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The feeding behaviour of cultured and wild Atlantic salmon, *Salmo salar* L., in the Louvenga River, Kola Peninsula, Russia

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An underwater survey was conducted in the Louvenga River to investigate the behaviour and distribution of juvenile Atlantic salmon, *Salmo salar* L., and the adaptation of cultured fish to the natural environment. The food and feeding habits of 34 wild and 44 cultured parr released from the Kandalaksha hatchery were also studied. The cultured salmon fed mostly in the bottom 15 cm of the water column in current velocities of 0.2–0.35 m s^{-1}. In contrast to wild fish, when cultured fish moved away from these areas and into areas with higher current velocities (average speeds of 0.52 m s^{-1}) and lower drift density (2.66 particles m^{-3}), they did not show a tendency to return to slower moving water. The diet of cultured parr was made up of benthic invertebrates (20%), terrestrial insects (32%), and drift items (33%), but these proportions were different in the diet of wild parr (2%, 24%, and 67%, respectively), with drift items predominating. The mean quantity of food per stomach indicated that the wild parr were feeding more actively than cultured parr. Invertebrates made up 3% of items in the drift, with the remaining 97% being exuvia of aquatic and terrestrial insects, algae, and various plant remains. Poor quality food items were found in 13% and 25% of the stomachs of wild and cultured parr, respectively, demonstrating that the cultured parr were less able to differentiate food items in the water column and made 20–30% more false feeding attempts than wild fish. The cultured parr were also more aggressive in terms of the frequency of aggressive interactions and reacted to each other at greater distances than wild fish. Thus, wild parr were able to optimize their feeding conditions by choosing habitats with preferred sizes of food items, higher densities of drift items, and current velocities that allowed them to maintain station and to feed more effectively. Conversely, cultured parr usually occupied suboptimal areas.

Keywords: behaviour, feeding, foraging behaviour, hatchery parr, salmon, swimming capacity, underwater surveys, wild parr.

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Introduction

The declining abundance of many populations of Atlantic salmon has increased interest in stock rebuilding programmes, involving the release of cultured fish and other management actions. However, the survival of cultured fish following their release into the wild remains low. There is a substantial amount of literature documenting the negative aspects of cultured fish, such as physiological and behavioural characteristics that could contribute to their low survival in the wild (Greene, 1952; Vincent, 1960; Flick and Webster, 1964; Moyle, 1969; Bachman, 1984; Nikonorov and Vitvitskaya, 1993; Klovach, 2003).

Foraging efficiency is one factor that affects the survival of cultured fish in the wild. The feeding intensity of cultured juvenile salmon following release into the wild is extremely low, and the composition of their diet is more restricted than that of wild fish (Sosiak *et al.*, 1979).

Following release into the wild, hatchery-reared salmon parr fed mainly on adult dipteral and benthic organisms, while wild parr consumed mostly drift items (Mitans, 1970; Smirnov *et al.*, 1985; Orlov, 2005). Cultured salmon also lack a diurnal feeding rhythm corresponding to the variable abundance of drift items, which is characteristic of wild juveniles (Zadorina, 1985). In this paper, we compare the feeding efficiency and behaviour of wild and cultured salmon under natural conditions in the Louvenga River, on the Kola Peninsula, Russia.

Material and methods

The study was conducted in the Louvenga River (Figure 1), which is stocked annually in June with 2+ year-old cultured salmon (70% parr, 30% smolts) from the Kandalaksha hatchery. The resident wild parr were derived from the natural spawning of wild fish. The age of the wild parr varied from 1+ to 3+ years. The study was conducted in July (1991–1996), one month after the release of cultured salmon from the hatchery when the wild and cultured fish occupied similar habitats. Chosen for the investigation was a section of river situated between two riffles, 1.5 km from the river mouth, with a total study area of 60 m^2 and a maximum water depth of 1.2 m. The river bed was composed of large- and medium-sized pebbles (3–6 cm) and boulders. Underwater observation of fish behaviour, sampling of drift particles, and measurements of current velocities were made, and samples of wild and cultured parr were collected to compare their diets. Following capture, the sampled parr were measured (fork length) and weighed (Table 1).

Figure 1. Map showing the location of the Louvenga River.

Table 1. Mean fork length (cm) and weight (g) with standard deviations (s.d.) for wild and cultured salmon in this study. The sample sizes are also given.

