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Differentially directed startle response in alevins of three salmonid species

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We studied responses of yolk-sac fry of three salmonid species to simulated predator attacks. Remaining motionless after tactile stimulation was more common in arctic charr alevins than in brown trout or Atlantic salmon. When stimulation was followed by a startle response, arctic charr predominantly responded with an upward swimming burst, whereas fry of brown trout and Atlantic salmon mainly performed a short swimming burst near the aquarium bottom. We suggest that differences between species in flow and predator regime may explain the differential behaviour between the three salmonids.

1. Introduction

The antipredator behaviour of juvenile salmonids differs between species (Magnhagen 1988, Abrahams & Healey 1993). However, very little is known about the responses of earlier life stages (but *see* Taylor & McPhail 1985). Since alevins (yolk-sac fry) of salmonids are relatively passive, the differences in antipredator behaviour are most likely to be detected in their escape response. Startle response, i.e. rapid swimming burst after external stimulation, is an important component of fish antipredator behaviour (Webb 1978). We studied the startle response in alevins of arctic charr (*Salvelinus alpinus*), Atlantic salmon (*Salmo salar* m. *sebago*) and brown trout (*Salmo trutta* m. *lacustris*) derived from landlocked stocks of Lake Saimaa, Eastern Finland. These species differ in their breeding habitat selection and breeding behaviour and this may be reflected in the antipredator behaviour of the alevins. We simulated predator attacks in the laboratory by tactile stimulation and studied whether the escape response differs between species.

2. Materials and methods

The experimental fish originated from artificially fertilized hatchery strains. The alevins were held in standard hatchery conditions in darkened plastic tanks (218 × 40 × 25 cm) at a density of several thousand individuals per tank. There was a continuous flow-through of lake water (temperature

+ 2°C) in the holding tanks. Hatching occurred relatively synchronously in different species and the study fish were therefore considered to be at roughly matching developmental stage. During the time of the study all the fish were still completely dependent on their yolk sacs.

As the experimental arena we used 20 glass aquaria (35 × 20 × 25 cm) filled with 20 cm of lake water (temperature + 2°C). The aquaria were placed in a dim hatchery room with an ambient temperature of + 5°C. We did not provide gravel or any other structure in the aquaria because the fish had been hatched and reared in an unstructured hatchery environment. For behavioural analysis we divided the water column into three horizontal sectors of equal depth: bottom, midwater and surface.

Before the experiment the fish were taken randomly from the holding tanks and transferred to the experimental aquaria and allowed to settle for one hour. Only one fish was placed in each aquarium at a time. The predator attack was simulated by purposefully flicking the side of the fish's tail with a 30-cm stick made of plastic-covered wire. Tactile stimulus of this kind has been shown to induce escape responses in young fishes (e.g., Taylor & McPhail 1985). After the attack we recorded: (1) whether the fish reacted with an escape response, and if so, (2) what was the uppermost water layer the fish reached during its escape.

3. Results

The three species differed in their responsiveness to the simulated predator attack (Table 1; χ^2 = 11.265, df = 2, $p = 0.004$; the swimming activities are pooled together). The most clear difference is between charr and salmon alevins, charr being less likely to respond to simulated attack with a swimming response than salmon. The response of trout was intermediate. When responding, the alevins of the different species also differed in their type of response (Table 1; χ^2= 27.64, df = 4, $p < 0.0001$, only fish that swam after the attack are included). Charr was more likely to reach the surface compared with salmon and trout that started swimming with a low angle and mostly swam near the bottom. The charr's escape response was frequently directed steeply upward resulting in a higher swimming angle than in trout and salmon.

4. Discussion

Our principal finding was that charr was more likely to direct its escape response upward in the water column whereas salmon and trout mostly swam near the aquarium bottom. However, charr also remained more often motionless when "attacked" compared with either salmon or trout larvae.

There is indication that young fish larvae often do not show any escape response when attacked by the predator (*see* references in Fuiman & Magurran 1994). Remaining motionless might serve as an active avoidance attempt against predation (e.g., Huntingford *et al.* 1994). However, this behaviour has also been attributed to developmental constraints of young fish larvae, as there seems to be a clear survival advantage to actively responding individuals under attack (Fuiman & Magurran 1994). For example, young coho salmon (*Onchorhynchus kisutch*) increases its responsiveness to tactile stimulations as development progresses towards emergence from the gravel (Taylor & McPhail 1985). We considered the alevins of the three species to be at roughly matching developmental stage. Nevertheless, we can not rule out that there might have been some differences in their developmental stage that could have caused their different tendency to actively respond to the simulated attack. However, the percentage of coho salmon responding to tactile stimuli did not exceed 40% even 50 days after emergence (Taylor & McPhail 1985), whereas in our study the three species exhibited response rates from 67.8% (charr) to 93.0% (salmon). Thus the re-

Table 1. The uppermost water layer reached during the escape response after tactile stimulation in the three salmonid species.

		Swimming			
Species	No response	Bottom	Midwater	Surface	Total
Charr	18	15	6	17	56
Salmon	4	45	2	6	57
Trout	11	36	3	4	54

sponsiveness to tactile stimulation may also vary between species.

Differences in breeding habitat selection of the three salmonid species may explain the observed differences in larval escape behaviour. In all three species, females dig a nest in the bottom gravel where the larvae hatch and remain until the end of the yolk-sac stage. However, salmon and trout spawn in rapids with considerable water flow, whereas charr in Lake Saimaa reproduces in rocky or stony areas of the lake bottom (Piironen 1990).

Little is known about the behaviour of the three species at the yolk-sac stage in nature, but as nests of both salmon and trout are usually covered with thick layer of gravel, the risk of predation on young larvae may be relatively low until the fish move into upper layers of the gravel at the end of the alevin stage (Dill & Northcote 1970). However, predation on eggs and alevins hiding within the gravel has been reported (Phillips & Claire 1966, Clary 1972, Savino & Miller 1991). If salmon or trout larvae hiding in the upper gravel layer are attacked by a predator, the low starting angle of their escape response may keep the alevins within the gravel and, perhaps more importantly, ensure that the water flow will not carry the fish away.

The propensity of the charr to swim upwards presumably indicates that it is willing to spend more time in the water column than the two other species. Charr alevins living in the lake bottom do not face the risk of being washed away with the stream. Furthermore, evidence from the field suggests (*see* Rubin 1994 and references therein) that in charr, nest digging by females is largely dependent on gravel size, being only weakly performed, if occurring at all, in such rocky and stony spawning grounds as in Lake Saimaa (Piironen 1990). The charr eggs and alevins are therefore probably more exposed to predation than those of salmon and trout. For example, Rubin (1994) reported that burbot (*Lota lota*) digs out the gravel or pushes the stones away to get access to charr eggs. Also in the Lake Saimaa water system burbot as well as sculpins (Cottidae) are present and probably prey on young salmonids. The abrupt upwards directed swimming burst by a charr alevin may surprise the predator and allow the alevin to escape from the predator's sensory field. This behaviour may thus be an efficient response towards predators searching for prey from the upper gravel layer.

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