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Synergistic effect on mortality in Atlantic salmon, *Salmo salar*, smolt caused by osmotic stress and presence of predators

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Synopsis

The hypothesis that an increase in the mortality rate of Atlantic salmon would be produced by the synergistic effect of osmotic stress and of stress due to the presence of predators was tested by putting two groups of smolts (one acclimated to seawater and the other not acclimated) into a tank containing predators. These smolts were tested afterwards in a seawater-challenge test, together with smolts of the control groups for both experimental groups. The mortality rate of the non-acclimated and predator-exposed smolts was 90%, and that of the seawater acclimated and predator-exposed smolts 43%, compared to no mortality among the control groups. Lack of acclimation to seawater did not in itself induce any lethal stress, but in conjunction with predator-stress there was a synergistic effect, leading to an increase in the mortality rate. The hypothesis is therefore considered to be valid.

Introduction

When Atlantic salmon, *Salmo salar,* smolts were placed in a tank together with cod, *Gadus morrhua,* they displayed different antipredator behaviour according to whether or not they had previously become acclimated to seawater (Järvi, unpublished). It was thus concluded that the difference in the anti-predatory behaviour of the two groups of smolts was due to osmotic stress. Although seawater acclimated (= adapted) smolts behaved in a significantly different way to non-adapted smolts, there was a great variation in the response found within the two groups. A reasonable suggestion is that the presence of the predator per se and the osmotic stress are two important stress factors that can affect prey species. This hypothesis is based on the fact that plasma concentration of the 'stress' hormone cortisol in the blood is known to increase during the process of adaptation of Atlantic salmon smolt to seawater (Nichols & Weisbart 1985), taken together with the fact that chemical stimuli from predator fish may induce stress response, indicated by an elevation of the cortisol and glucose levels in the blood plasma (Rehnberg & Schreck 1987).

When fish are exposed to stress their physiology is individually affected. In general, stress will induce changes in the metabolic rate (Barton & Schreck 1978) and the hydromineral balance (Schreck 1981), for example, by its effect on the rate of sodium exchange across the branchial epithelium (e.g. Evans 1980, Lahlou 1980). If glycolysis becomes anaerobic, due to an increase in the metabolic rate, it will ultimately cause an increase in the lactic acid content of the blood and tissues (e.g. Heisler 1980). Such an accumulation of lactic acid may eventually lead to acidosis and death.

Acidosis can be caused by a single stress factor as well as being caused by the sum of various stress factors (e.g. Barton et al. 1986). Thus, one would expect that the mortality rate due to predator-stress should increase when osmotic stress is also present.

The aim of this study was to test whether smolts previously exposed to the presence of predators survived a seawater-challenge test less well than a control group, and, whether such predator-exposed smolts, previously unadapted to sea-water, survived a seawater-challenge test less well than a group of smolts both predator-exposed and seawater-adapted.

Material and methods

The experiments were carried out during May 1987, at the Research Station for Freshwater Fish, Ims, near Stavanger in south-western Norway. The fish used were two – years – old Atlantic salmon smolts originating from the river Imsa and reared under normal rearing conditions. Before making the experiments, a large number of smolts was divided into two groups (>>1000 individuals each). One group was kept for three weeks in the diluted natural seawater (salinity = 25‰; temperature = 8–10° C) normally used by the Research Station at Ims for adapting smolts to seawater conditions before release (the seawater-adapted group). The other group was kept in freshwater (alkalinity = 130 μekv/l; salinity = 0.02‰; temperature = 14–16° C) for the same length of time (the osmotically unadapted group). Six live cod, each weighing between 1.0 and 2.5 kg, bought from the local Fishermens' Association, were used as predators. Prior to the present experiments, these cod had been used in a study of the anti-predator behaviour of Atlantic salmon smolts in 10 consecutive trials, during the course of which the cod were placed together with six smolts in each trial.

In order to test the effects of stress caused by the presence of a predator and/or osmotic stress, a seawater-challenge test was devised. Two groups of smolt, one taken from the freshwater tank (N = 39) and one taken from the seawater tank (N = 40), were put into a circular tank filled with seawater (area = 72 m^2; waterlevel = 0.6 m; water-velocity $\approx$ 0; salinity = 32‰) and containing the six cod. Each trial exposure to the predators lasted for one hour. Because of their training in the previous experiments the cod did not subsequently alter their behaviour towards the smolts; they swam about actively in the tank, but without, actually hunting the smolt, so far as we could see. This was probably because they had eaten to satiety during the previous series of anti-predator behaviour experiments. After an hour's exposure to the predator, the smolts were caught and transferred to a rearing tank (2.0 × 2.0 m), filled with natural seawater (32‰ salinity) to a depth of about 0.4 m. The water-exchange rate was 20 l/min. The time elapsing between the two consecutive experiments was one day. Two control groups, one taken from a freshwater tank (N = 40) and one taken from a seawater tank (N = 20) were also treated and tested in the same way as the experimental groups of smolts except that they were not subjected to exposure to the predators. Thus, the physical stress caused by handling should have been similar for all the test groups and the control groups. The numbers of smolts in each of the four different groups that subsequently died during the 24 hour seawater-challenge test were noted.