		Fork length (cm)		Weight (g)	
Origin of fish	Sample size	Mean	s.d.	Mean	s.d.
Cultured	44	11.3	4.22	14.9	5.7
Wild	34	8.9	1.46	9.6	1.3

Underwater investigations were carried out twice daily, more than 40 in all, with 345 cultured and wild salmon parr being observed. Observations were performed by a scuba diver lying in the river close to the river bed in depths not exceeding 0.3 m. The water's clarity allowed observations from distances of 1.5–2.0 m, which were recorded using a slate and pencil without affecting the behaviour of the observed fish. Their origin (i.e. cultured or wild) was identified. All cultured fish were adipose fin-clipped before release, facilitating their identification. Furthermore, cultured fish were characterized by scale loss, uneven and relatively short fins, and often by necrosis of the dorsal fin. During observation, the number of successful and unsuccessful feeding attempts was noted together with the frequency of acts of aggression. Aggressive behaviour included threatening poses, charges, chases, and nips. False feeding attempts were recorded when fish discarded particles from their mouths.

Drift particles were sampled using a drifter-trap consisting of a wooden frame (20 × 60 cm) covered with filtering fabric (23 meshes cm^{-1}). Each trap set lasted 15 min, and 62 drift samples were collected. Current velocities in the areas occupied by the salmon were measured using a standard current meter.

Samples of both cultured and wild juvenile salmon were collected from the river using a specially constructed landing net with 10-mm mesh netting. The stomach contents of 34 wild and 44 cultured fish were examined. The feeding rate was estimated from the indices of stomach fullness expressed in parts per thousand (‰ mass estimates).

Results

All the wild fish were territorial. In contrast, one month after their release into the river, the cultured fish remained in groups at significantly higher densities than the wild fish (Mann–Whitney test, $U = 22.5$, $p < 0.01$) (Table 2).

One month after release, the cultured juveniles were feeding actively. However, based on the average amount of food per stomach, the wild fish fed more intensively than cultured juveniles. The index of stomach fullness in cultured fish (57‰) was significantly lower than that in wild specimens (154‰) (Mann–Whitney test, $U = 2.1$, $p < 0.001$).

Table 2. Mean density (number of fish m^{-2}) of cultured and wild Atlantic salmon parr in the Louvenga River. The standard deviations (s.d.) and the 95% confidence limits (CL) are also shown. The difference between the compared samples is statistically significant (Mann–Whitney test, $U = 22.5$, $p < 0.01$).

Origin of fish	Number of study sites	Mean density (fish m^{-2})	95% CL	Min–max	s.d.
Cultured	20	0.35	0.25–0.45	0.08–0.8	0.21
Wild	20	0.06	0.04–0.08	0.02–0.18	0.05

Aquatic organisms and the exuvia of aquatic and terrestrial insects together with algae and various plant remains made up 3% and 97%, respectively, of the total number of sampled particles in the water column. The exuvia, algae, and plant remains are of low nutritional value and occurred more frequently in the stomachs of the cultured ($n = 11$) than the wild fish ($n = 1$). Cultured salmon rarely distinguished between high and low quality food items in the water column and consumed 20–30% more poor quality items than wild fish (Mann–Whitney test, $U = 8.5$, $p < 0.001$). In areas with higher current velocities, and consequently faster movement of drift items, this situation was more pronounced. The number of false feeding attempts for wild fish was independent of current velocity (ANOVA, $F = 1.19$, d.f. = 3, $p = 0.23$), while for cultured fish this relationship was significant (ANOVA, $F = 48$, d.f. = 3, $p < 0.01$).

Data on the feeding activity of cultured and wild salmon, particularly the comparative analysis of the relationship between number of feeding attempts and drift density, indicate that for cultured salmon, feeding attempts correlated significantly with the density of food items in the drift, both for edible items ($r = 0.65$, $F = 10.4$, $p < 0.05$) and total (edible and inedible) drift items ($r = 0.52$, $F = 5.2$, $p < 0.05$). In contrast, for wild fish, the relationship between the number of feeding attempts and total drift density was not significant ($r = -0.18$, $F = 0.5$, $p = 0.49$), and the correlation between the number of feeding attempts and edible drift density was stronger ($r = 0.92$, $F = 80.8$, $p < 0.001$).

Stomach content analysis revealed clear differences in the food selected by wild and cultured fish. Stomachs of cultured parr contained 16% (by mass) cased caddis fly larvae (Trichoptera) (cf. 0.9% in wild fish), 32% aerial insects (24% in wild fish), 3.6% molluscs (0.6% in wild fish), and 16% inedible items (7% in wild fish) (Table 3).

