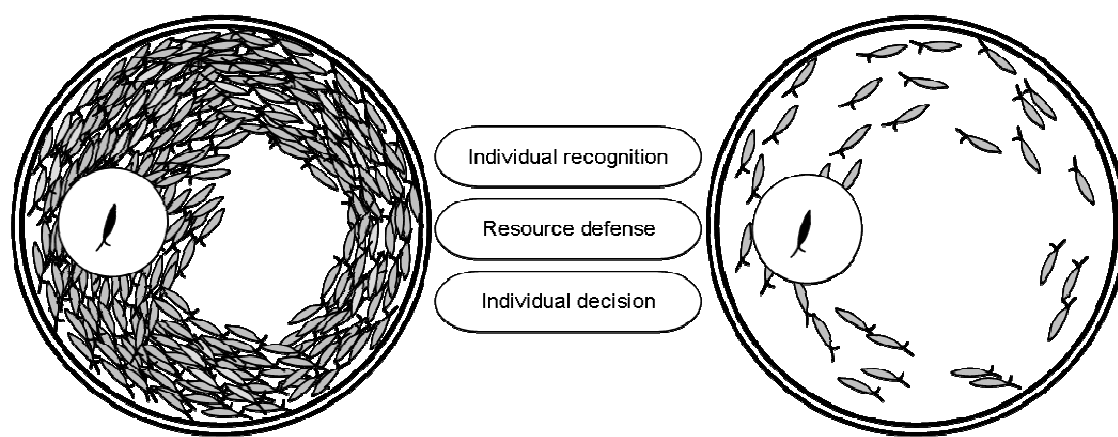


Figure 1. Density conditions may influence behavioural development by altering the conditions for key factors such as individual recognition, resource defence and decision making. The figure illustrates conventional hatchery densities (left) and reduced hatchery densities (right).

Third, group size and density conditions can affect individual learning, as increased density facilitate flocking/schooling and associated copying behaviour (*reviewed by* Couzin et al. 2006; *and* Fernö et al. 2006). One way of coping with the cognitive demands associated with high densities would be to leave the individual control and use social information (Camazine et al. 2001), which may facilitate food localisation and enhance predator detection (*i.e.* the many-eyes hypothesis, *reviewed by* Krause and Ruxton 2002). However, prolonged loss of individual control in high-density groups may gradually impair the development of individual learning ability.

Salmonids as model species

Salmonid species are particularly useful models to study evolution and phenotypic plasticity, as they adapt to a wide range of environments over their life history. Salmonids have been exploited since the eighteen-century and are an important resource for commercial and recreational fishing around the world (*reviewed in* Verspoor et al. 2007). In this thesis two species of the *Salmo* family, the brown trout (*Salmo trutta*) and the Atlantic salmon (*Salmo salar*), are examined.

The biology of the Atlantic salmon and the brown trout

The historical distribution of the Atlantic salmon is the North Atlantic with associated coastal drainages, but many populations in the native range are today threatened by extinction. Most populations are anadromous (*i.e.* sea-migrating), spending the adult growth stage in the sea before migrating up their natal stream to spawn. A few populations complete their entire life cycle in freshwater as landlocked forms, as found for example in lake Vänern, Sweden (Klemetsen et al. 2003).

The native distribution of the brown trout was restricted to Europe, but over the last century the species has been introduced by humans in most continents (Elliott 1994). Brown trout is not considered endangered, although some populations do suffer from various degrees of stress from environmental degradation and over-fishing. Populations are found both as freshwater resident forms in streams and lakes, or as anadromous (*i.e.* sea trout). The following part will focus on the biology of anadromous brown trout and Atlantic salmon.

After one to four years of feeding in the ocean, sexually mature anadromous salmonids return to their natal river to spawn. During homeward migration they cease feeding, and begin to develop sexual characteristics, such as

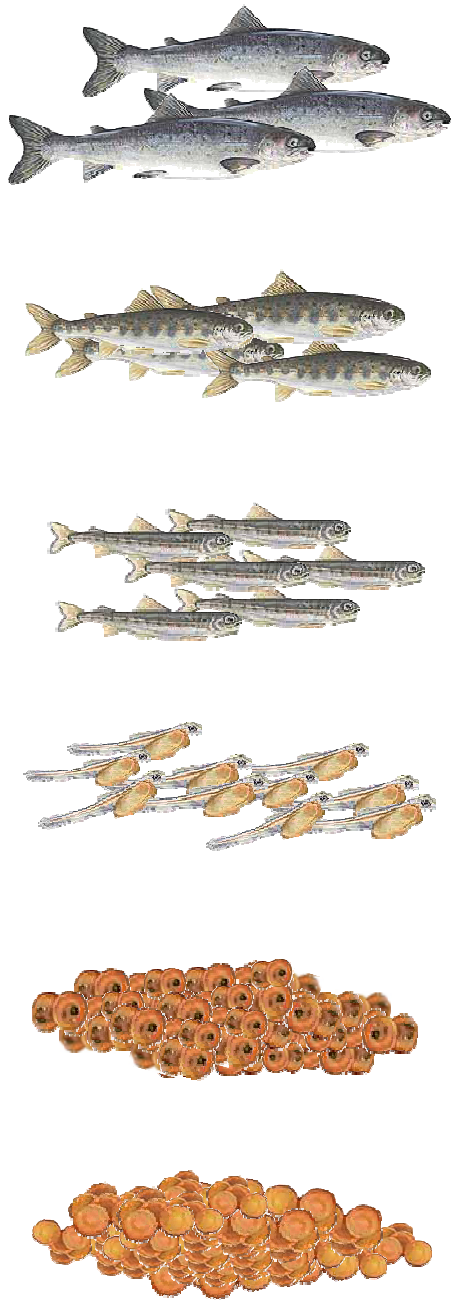


Figure 2. The freshwater life stages of an anadromous salmonid, the Atlantic salmon. From below: eggs, eyed eggs, yolk sac alevins, fry, parr and smolts. Modified from the Atlantic salmon life cycle (ASF).

