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Rapid growth of Atlantic salmon juveniles in captivity may indicate poor performance in nature

Arto Saikkonen[a,1], Jukka Kekäläinen[a,b,*], Jorma Piironen[c]

[a] Department of Biology, University of Eastern Finland, P.O. Box 111, FI-80101 Joensuu, Finland
[b] Department of Biological and Environmental Science, University of Jyväskylä, P.O. Box 35 (YAC-315.2), FI-40014 Jyväskylä, Finland
[c] Finnish Game and Fisheries Research Institute, Joensuu Game and Fisheries Research, Yliopistonkatu 6, FI-80100 Joensuu, Finland

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ABSTRACT

The hatchery environment often favours completely different traits than natural selection in the wild. Consequently, hatchery-reared fish are usually larger and more aggressive than their wild counterparts. Increased growth rate and aggression are predicted to be beneficial in feeding competition in hatcheries, but not necessarily in nature, where food resources are spatially and temporally more variable. We compared the growth, condition and mortality of landlocked Atlantic salmon (*Salmo salar* L.) juveniles in a common hatchery environment and when feeding on natural prey in semi-natural channels. We found that the growth and survival probability of the fish in the hatchery was negatively associated with their performance in the semi-natural channels. Furthermore, we found tendencies for directional selection (linear selection differential and gradient: $P < 0.1$, in both cases) against large body size in semi-natural channels, but not in the hatchery. Therefore, good performance during hatchery rearing may indicate reduced performance in food-limited natural conditions, where selection may favour smaller individuals that have a lower standard metabolic rate (higher growth efficiency). If our results are also valid in fully natural conditions, they suggest that selective stocking of the most successful hatchery phenotypes may not be an optimal strategy to conserve endangered natural salmonid populations.

1. Introduction

Stocking of captive bred individuals to their original habitats is a commonly used method to support or reintroduce natural fish populations. The primary aim of captive breeding programs is to maintain populations that are unable to survive in the wild, until the naturally reproducing population is again re-established (Utter and Epifanio, 2002; Fraser, 2008). Unfortunately, the fitness of the hatchery-reared fish can decline extremely rapidly which can severely impede the recovery of natural populations (Araki et al., 2007, 2008; Blanchet et al., 2008; see also Wang and Ryman, 2001). Due to unnatural hatchery environments, hatchery-reared fish encounter radically different selective forces than their wild counterparts (Hindar et al., 1991; Waples, 1991; Fleming and Gross, 1993; Snyder et al., 1996; Reisenbichler and Rubin, 1999; Frankham, 2008; Robert, 2009; see also Carlson et al., 2007). At the worst, artificial selection may promote fixation of alleles that are even deleterious in the nature (Olla et al., 1998; Lynch and O'Hely, 2001; Jonsson and Jonsson, 2006). The avoidance of detrimental genetic changes requires that any kind of artificial selection during hatchery rearing is minimised. Unfortunately, recent hatchery practices have been demonstrated to cause significant maladaptive changes in various morphological, behavioural and physiological traits (Fleming et al., 1994; Jonsson, 1997; Kallio-Nyberg and Koljonen, 1997; McDonald et al., 1998; Johnsson et al., 2001; Brockmark et al., 2007; Brockmark and Johnsson, 2010). For example unnaturally high rearing densities in hatcheries may select for fish phenotypes that have reduced feeding and predator avoidance ability as well as survival in the wild (Brockmark and Johnsson, 2010; Brockmark et al., 2010).

In nature, only a minor proportion of fish larvae are able to survive to reproduction, which means that the surviving phenotypes are only a minor subset of all available phenotypes. Instead, due to unnaturally favourable conditions, a much larger fraction of these phenotypes can survive in captivity (e.g. Braithwaite and Salvanes, 2005). Thus, most of the hatchery phenotypes must be eliminated in nature (Weber and Fausch, 2003). This raises the possibility that the phenotypes which are successful in captivity are not necessarily the best phenotypes in natural conditions. The common practice of supportive breeding programs is to selectively use the best phenotypes for restocking

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* Corresponding author at: Department of Biology, University of Eastern Finland, P.O. Box 111, FI-80101 Joensuu, Finland. Tel.: +358 13 251 4577; fax: +358 13 251 3449.

E-mail addresses: arto.saikkonen@metsa.fi (A. Saikkonen), jukka.s.kekalainen@uef.fi (J. Kekäläinen), jorma.piironen@rktl.fi (J. Piironen).

[1] Present address: Metsähallitus, PL 36 (Ivalontie 10), FI-99801 Ivalo, Finland.

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natural habitats, which in practice frequently means selective use of individuals with a high growth rate. Large body size may potentially confer some fitness benefits in the nature (e.g. give some protection against gape-limited predators). However, in hatchery conditions, aggression is positively associated with body size and large body size is in turn associated with decreased wariness in the vicinity of predators (Martel and Dill, 1993; Johnsson et al., 1996; Fleming and Einum, 1997; Olla et al., 1998; Weber and Fausch, 2003). This suggests that large body size may ultimately have a negative effect on predator avoidance behaviour and overall fitness of the hatchery fish (Munch and Conover, 2003; Biro et al., 2005; Stoks et al., 2005; Sundt-Hansen et al., 2009).