Wild fish consumed significantly more mayfly (Ephemeroptera) larvae (42%), uncased caddis larvae (24%), and chironomid and Trichoptera pupae (1.2%) than cultured parr. These groups occurred in the diet of all wild fish and in the drift. Wild parr, therefore, consumed mainly the edible items in the drift.

Table 3. Diet composition (mean % of the total mass of stomach contents) in juvenile wild and cultured salmon from the Louvenga River. *p*-level, significance level of comparison between the samples (Mann–Whitney *U* test), bold values are statistically significant.

Item in stomach contents	Cultured salmon	Wild salmon	*p*-Level
Mayfly larvae	15.3	41.9	<**0.01**
Trichoptera larvae	15.1	23.8	<**0.05**
Trichoptera larvae with lodges	16.1	0.9	<**0.01**
Diptera larvae (Simuliidae and Chironomidae)	2.2	0.4	0.07
Pupae (Chironomidae and Trichoptera)	0.3	1.2	<**0.05**
Imagos (aerial insects)	31.7	24.2	0.11
Molluscs	3.6	0.6	<**0.05**
Inedible particles	15.7	7.0	<**0.01**

The diet of cultured fish was similar to that of wild salmon, but the main food items for wild fish occurred less frequently in the stomachs of cultured parr. A significant proportion of the diet of cultured fish was composed of the less-favoured food items of wild parr, such as cased caddis fly larvae, and pupae and imagoes of various insects. In contrast to wild parr, cultured fish obtained a significant proportion of their diet from the river bed rather than from the drift. Cultured salmon also consumed more sand, detritus, and algae, with levels reaching 8% of the total weight of food consumed.

The average number of food organisms per stomach was 10 and 128 for cultured and wild parr, respectively. The stomach fullness index averaged 82% and 94% for cultured and wild fish, respectively. The mean index for a single food organism (estimated by weight) amounted to 6.6‰ in cultured fish and 0.7‰ in wild fish. These data indicate that food organisms with greater individual mass, i.e. primarily molluscs and cased caddis fly larvae, are most frequent in the diet of cultured fish (Table 3).

These differences in diet between cultured and wild salmon are closely linked to their swimming ability and feeding behaviour. Cultured salmon fed mostly in the bottom 15 cm of the water column in current speeds of 0.28 m s^{-1}, while wild parr occupied habitats with an average current velocity of 0.47 m s^{-1} (Mann–Whitney test, $U = 49$, $p < 0.01$). The habitats selected by wild salmon were characterized by high drift density (3.2 ± 0.48 particles m^{-3}), and items from the drift made up the main component of their diet. Habitats occupied by cultured parr had low densities of food items in the drift, and these parr fed on benthic invertebrates and terrestrial insects that had fallen onto the water surface. On occasion, cultured parr encountering faster flow (0.52 m s^{-1} on average) with lower drift density (2.66 ± 0.18 particles m^{-3}) did not attempt to return to more favourable habitats.

There was a weak but statistically significant relationship between the number of aggressive acts and wild parr density ($r = 0.51$, $F = 5.91$, $p < 0.05$). The relationship between the level of aggression and drift abundance (r_1) and current velocity (r_2) was not significant for wild fish ($r_1 = -0.47$, $F = 4.17$, $p = 0.06$; $r_2 = -0.12$, $F = 0.23$, $p = 0.64$). In contrast, there was a significant relationship between the level of aggression and parr density for cultured parr ($r = 0.97$, $F = 252$, $p < 0.01$). There was also a significant correlation between levels of aggression in cultured parr and drift abundance (r_1) and the current velocity (r_2) ($r_1 = 0.95$, $F = 138$, $p < 0.01$; $r_2 = -0.90$, $F = 65$, $p < 0.01$).

Discussion

It is generally recognized that the feeding and territorial behaviour of cultured Atlantic salmon parr only equals that of wild parr after a period varying from several days to one month post-release (Mitans, 1970; Shustov *et al.*, 1980; Ermolayev, 1982; Bakshtansky and Nesterov, 1985; Zadorina, 1985; Bougayev *et al.*, 1987; Shchurov, 1987). In this study, the density of cultured parr was five times higher than that of wild parr one month after their release (Table 2).