spawning colouration and the male hooknose. The mature salmonids often stand in the river mouth, adjust to the freshwater and wait for appropriate conditions before they migrate upstream to the spawning grounds. The time of spawning varies with water regime and temperature, but often occurs within a period of ten weeks between September and December in northern latitude populations. Females compete for spawning sites, and excavate gravel nests (i.e. redds) in riffle areas, where stable water flow provides the eggs with oxygenated water and prevents sediment infiltration. Males compete for access to females in effort to fertilise eggs as they are deposited. Some early maturing stream-resident males adopt an alternative strategy using ‘sneaking mating tactics’ to avoid confrontation with much larger adult males (Fleming 1996; Gross 1985). The spawning may be delayed by females when they are approached only by small or low-status males. After mating, the female cover the eggs with gravel using the caudal fin. This mating procedure may be repeated until a series of egg batches are laid.

The eggs hatch the following spring and the resulting yolk sac alevins remain buried in the gravel, protected from predation and displacement, feeding endogenously for a period of five to six weeks. As yolk reserves are depleted, young salmonids, now referred to as fry, emerge from redds and start to search for food. This is a critical period associated with increased predator exposure and intense fights over profitable feeding territories, where a large proportion of the fry will die from starvation or predation during their first summer (Elliott 1994; Einum and Fleming 2000; Einum and Nislow 2005). Fry that emerge early have a competitive advantage due to the ‘prior residence-effect’ (Bradbury and Vehrencamp 1998; Johnsson et al. 1999) with benefits of faster growth and lower mortality compared to displaced late-emerging fry (Brännäs 1995, Harwood et al. 2003). During the first summer, the fry quadruple in length and develop into parr. As the density increases, the cost of

maintaining feeding territories may become too high where fry/parr are more likely to form dominance hierarchies (Keeley 2000). The parr are cryptically coloured (Donnelly and Dill 1984).

After 1-4 years, depending on the growing conditions, the parr undergo a series of behavioural, morphological and physiological changes to prepare for the sea (*i.e.* smoltification or parr-smolt transformation, see McCormick and Saunders 1987). This process is mediated by seasonal environmental cues, primarily photoperiod (Saunders and Henderson 1970) and water temperature (Johnston and Saunders 1981). As parr transform to smolt, they change from territorial to shoaling behaviour, lose their parr marks for a silvery body colouration and increase their hypoosmoregulatory capacity. After having left their natal stream, salmonids experience a period of rapid growth of one to four years in the ocean.

Hatchery rearing

Aquaculture is broadly defined as breeding and raising aquatic organisms in captivity as part of their life cycle (Stickney 2005). The breeding environment ranges from semi-natural ponds to intensive high-technologic farms using water-recirculation systems. Aquaculture has seen a world wide rapid expansion during the last twenty years, which is likely to continue to over the foreseeable future (FAO 2004). Fish farmed for the table market (*see* Brännäs and Johnsson 2008) are often selected for specific economically profitable characters (*i.e.* domestication), such as rapid growth, stress tolerance and late maturation (Stickney 2005). However, fish are also reared in hatcheries for release to supplement wild populations (Waples et al. 2007), which is the focus of this thesis.

Over the last two centuries, salmonids have been extirpated from a large part of their natural range as a result of exploitation, industrial pollution, agriculture and damming (Parrish et al. 1998; Lackey 2002). Regulations in rivers due to

power plants is a well-known problem for smolts migrating to sea (*e.g.* Thorstad et al. 2003) and adults migrating to spawning grounds (*reviewed by* Coutant and Withney 2000). Hatchery rearing originated as a means to increase the abundance of fish solely for fishery opportunities, but an increasing number of hatcheries have now the explicit mission to compensate for decline in the natural production or to sustain valuable populations (Aprahamian et al. 2003). The different types of hatchery programs are primarily based on the species vulnerability to extinction (Fraser 2008). For example, hatchery reared fish can be used to mitigate loss of natural production, to enhance populations above their natural carrying capacity, or to reintroduce fish in rivers where native populations are extinct (*reviewed by* Cross et al. 2007).

The value and efficiency of hatchery release programs are debated, and it has been questioned whether hatchery and wild fish are ecological exchangeable (Waples 1999; Levin et al. 2001; Bisson et al. 2002; Brannon et al. 2004; Araki et al. 2008). Studies have shown that released fish interfere (*i.e.* compete and/or interbreed) with wild counterparts (McGinnity et al. 2003; Bohlin et al. 2002; *reviewed by* Weber and Fausch 2003), which can have negative effects on the natural population (Fleming et al. 2000; Lynch and O'Hely 2001; Ford 2002; Araki et al. 2008). In addition, released fish often have poor survival in the wild resulting in poor contribution to the wild populations (*reviewed by* Olla et al. 1998; Brown and Laland 2001).

Why do hatchery and wild fish differ?

Both environmental and genetic factors can cause differences between wild and hatchery-reared fish. Environmental and genetic differences can arise separately or through a number of interlinked processes. *First*, naturally spawning fish invest considerable time and energy in mate acquisition, while mature hatchery fish are selected by humans for artificial propagation. However, little is still known about the consequences of neglecting sexual selection in most breeding programs (Berejikian et al. 2001;



Figure 3. Juvenile brown trout typically inhabit small streams (River Norumsån, SW, Sweden), whereas juvenile Atlantic salmon generally prefer larger rivers. The species often coexist in watercourses of intermediate size. Hatchery fish reared for supplementation purposes are commonly reared in indoor tanks throughout the juvenile stages (former Swedish Board of Fisheries research station, Kålarne, Sweden). Photo: Sofia Brockmark.