Growth rate is generally thought to be positively associated with individual dominance status. However, earlier studies investigating the influence of the dominance status on individual growth rates in nature have found conflicting results (Nakano, 1994; Höjesjö et al., 2002; Martin-Smith and Armstrong, 2002; Harwood et al., 2003). Dominance status seems to predict individual growth rate in some conditions, but not in others. Dominants often have a higher standard metabolic rate (SMR) than subordinates, which can be beneficial in conditions where dominant individuals can easily increase their food intake to compensate their higher energy expenditure (Metcalfe, 1986; Cutts et al., 2001; Lahti et al., 2002). Thus, large body size is predicted to be beneficial in feeding competition in hatcheries where food is delivered in highly predictable locations, but not necessarily in more unpredictable, food-limited habitats where the monopolisation of resources and high food intake is not possible (Niva and Jokela, 2000; Harwood et al., 2003; Vøllestad and Quinn, 2003). Höjesjö et al. (2004) also demonstrated that the relative competitive ability of dominant and subordinate individuals can change in response to habitat complexity per se. The authors showed that habitat complexity decreases the growth rate of dominant individuals in relation to subordinates, but that in structurally simple habitats, the pattern is reversed. Together, these studies indicate that even if large (dominant) individuals often win the feeding competition in structurally simple conditions, large body size does not necessarily predict their competitive ability in structurally complex natural habitats.

Many wild Atlantic salmon populations are endangered, which partly explains why it is one of the most widespread species in hatcheries throughout the world (Lackey et al., 2006; Williams, 2006). Atlantic salmon are also an ideal model species to study the potential fitness effects of hatchery selection, since salmonids seem to be particularly susceptible to fitness loss during captivity (Araki et al., 2008). Even if vast numbers of studies have hypothesised that hatchery fish have lower fitness than wild fish (e.g. Lynch and O'Hely, 2001; Ford, 2002; Frankham et al., 2002; Araki et al., 2008), the present knowledge does not allow us to make firm conclusions about how useful captive-reared individuals really are in the restoration of endangered populations (Ryman and Utter, 1987; Araki et al., 2008). More studies are required to discover the ultimate mechanisms that may lead to reduced fitness of hatchery-reared fish in the wild (Araki et al., 2008).

In the present study, we investigated the growth, body condition and mortality of endangered Lake Saimaa (Finland) landlocked Atlantic salmon juveniles in a common hatchery environment and in semi-natural stream channels. More specifically, we studied whether performance (body size, condition and survival) in hatchery conditions is associated with increased performance in more natural feeding conditions. Since selection is expected to favour different traits in these two environments, we predicted that the same phenotypes could not have the highest success in both environments.

2. Materials and methods

2.1. Experimental fish

In the autumn of 2000, sexually mature landlocked Atlantic salmon males ($n = 8$) and females ($n = 15$) were gill-netted from the Pielisjoki River, downstream from the Kuurna hydropower station (62°42 N, 29°52 E). The milt of each male (except one individual) was used to fertilise the eggs of two females to create half-sibling families for later experiments. All the eggs were transported to the Finnish Game and Fisheries Research Institute's Enonkoski aquaculture station, where the eggs were incubated in family-specific containers until hatching next spring. After hatching, a haphazard sample of 150 offspring was collected from each family for further rearing. All the families were maintained in identical ca 0.1 m^3 circular tanks with continuous water flow (18 cm water depth) until March 13th 2002 when the first stage of the experiment was started. On the same day, all the fish were tagged with fluorescent elastomer tags (Northwest Marine Technology Inc., USA) (family-specific tag) and with passive integrated transponders (Trovan Ltd., UK) (individual tag). The length of the individual tag was only 12 mm, so that it could be placed in the body cavity via a small incision. Because of the high costs of the individual tagging, most of the fish were tagged by family-specific tags only. Prior to tagging, all the fish were anesthetised with tricaine methanesulfonate (MS-222, Sigma®, Sigma Chemical Co., St. Louis, Missouri, USA) and measured for total length and fresh mass. After tagging, the salmon families were divided into experimental groups, by taking a haphazard sample of 10 individuals from each of the 15 family groups. These fish were placed in separate ca 0.4 m^3 circular tanks (150 individuals/pool, rearing density: 375 individuals m^{-3}). The same procedure was replicated nine times (nine individual fish pools). In two pools, fish had been marked both with family-specific and individual tags, whereas in seven pools only family-specific tags were used. Fish from six pools were placed in six independent semi-natural stream channels in June 2002, while three groups were left in their pools in the hatchery (control groups). Due to technical difficulties in water flow control in one semi-natural channels, this channel was omitted from further analyses.

2.2. Experimental channels and fish feeding

Approximately 30 days prior to semi-natural experiments, the bottom of the six 2.5 m wide, 30 m long (ca 25 m^3, fish density: 6 individuals m^{-3}) concrete channels was covered with 10–60 mm gravel and stones. In addition, bigger stone piles were constructed throughout the channels to provide microhabitats for the fish. The stream velocity was approximately similar (ca. 20 l s^{-1}) in all five stream channels. Each channel was covered with overhanging nets to provide shading and shelter against bird predators. The primary aim was to make conditions between the channels as identical as possible. Five fold-down barriers were built in each channel to separate the channel sections prior to electrofishing (see below). Soon after the construction of the semi-natural channels, a natural benthic fauna emerged in the channels, including several taxa: Hirudinea, Gastropoda, Ephemeroptera, Trichoptera and Diptera. Fish were not fed in the channels. In the hatchery (control) groups, fish were maintained in 0.4 m^3 circular pools with continuous water flow. Fish were automatically fed daily with commercial fish food (Rehuraisio Oy, Raisio, Finland). Pellet size was 1.7 mm during the spring period (Until June 9th) and 3.5 mm during the summer (after June 9th). All incoming water of the Enonkoski aquaculture station is taken from the nearby Lake Ylä-Enonvesi. Thus, the water temperature in experimental and control environments did not differ each others and followed the natural rhythm during the whole study period (temperature range 1.6–21.0 °C).