Wild parr occupied habitats with optimum current velocities and higher densities of drift items, whereas cultured fish occupied habitats with slower currents and lower drift densities. For feeding, hatchery-reared parr preferred current velocities <0.22–0.23 m s^{-1} by day (Bakshtansky *et al.*, 1980; Safonov, 1981; Safonov *et al.*, 1985) and 0.27 m s^{-1} at night (Safonov *et al.*, 1985). In this study, however, cultured parr occurred frequently in habitats with higher current velocities in which the number of their false feeding attempts increased significantly and, in contrast to wild parr, they did not attempt to leave these areas. There was some evidence that cultured fish could not feed on drift in these higher current velocities and adopted a benthic feeding mode. Wild parr were able to optimize their feeding conditions, occupying habitats with the preferred size of food items, greater density of drift, and current velocities that allowed them to remain in the selected parts of the river and to feed effectively, while cultured fish usually occupied suboptimal areas.

Previous studies have indicated that only 50% of cultured smolts were able to maintain position in a stream at current velocities of 0.5 m s^{-1}, 40% remained close to or on the substratum, and 10% were displaced by the current (Ermolayev, 1982). When parr make their feeding attempts at an angle to the current, the probability of current-mediated displacement increases. Safonov *et al.* (1985) found a negative correlation between the current velocity selected by juvenile salmon and the distance of their feeding attempts. This relationship is more pronounced for cultured fish ($r = -0.63$) than for wild fish ($r = -0.51$) and suggests that cultured fish have poorer foraging ability at higher current velocities and that, possibly as a result, cultured fish obtain a considerable part of their diet by feeding on the river bed. Wild fish, in contrast, rarely feed on the river bed. Therefore, even when cultured fish feeding rates approached those of the wild fish, they mainly consumed larger organisms living on the river bed, such as cased caddis fly larvae and molluscs, which do not occur in the drift. The lack of morphological adaptations in salmon that allow grinding of the cases and shells of these organisms (cf. pharyngeal teeth in cyprinids) prevents the digestion and assimilation of such food items.

At low current velocities, the efficiency of the feeding behaviour of cultured parr declines, because they must feed on the finest drift particles or take aerial insects floating on the water surface. Wankowski and Thorpe (1979) found that the diameter of food particles carried by a stream at current velocities <33 cm s^{-1} does not exceed 1 mm, while juvenile Atlantic salmon >12 cm in length prefer larger food items, (Wankowski, 1979). Therefore, at their preferred current velocities of up to 0.27 cm s^{-1} for cultured fish, optimally sized food particles are lacking, and cultured fish must consume smaller, energetically less-favourable items, or take terrestrial insects that have fallen onto the water surface. The relative mass of these food items in the diet of some cultured fish was as high as 40%.

Based on comparative studies of feeding efficiency and the behaviour of cultured juvenile salmon held in a pond before release into a river and in the river post-release, Mitans (1970) emphasized that, regardless of the cultivation technique employed, cultured fish released into the wild would be less well-adapted for drift feeding than wild fish.

The feeding behaviour of cultured fish in this study was characterized by lower selectivity of feeding attempts than that of wild fish. Cultured fish failed to differentiate between food objects in the water column and, as a result, they consumed many items of low nutritional value. Furthermore, cultured parr displayed poor orientation in the current and could not remain in optimal river habitats having moderate current velocity and a high density of drift particles. Even after acclimation to conditions in the wild, the diet of cultured fish comprised of food items avoided by wild fish, such as molluscs, cased caddis fly larvae, pupae and imagos of various insects, and inedible particles.

The distribution pattern and dynamics of the downstream movements of wild fish depended on environmental factors, such as food abundance, availability of shelter, current velocity, and the presence of predators, whereas in cultured parr, the main factor limiting their distribution and affecting their downstream displacement was the maximum tolerable current velocity. Although wild parr actively selected areas with optimal feeding conditions, cultured fish usually occupied sites irrespective of feeding opportunities.

If habitat selection in cultured parr was determined by the same factors as for wild fish, the correlation between the densities of these two groups in habitats with different feeding opportunities would be relatively strong. However, the correlation was not significant (Figure 2).

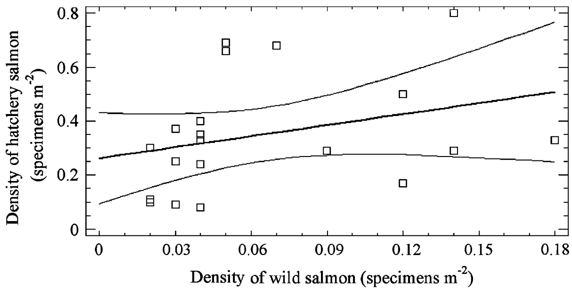

Figure 2. Correlation between the densities of wild and cultured Atlantic salmon in the same habitats in the Louvenga River ($r = 0.30$, $F = 1.88$, $p = 0.18$). The two fainter lines indicate the 95% confidence limits.