2009). *Second*, the relaxed selection is a natural consequence of the safe hatchery environment. Hatchery fish are provided an abundance of nutritious pellets, are protected from predators, and treated for diseases. Therefore, individuals with genotypes that otherwise would have been eliminated by natural selection in the wild, survive and are released at later life stages when density-dependent mortality has been reduced (Milner et al. 2003). Survival from egg to smolt stage is usually 85-95% in hatchery but only 1-5% in the wild (Reisenbichler et al. 2004).

Third, genetic variation within and among populations, reduced gene flow and environmental variability provide ample opportunities for local adaptation to evolve in the wild (Allendorf and Waples 1996). Directional selection for preferred traits, such as growth, causes hatchery fish to diverge genetically from fish of wild origin (Gross 1998; Tymchuk et al. 2009). Genetic differences between hatchery- and wild fish can also arise intentionally due to repeated use of hatchery-reared parental fish. Indeed, changes from the wild phenotype can occur rapidly, even in the second generation of hatchery fish (Araki et al. 2007a). Domestication selection may also result from inadvertent selection for non-target traits advantageous in captivity (Waples 1999). For example, rapid growth may promote increased risk taking, such

as the tendency to forage under risk of predation (Johnsson et al. 1996; Jönsson et al. 1996). Consequently, salmonids selectively bred for several generations tend to diverge behaviourally (Johnsson et al. 2001; Sundström and Johnsson 2004), morphologically (Fleming et al. 1994), physiologically (Fleming et al. 2002) and ecologically (Fleming and Gross 1993; Marchetti and Nevitt 2003; Araki et al. 2007b) from their wild counterparts.

Fourth, adaptive behaviour not only requires the genetic predisposition, but also depends on ontogenetic experience. In general, fish have a high phenotypic plasticity, and hatchery and wild fish experience substantially different environments as juveniles. Hatchery fish are often reared at high densities in barren tanks containing no live food and/or predators. Thus, hatchery-reared fish may be deprived of the experience of actively searching and handling live prey, as well as the experience of encountering potential predators (*reviewed by* Brown and Laland 2001). The hatchery rearing environment generally has a negative impact on fish welfare, mainly caused by high rearing densities and decreased water quality (*reviewed by* Ellis et al. 2002). High rearing densities can result in increased chronic stress, which in turn make fish more susceptible to diseases (Iguchi et al. 2003; Sundh 2009). However, the effects of

high stocking density appear to be species-specific. For example, Arctic charr (*Salvelinus alpinus*) is a shoaling species favoured by high rather than low densities (Jørgensen et al. 1993). The constant hatchery environment, lacking structural complexity, also does little to stimulate flexible behaviour (Braithwaite and Salvanes 2005; Salvanes and Braithwaite 2005; Salvanes et al. 2007; Lee and Berejikian 2008).

It is this fourth aspect, the environmental effect on phenotypic development that this thesis mainly deals with.

What can we do about it?

To maintain the genetic diversity in captive populations and to use fish of local origin have been considered critical to the success of hatchery programs (e.g. de Leaniz et al. 2007). By using adipose fin clipping in combination with micro-tagging or genetic marking, many supplementary and conservation programs today have a larger control and potential to maintain genetic diversity (Cross et al. 2007). Most hatchery programs, however, still neglect the effects of the captive environment on phenotypic development.

Planting eggs directly in the watercourse (Barlup & Moen 2001) or releasing hatchery-fish to their ancestral environments earlier than the smolt stage (Reisenbichler, 1997) might reduce opportunities for developmental divergence from the wild type. Indeed, hatchery reared brown trout of the seventh sea-ranched generation performed as well as their wild progenitors when both strains were planted out as eyed eggs (Dannewitz et al. 2004; Dahl et al. 2006). However, releasing fish prior to smolting is often not possible in regulated watercourses, which often lack proper nursing habitats and/or migration routes for anadromous fish (Cross et al. 2007).

Behavioural aspects has traditionally been largely neglected in aquatic conservation efforts (Shumway 1999), but there is now a growing interest in preparing naïve fish for the wild (reviewed by Griffin et al. 2000, Brown and Laland 2001). Life-skills training is here defined as an active training procedure to teach naïve fish

essential behaviours needed in the wild. Up to date researchers have mostly focused on learning naïve fish to respond to ecologically relevant stimuli, including foraging on live prey (Olla et al. 1994), predator recognition and proper anti-predator responses (e.g. Berejikian et al. 2003; Vilhunen et al. 2005). Even though it is commonly thought among the public that fish have “three second memory”, an expanding number of studies show that fish are capable of different types of learning and can use past experience to alter their behaviour (Brown et al. 2006). Attempts to train hatchery-reared animals have, however, yielded inconsistent results. According to Braithwaite and Salvanes (2005), efficient behaviour in the wild requires more than the ability to recognise a specific food type or predator, as the animal must be able to respond to a variety of challenges in a flexible manner. Therefore, an alternative approach may be to manipulate the hatchery environment to promote behavioural flexibility. For example, juvenile cod (*Gadus morhua*) reared with experience of variable food and spatial cues were faster to investigate and consume live prey than fish from conventional hatchery tanks (Braithwaite and Salvanes 2005). Also, the ability to forage on novel prey was enhanced in juvenile Atlantic salmon reared in enriched tanks (containing plants, rocks and novel objects) and exposed to live prey, compared to fish reared in conventional hatchery tanks feeding on pellets (Brown et al. 2003a). Thus, it seems reasonable to assume that more nature-like rearing environments can help hatchery fish to cope with novel cues more properly and hence adjust their behaviour to better adapt to the wild upon release. However, few studies have investigated effects of manipulations of the hatchery environment on post-release survival.