Results

Because no difference was found between the mortality rates of the two control groups (none of the smolts in either group died), it is evident that the osmotic stress per se had no effect on the mortality rate (Table 1). The fact that the seawater-adapted group, when exposed to predators, suffered such a significant mortality rate in the osmotic-stress test subsequently (43%), suggests that the predator-induced stress had had some effect on mortality, particularly since the mortality rate of the non-adapted and predator-exposed group was even higher (90%). The difference in the mortality rates of these two experimental groups was highly significant (χ^2 = 19.6, df = 1, $P<0.0001$), suggesting that osmotic stress does have a synergistic effect on mortality.

Discussion

The causes of death

Because mortality rate of the seawater adapted and predator-exposed group was significantly higher than the corresponding control group, it is reasonable to suggest that smolts are under stress when faced with the presence of predators. The effect of the predator-induced stress on mortality may be caused in one of two ways:

(1) When a prey becomes aware of the presence of a predator, it becomes alert. The simple fact that a predator is in the vicinity causes the stress reaction. The underlying physiological mechanism, to my knowledge, is still unknown. However, Rehnberg & Schreck (1987) have shown that chemical stimuli produced by the predators caused an elevation in the cortisol and glucose levels in the blood plasma of juvenile coho salmon, *Oncorhynchus kisutch*, indicating a stress response. The same kind of physiological response has been reported in social interactions among fish. For example, when subordinates are in conflict with dominants they experience stress. This leads to increases in both the cortisol and the adrenaline levels in the blood plasma. These changes disturb normal glucose metabolism and may eventually lead to acidosis, by causing an increase in the concentration of lactic acid in the blood and tissues (e.g. Mazeaud et al. 1977, Schreck 1981).

(2) When a predator hunts, but fails to capture, its prey, the prey will have been obliged to be physically active. It is known that fish may die several hours after being forced to undergo severe physical exercise. Black (1958) and Bennett (1978) have suggested that the physiological cause of death may be associated with lactic acid diffusion into the blood. Besides lactic acid, another organic acid, or acids, may also be involved in the induction of such acidosis (Wood et al. 1983). Whether the prey suffers more stress from the simple presence of a predator, or by being actively hunted, can not be decided from the results of the present study.

Although it is known that when smolts migrate from freshwater to seawater they suffer osmotic stress, caused by an increase in the level of the stress hormone cortisol in the blood (see e.g. Specker 1982, for a review). The results of the present study have shown that such osmotic stress alone did not lead to any increase in mortality. However, because the mortality rate of the freshwater-adapted, predator-exposed group was significantly higher than that of the seawater-adapted, predator-exposed group, osmotic stress obviously had a synergistic effect on mortality.

Ecological perspectives

The density of predators is very high in the river estuaries through which salmon smolt have to pass on their seaward migration (e.g. Hvidsten & Møkkelgjerd 1987, Hvidsten & Lund 1988). This means that both hatchery-reared and wild smolt will be exposed to a similar and very high predation pressure (Hvidsten & Lund 1988). This high rate of predation can be accounted for in one of two ways, either the predators are quite capable of hunting and catching physiologically-normal smolt, or, alternatively, the smolt are more easily caught by the predators because the normal escape-behaviour of a greater number of individual smolts is inhibited when they are attacked, due to the physiological

Table 1. The Atlantic salmon smolt, seawater acclimated or otherwise, that survived, and those that died, during an experimental, 24 hour, seawater-challenge test, according to whether or not they had previously been exposed to the presence of predators.

	Non-acclimated		Sea-water acclimated	
	Predator exposed	Control group	Predator exposed	Control group
Survived	4	40	23	20
Died	35	0	17	0

effects of stress. Based on the results of the present study, I suggest that the high predation rate is better explained by the latter alternative, i.e. the inhibition of normal anti-predatory behaviour. For example, when smolts are exposed to predators, they normally shoal (Jakobsson & Järvi 1977, Järvi, unpublished). However, when in the same situation, but under physiological stress, they shoal to a much lesser extent. Cod are known to take longer to catch an individual prey when it is in a shoal than when it is alone (Radakov 1958). One reason for this may be the confusion effect, i.e. each member of a shoal acts and looks alike, which makes it difficult for the predator to pick out one particular prey to attack (Radakov 1973). If a prey behaves in an incongruent manner, compared to other prey, it will be much more easily picked out by the predator (Milinski & Lövenstein 1980). Thus, any smolt liable to such physiological stress in the presence of predators will be an easy victim for a cod.

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