This comparative analysis indicates that the wild parr displayed stronger territorial behaviour, occurring at relatively low densities and occupying optimal habitats with moderate current velocity and high densities of drift particles. As a result, the level of aggression in wild parr is extremely low, and the number of territorial conflicts is independent of current velocity or feeding conditions. In contrast, cultured parr form dense aggregations and, consequently, demonstrate greater levels of aggression, depending on both current velocity and drift density. On one hand, the higher the current velocity, the lower the number of feeding attempts made by cultured parr, which leads to a decrease in the frequency of contacts and, consequently, of aggressive acts. On the other hand, as cultured parr are less capable of differentiating food in the water column, the frequency of their feeding attempts increases as a result of many false attempts, and the number of contacts between individuals increases. Conflicts in wild fish are limited to threatening poses (95% of incidents). In addition, wild parr displayed equal numbers of aggressive and defensive acts during their conflicts, while in cultured fish the number of aggressive acts was nine times greater than the number of defensive acts (Safonov *et al.*, 1985). The increased aggressiveness of cultured fish together with their less effective feeding behaviour apparently leads to an increase in energy expenditure, and because of their higher motor activity, increased exposure to predators during acts of aggression.

Thus, our results show that the feeding behaviour of cultured fish is less effective than that of wild salmon. Other studies have indicated that cultured Atlantic salmon can lose up to 50% of their visceral fat in the first 40 days after being stocked into the wild (Mitans, 1970; Shustov *et al.*, 1980; Bakshtansky *et al.*, 1981; Ackman and Takeuchi, 1986). In addition to the lower efficiency of feeding behaviour, cultured parr exhibit the other negative characteristics of low efficiency of defensive behaviour and poor swimming ability, which lower their chances of survival (Mitans, 1970; Bakshtansky *et al.*, 1980; Safonov, 1981; Bakshtansky and Chernitsky, 1983; Loenko, 1985; Valetov and Movchan, 1985; Bougayev *et al.*, 1986; Mayama, 1990; Brauner *et al.*, 1994; Jepsen *et al.*, 1998; Koed *et al.*, 2002; Poole *et al.*, 2003). Consequently, many cultured juvenile fish die shortly after their release into the wild. Despite the low survival rate of cultured parr, many authors believe that there may be opportunities to increase their performance to levels similar to those of wild fish (Mitans, 1970; Shustov *et al.*, 1980; Ermolayev, 1982; Bakshtansky and Nesterov, 1985; Zadorina, 1985; Bougayev *et al.*, 1987; Shchurov, 1987), although high levels of mortality immediately post-release remain a problem.

Many studies have documented the loss of genetic variability in artificially restored populations (Allendorf and Phelps, 1980; Cross and King, 1983; Vuorinen, 1984; Vespoor, 1988; Fleming and Einum, 1997), and genetic divergence between wild and hatchery populations of salmon (Ryman and Stahl, 1980; Kazakov and Lyashenko, 1987; Crozier, 1998; Kazakov and Titov, 1998). The possible negative consequences of interbreeding between wild and cultured salmon are a concern (Helle, 1981; Larkin, 1981; Ryman and Stahl, 1981; Simon *et al.*, 1986; Harada *et al.*, 1998), and some authors have proposed that spawning of hatchery-origin salmon in the wild should be prevented (Bisson *et al.*, 2002). Mitans (1970) noted that it is possible to adjust the conditions and feeding regime in the hatchery to better acclimate cultured salmon for release into the wild, but doubted if such an approach would be profitable. It remains to be seen if such measures will be biologically effective.

In our opinion, and as previously noted by several authors (Smirnov *et al.*, 1985; Bielak, 1998; Gwak *et al.*, 2003), one potential method to increase the rate of acclimation, and therefore the survival of cultured salmon, would be to introduce hatchery-reared fish into the wild at an earlier stage of development, thus reducing the possibility of inappropriate behaviour learned in the hatchery and avoiding the survival of poor quality fish that can occur under hatchery conditions. It may be desirable, in future programmes intended to conserve, maintain, and restore wild salmon populations, to use "semi-natural" cultivation techniques such as the incubation of eggs in artificial redds in natural spawning grounds and methods that do not involve manipulation of the fish in the hatchery.

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