AIMS AND OBJECTIVES

The overall aim of my thesis is to improve the understanding of how structural complexity, density and the social environment influence the

phenotypic development of juvenile brown trout and Atlantic salmon, and how this understanding can be used to enhance the quality and post-release performance of hatchery fish.

Due to limited attention abilities only a certain amount of information can be processed at once. An individual's behaviour is constrained when a task becomes cognitively demanding and further reduced when the attention is divided between several tasks. In territorial juvenile trout, where the aggression is lower among familiar individuals, the decision to associate with familiar individuals may allow the attention to be focused on predator vigilance and feeding rather than aggressive interactions. The following prediction was tested:

Reduced aggression and increased vigilance in socially stable groups lead to more efficient predator detection .

High rearing densities and lack of physical structure are addressed as potential key factors in the hatchery environment responsible for impairing the phenotypic development important for surviving in the wild. Based on general constraints on the phenotypic development, resource defence theory, the theory of limited attention, and learning theory the following predictions were tested:

Reduced conventional hatchery densities facilitate the ability to cope with social situations, including the ability to defend contested resources, with subsequent positive effects on growth and survival in the wild.

Reduced conventional hatchery densities and increased structural complexity facilitate the ability to develop adaptive behaviour, including novel prey foraging, food location ability and anti-predator response, with subsequent positive effects on growth and survival in the wild.

Reduced conventional hatchery densities and increased structural complexity facilitate smoltification.

METHODS

Experimental fish

My studies were carried out using two species of the *Salmo* family: the brown trout, *Salmo trutta* (papers I-III) and the Atlantic salmon, *Salmo salar* (paper IV). The experimental fish were either offspring of wild naturally spawning parents (paper I) or artificially fertilized sea-ranched parents (papers II-IV). Sea-ranched fish refer to fish that have been reared in the hatchery from egg to smolt stage before release into natural waters (Sundström 2004). Compared to wild fish, which are shaped by sexual and natural selection, sea-ranched fish are artificially selected, and experience relaxed selection in the hatchery, followed by natural selection after release. Sea-ranched fish are commonly released in regulated waters with water court decisions and/or in waters with few adequate spawning grounds. The sea-ranched fish used in papers II-IV may have interbred with wild fish in tributaries or downstream the power plant.

Rearing conditions

The behavioural studies in paper I were performed at the Department of Zoology, University of Gothenburg using anadromous brown trout originating from river Jörlanda (58° N), south-western Sweden. In papers II-III, studies were conducted at the Swedish Board of Fisheries in Kälarne, mid-Sweden, using anadromous brown trout originating from river Dalälven (60°N). Eggs were first incubated at the Swedish Board of Fisheries in Älvkarleby before transported to Kälarne in late winter. The study presented in paper IV was performed at E.on's fish farm in Laholm, south-western Sweden using salmon fry originating from River Lagan (56°N).

In papers II-IV we compared the performance of fish reared at different densities. The conventional stocking densities (paper III-IV) were set according to the local practice at E.on's fish farm in Laholm (~1050 individualsm⁻³, paper IV) and the Swedish Board of Fisheries in Kälarne (425 individualsm⁻³, papers II-III).

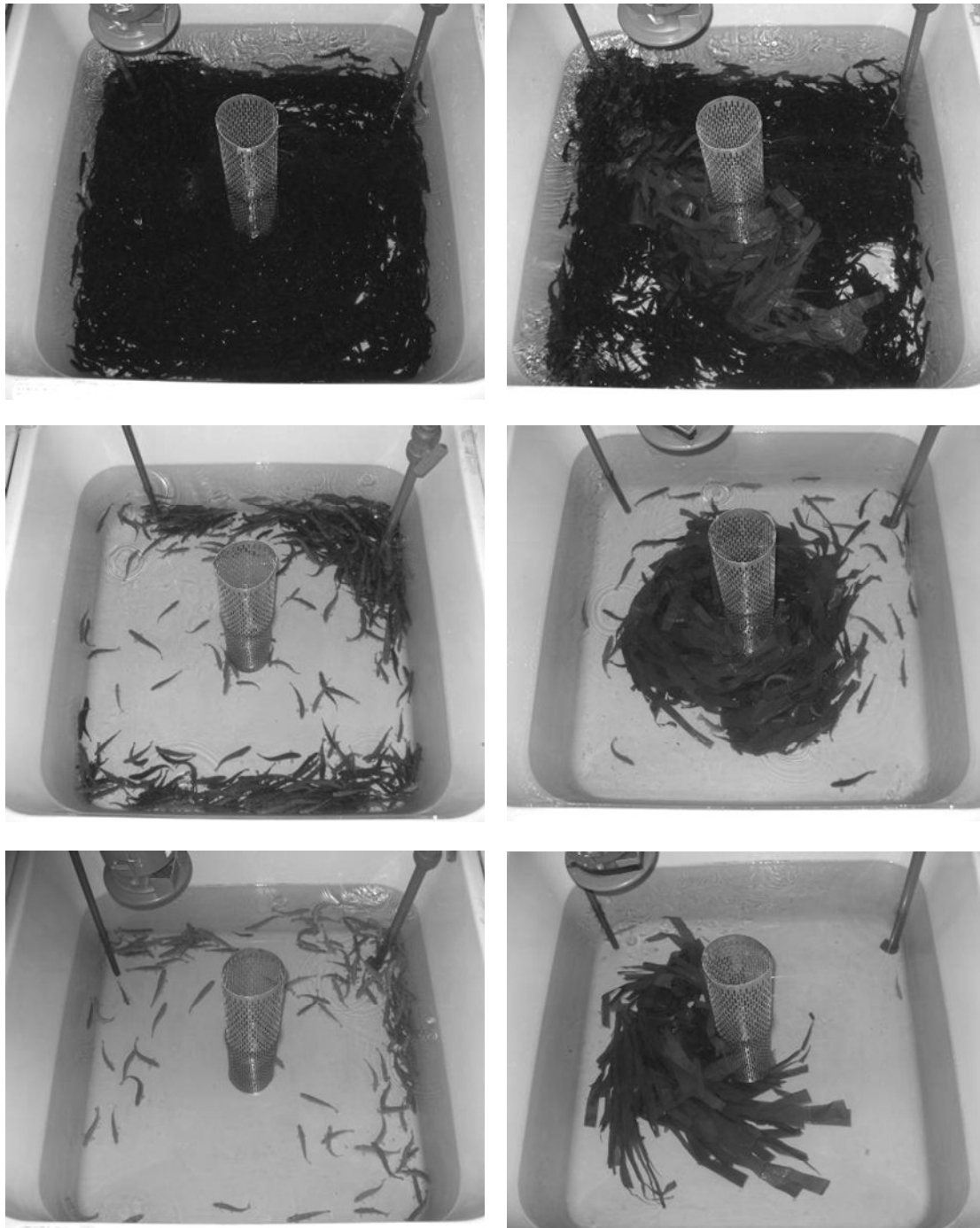


Figure 4. Rearing treatments used in the experiment presented in paper III. From the top: conventional hatchery density, approximately a third of conventional hatchery density and natural density. Pictures to the left show barren tanks and pictures to the right show tanks with structure. Photo: Bart Adriaenssens.

Conventional hatchery densities often differ between hatcheries, and it should be pointed out that hatchery densities for fish reared for supplementation are commonly lower than fish farmed for the table market. The natural rearing density was chosen according to Elliott's case study of migratory brown trout in a natural stream (Elliott 1994). Medium density (paper II-IV) was set to half of conventional density (paper II), or approximately a third of conventional density (paper III-IV).

In papers III-IV we also compared fish performance under different levels of structural complexity. Tanks were structured using green plastic bags, sliced up to resemble water-plants and provided with a stone ballast to keep them in place (see fig 4.). The bags provided tanks with protective shelter for the fish and more heterogeneous water flow dynamics compared with the barren tanks. Fish were reared from egg until the parr stage (papers II-III), or from fry until smolt stage (paper IV) in conventional hatchery tanks.

Field and laboratory procedures

In papers II-IV we evaluated the effects of rearing conditions (density and structure) on performance in natural streams. Fish were stocked in an enclosed section of river Aneråsån (63°N, paper II-III), or in river Smedjeån (56°N, paper IV), a tributary stream to river Lagan in southwest Sweden. Fish in both streams were exposed to predation from mink (*Mustela vison*) and heron (*Ardea cinerea*), and in Smedjeån also from northern pike (*Esox lucius*), European eel (*Anguilla anguilla*), pike perch (*Lucioperca lucioperca*) and resident brown trout. As the stream section in river Aneråsån was closed off by net, no fish could escape or invade the stream section.

In papers I-III behavioural data were either recorded manually, or by using a video camera. To document fin damage and silvering (paper IV), photos were taken using a digital camera. Plasma insulin-like growth factor I (McCormick 1993) and gill Na^+K^+ -ATPase activity (Moriyama et al. 1994) were measured according to standard protocols.

To capture wild fish (paper I) and to recapture released fish (papers II-IV), electrofishing was used (LUGAB 1000, straight DC, 200-400V (papers I and IV); 1000-1200V (papers II-III). The stream sections were repeatedly fished to increase recapture rates (paper IV), or to make sure that all fish were recaptured (papers II-III).

In the behavioural study (paper I) and in the field studies (papers II-IV), the adipose fin was removed to identify focal fish. In addition, the released fish were tagged using passive integrated transponder tags (PIT) inserted into the body cavity to enable individual identification (papers II-IV). Fish in the behavioural studies in paper II were also individually marked with a coloured pearl inserted below the dorsal fin.

When evaluating possible treatment effects it is of great importance to obtain a representative sample of fish (Barnard et al. 1993). In papers II-IV a standardised procedure was designed to minimise any sampling bias. Before sampling fish, the water level was lowered in the tank, and fish were subsequently caught by rapidly pulling the net from side to side two times. The sample was then released in a bucket filled with water and the fish were again netted, but now diagonally from bottom to top. This procedure was repeated three times until a sufficient number of fish were sampled. Moreover, fish were measured using the same anaesthetic and scale throughout a given study. The procedure was standardised by allowing superfluous water to be absorbed by a wet cloth before measuring the fish.

RESULTS AND DISCUSSION

Density and the social environment

The importance of social stability for adaptive behaviour

The ability of an animal to perform a task successfully is limited by the amount of attention being simultaneously focused on other activities. Individuals exposed to several tasks often choose

to allocate most of their attention on one of them. The potential fitness consequences of processing information from more than one source are considerable. We show that social stability can be of vital importance for survival under conditions of high predation risk (paper I). Groups of familiar brown trout were, on average, faster to escape a simulated predator attack from a heron model compared to groups containing an unfamiliar dominant individual. In addition, familiar groups were less aggressive and showed higher feeding activity than unfamiliar groups (paper I). Our results suggest that familiarity-biased association confers advantages through direct fitness benefits afforded by faster predator evasion responses and long-term benefits provided by increased feeding opportunities.

Manipulations with hatchery densities

In general, the results presented in this thesis reveal that reduced hatchery densities facilitate the development of adaptive behaviours

important for growth and survival in the wild. Several not mutually exclusive mechanisms are likely responsible for the strong effects of density, but before going into details, I would like to introduce a hypothetical model that can underlie further discussions below.

Figure 5 illustrates the pattern of phenotypic expression (*i.e.* reaction norm) of “the average genotype” across a range of densities (Pigliucci 2001). The variation in natural density (x-axis) gives a variation in the phenotypic expression (y-axis). Fish, reared at densities substantially higher than they are adapted for (*i.e.* conventional hatchery densities), will presumably express a phenotype outside the range of adaptive phenotypic variation in the wild. This may hypothetically explain why hatchery-reared fish generally have low fitness in the wild. If the genotype is less plastic (straightened curve) in extreme environments, hatchery densities may need to be decreased drastically to produce phenotypes that survive in the wild.

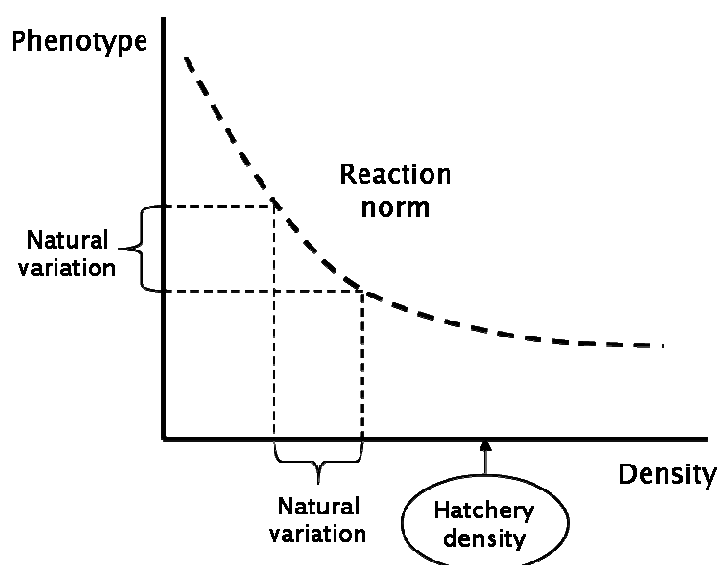


Figure 5. The reaction norm of a genotype transforms environmental variation into phenotypic variation. Hatchery density is an outlier that does not fit into the natural variation found in wild populations. This schematic model is modified from Suzuki et al. (1986).

Pre-release performance

Effects on behaviour

My results demonstrate density-dependent effects on competitive ability, the ability to forage on novel prey, spatial orientation, and adaptive anti-predator response (paper II-III). These behaviours are important life-skills for growth and survival in the wild.

I suggest that these density effects on behaviour can be explained by three not mutually exclusive mechanisms (Fig 1.). *First*, the potential for individual recognition decreases with increasing density due to cognitive constraints, reducing the capacity to develop recognition-based social systems and relations with specific individuals (*reviewed by* Griffiths and Ward 2006). It is therefore reasonable to believe that the development of competitive skills is influenced by density, which may help explaining why trout reared in natural-density tanks were more efficient competitors for food than fish reared at conventional densities (paper II). As previously discussed, familiarity can increase food intake, reduce aggression and increase vigilance towards predators (paper I), suggesting a general link between adaptive social behaviour and natural density conditions (paper II).

Second, the benefit of resource defence is expected to decrease with competitor density up to the threshold where resources are no longer economically defendable (Grant 1997). Fish reared in high-densities may be less likely to develop and express territorial behaviour, which may further explain why trout reared in natural densities were dominant in competition for food over conspecifics from the higher density treatments (paper II). Hatchery-reared salmonids have previously been shown to be less efficient in settling aggressive interactions than wild-reared conspecifics (Metcalfé et al. 2003), spending more time in territorial contests without increased probability of winning (Deverill et al. 1999; Sundström et al. 2003). This may suggest that the hatchery environment impairs the efficiency of contest assessment (Leimar and Enquist 1984).

Third, in a crowded environment physical

and cognitive constraints may lead to reduced individual control, switching from the use of private information and individual decisions to copying others (*e.g.* shoaling behaviour) (*reviewed by* Couzin et al. 2006; Volpato 2009). This possibly explain why fish reared at high densities consumed less novel prey, fled more rapid to refuges after a predator attack, and were faster to locate food in a maze compared to fish from reduced densities (paper III). Thus, behavioural responses to crowding (*i.e.* conventional hatchery densities) may constrain both social competence, as discussed above, and the development of individual behaviour skills.

Effects on growth

Hatchery fish grow faster due to high abundance of nutritious pellets, and are therefore generally larger than their wild counterparts at a given age. Generally, trout and salmon reared at lower densities grew faster than fish at higher densities, although all density treatments received the same feeding rate (paper II-IV). There are several possible mechanisms that may explain the density effect on growth. High densities can induce exploitation competition where individuals are getting in each others way, causing losses of a larger proportion of the food from the hatchery tank (Ruxton 1993). Related to this is the phenomenon of shadow interference where some individuals may experience reduced food intake from being “shadowed” by competitors (Elliott 2002; Krause and Ruxton 2002). Additionally, acute and chronic stress are known to reduce individual growth (*reviewed by* Ellis et al. 2008), which may explain the reduction in growth found in conventional densities (paper II-IV). However, in contrast to our results, several studies have reported negative effects of low rearing densities on growth rate (Ellis et al. 2002). In rainbow trout, for example, low stocking densities can lead to increased size variation (North et al. 2006).

Effects on smolt characteristics

Wild anadromous salmonids generally undergo parr-smolt transformation after one to five years,

whereas hatchery reared salmonids normally smoltify after one to two years. In Paper IV we investigated the effects of density conditions on smoltification. Prior to release, fish in reduced hatchery densities had higher plasma IGF-1 (paper IV), a hormone which is stimulated by temperature and photoperiod, and increases under parr-smolt transformation (Beckman et al. 2000). No difference was found in gill Na^+K^+ -ATPase activity between fish exposed to a seawater challenge test and fish kept in freshwater. However, seawater survival and silvering (i.e. adaptation to sea water) were significantly higher among fish reared at reduced densities (paper IV). Together this suggests that fish reared at reduced densities show more complete parr-smolt transformation than fish from conventional densities (paper IV).

Effects on fin erosions

Fin erosion is a recognized problem in many hatchery-reared fish species, including brown trout and Atlantic salmon (reviewed by Ellis et al. 2008). We found that Atlantic salmon reared at reduced densities had less-fin damage than fish in conventional hatchery densities (i.e. amount of dorsal fin tissue loss, paper IV). Nipping and fin damage associated with scramble competition is common in high-density hatchery situations (McLean et al. 2000; Ellis et al. 2002). Similar to our findings (paper IV), MacLean and colleges (2000) reported that the relationship between fish size and fin damage became stronger over the growing season. However, other studies have reported no such relationship (e.g. Turnbull et al. 1998).

Post-release performance

Effects on survival and growth

Fish reared at reduced densities generally survived and grew better after release compared to fish reared at higher densities (paper II-III). However, in paper IV low recapture rates (0.05% and 0.03%, approximately two, resp. nine months after release), reduced the statistical power for detecting treatment effects on survival.

Larger fish generally survive better after

release (Holtby et al. 1990; Quinn and Peterson 1996), possibly as the risk to be predated may change dramatically as prey individuals grow (i.e. size dependent predation risk, Brönmark and Milner 1992). Fish reared at reduced densities were larger in size at release in some (paper II-III), but not all studies (paper IV). However, size at release had no significant effect on post-release survival (paper II-IV).

There are several possible explanations for the strong density effects on survival in the natural stream (paper II-III). In general, however, it appears that the enhancement of adaptive individual and social behaviour, mediated by low rearing densities, was translated to higher fitness upon release into the wild (paper II-III). Brown trout parr have previously shown to defend protective territories harder when predation risk increases in the habitat (Johnsson et al. 2004), which may further increase predation mortality for subordinates when protective cover is limited (paper II). Moreover, it is not surprising that the density-induced behavioural effects: (i) increased ability to feed on live novel prey; (ii) increased spatial orientation ability, and (iii) a more efficient anti-predator response translate into increased survival and growth in the wild (paper III).

Even though the wild and hatchery environment differ quite drastically, parallels can be drawn to animals that naturally undergo habitat shifts as a part of their life history. Habitat transitions phases are thus typically associated with high levels of mortality (Biro et al. 2003; Byström et al. 2003), as animals have limited ability to divide their attention between several novel tasks when shifting to a new environment (Clark and Dukas 2003; Dukas 2002; paper I). This is likely one of the most important explanations for the mortality of the released fish in my studies (paper II-III).

Physical structure

Somewhat surprisingly, we found few clear effects of structure (paper III-IV). In addition,

some of these effects were negative. For example, brown trout reared in barren tanks were faster in performing an escape response after a simulated predator attack than were fish reared in tanks containing structure (paper III).

However, we found that Atlantic salmon reared in low-density tanks with structure reached a larger body size at smoltification when compared with fish reared in conventional tanks (paper IV). Structural complexity in combination with low density may have reduced visual contact between individuals, which in turn may have allowed fish to spend more time feeding rather than interacting with conspecifics. An additional explanation may be that structure allowed fish to hold positions in low-velocity areas (*i.e.* behind the structure) and thus saved energy costs (Huntingford et al. 1998; Kalleberg 1958). Growth was, however, not affected by structural complexity at younger life stages (*i.e.* before first winter, paper III-IV).

Structural enrichment is a definition that has been used widely, ranging from introduction of physical structure *per se* (Kihlslinger and Nevitt 2006; Lee and Berejikian 2008), to structure in combination with an additional modifications. For example, cod (*Gadus morhua*) reared in tanks with variable structure (*i.e.* where structure periodically was moved around) appear to have more flexible behavioural repertoires than cod reared in conventional hatchery tanks (Braithwaite and Salvanes 2005; Salvanes and Braithwaite 2005). Moreover, a combination of live food and structure in rearing tanks improved foraging in Atlantic salmon (Brown et al. 2003). Also, the fin quality of juvenile steelhead reared in tanks containing wood, overhead shade and underwater feeders was similar to that of naturally reared steelhead (Berejikian and Tezak 2005, see also Berejikian et al. 2000). However, even though many studies refer to positive effects of structure, few have actually found effects of physical structure *per se*. These differences in design may explain the inconsistent results reported on structural manipulations, including the results in thesis.

Implications for hatchery rearing

To the best of my knowledge, the results presented in this thesis are the first showing that **a reduction of conventional hatchery densities drastically enhances the development of adaptive behaviour and post-release survival of hatchery-reared salmonids** (paper II-III). This result has important implications for hatchery rearing practices. Combining the survival data on brown trout parr from paper II and III suggests that post-release survival decreases exponentially over the range of densities used (Fig. 6). Concordantly, adaptive individual and social behaviour skills appear to deteriorate with increasing density (paper II and III). We found no effects when conventional hatchery densities were reduced to half (paper II), but a density reduction to a third of conventional densities resulted in significant enhancements of behaviour and survival (paper III). However, even stronger effects were acquired when densities were reduced to high natural levels (Elliott 1994, paper II-III). It can thus be speculated that the exponential decrease in survival with increasing densities is related to limited abilities to develop adaptive behaviour and/or, more generally, that conventional hatchery densities impairs phenotypic development, resulting in fish poorly adapted to the wild (Fig. 5).

Ecologically sound rearing methods are not only important to increase return rates of mature adult salmonids, but should also be considered from an ethical point of view (Shumway 1999; Branson 2008). In the context of the continuous growth of captive rearing and growing interest of fish welfare, behaviour should be taken into account when rearing fish. Together with previous studies (Braithwaite and Salvanes 2005; Salvanes and Braithwaite 2005; Salvanes et al. 2007; Lee and Berejikian 2008), the results presented in my thesis strongly suggest that simple manipulations of the hatchery environment can promote adaptive behavioural development resulting in increased survival of fish released into the wild.

Recent studies on fish have demonstrated

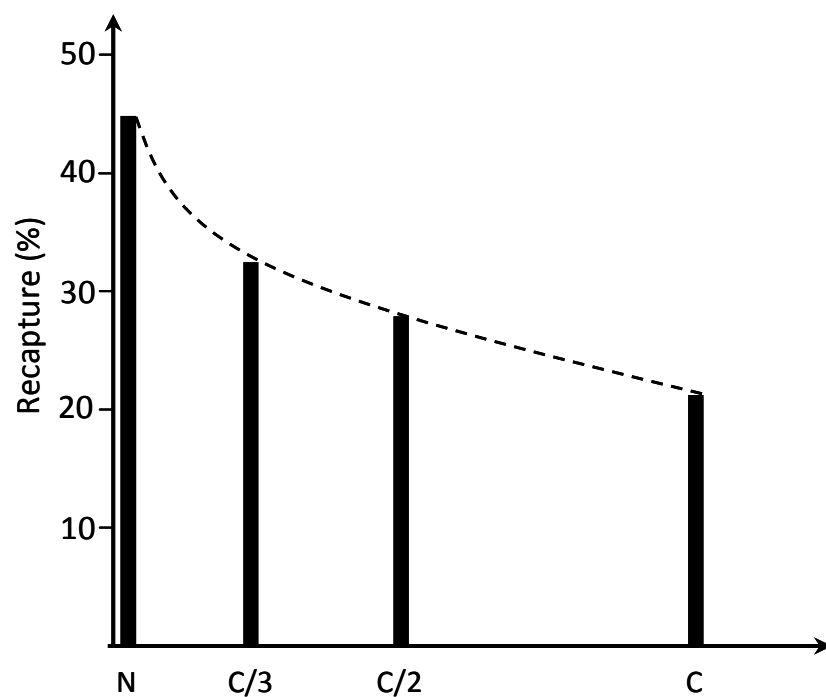


Figure 6. Recapture rates (%) of hatchery-reared brown trout parr released and recaptured after approximately a month in a natural stream. The trout were reared at the following densities: N (high natural densities), C (conventional hatchery densities), C/2 and C/3 (approximately half and a third of conventional hatchery densities). The figure is based on results presented in papers II and III. The extrapolated dashed line illustrates hypothetical return rates associated with different hatchery rearing densities.

that they are able to integrate and memorize complex information, abilities requiring advanced cognitive processing (Braithwaite 2006; Brown et al. 2006). In addition, fish show strong species-specific behaviours, including ontogenetic effects on sociality and habitat use (reviewed by Godin 1997; and Ruxton and Krause 2002; reviewed in Magnhagen et al. 2008). The high rearing densities used in traditional supplementation programs is unlikely to meet specific behavioural, especially in species with territorial juvenile stages, like many salmonids. The results in my thesis highlight the need to consider the behavioural requirements of young territorial salmonid species reared for supplementation. Thus, the ultimate aim of supplementation and conservation hatcheries should be to produce fish similar to those in the wild, whereas the table market requires fish that are well-adapted to the captive-environment (Brännäs and Johnsson 2008). However, power companies are generally

obliged to compensate for the loss of smolt production in regulated waters, based on the number of fish released, not on return rates. As an unfortunate result, smolt production has traditionally focused on quantity rather than quality. Adjustments in water court decision have recently been discussed by the Swedish Board of Fisheries (Fiskeriverket rapport 2007). Brown and Day (2002) have recently pointed at that government funding of supplementation hatcheries may cause similar problems.

Reducing hatchery densities is a relative simple method to practice in supplementary and/or conservation hatcheries. However, a drastic reduction might be economically demanding unless increased adult returns will compensate for the reduction in numbers of released juveniles. With this background, two points are important to make. *First*, the positive effects on post-release performance were only measured after short periods. Thus, long term cumulative effects on

growth and return rates could not be evaluated. *Second*, there is a growing public interest in the ethical aspects of captive rearing, where people are becoming concerned about fish welfare issues, demanding the right for captive animals to express their natural behaviour (Shumway 1999; Huntingford et al. 2006; Ashley 2007).

Finally, considering that only one of many interacting factors in the hatchery environment was manipulated in the present study, the scope for modifying the rearing methods of supplementary hatcheries to increase their contribution to natural production may be substantial (Braithwaite and Salvanes 2005; Salvanes and Braithwaite 2005; Lee and Berejikian 2008). There is, however, a limit to what we can accomplish with improving hatchery rearing methods (Waples 1999). Habitat restoration and preservation will always be critical to maintain viable natural populations. Hence, hatchery rearing should be a last-resort solution, a complement rather than an alternative to habitat conservation.

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