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Shelter selection in juvenile Atlantic salmon, or why do salmon seek shelter in winter?

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During winter, juvenile Atlantic salmon *Salmo salar* become nocturnal and seek refuge during the day in the stream bed gravel interstitial spaces. The function of this behaviour is unclear, but two major types of hypothesis have been proposed. One is that the fish are hiding from something (e.g. a predator) and the other is that the fish are seeking shelter from the water current. These hypotheses were tested by examining the selection of juvenile salmon for refuges that offered different degrees of concealment or shelter. The fish clearly preferred refuges that allowed them to hide (i.e. they were dark and opaque) but offered little shelter from the current. Therefore, it can be assumed that the primary function of this nocturnal behaviour during winter is most likely to hide from diurnal predators.   © 1998 The Fisheries Society of the British Isles

Key words: *Salmo salar*; sheltering behaviour; winter concealment; nocturnalism; antipredator behaviour; energetics.

INTRODUCTION

Stream-dwelling juvenile salmonids are sit and wait predators which forage by holding station in the water current and darting out to intercept prey (Wankowski, 1981). They maintain these stations on or just above the substratum both by day and by night for most of the year, but change in winter to hiding by day in streambed refuges from which they emerge at night. Therefore, it has been suggested that they switch from being perpetually active in the summer to being nocturnally active during the winter (Chapman & Bjornn, 1969; Fraser *et al.*, 1993, 1995; Griffith & Smith, 1993; Heggenes *et al.*, 1993; Richie & Griffith, 1993). The switch has been shown to be driven by temperature, with fish increasingly seeking refuge during the day when the water temperature falls below 10° C (Fraser *et al.*, 1995; Valdimarsson *et al.*, 1997). This nocturnal behaviour is unexpected, since salmonids are usually considered to be visual foragers (Keenleyside, 1962; Stradmeyer & Thorpe, 1987), and even under the brightest night-time conditions juvenile Atlantic salmon *Salmo salar* L. feed at only 35% of their daytime efficiency (Fraser & Metcalfe, 1997).

Several hypotheses have been proposed to explain the switch to nocturnal behaviour. These can be classified into two major types: hiding, such that the fish are concealing themselves from specific threats; and sheltering, where the fish are instead seeking refuge from harsh environmental conditions. However, it is important to stress that these types of explanation are not mutually exclusive.

The hiding hypothesis is that the juveniles are attempting to avoid predators (Bustard & Narver, 1975; Fraser *et al.*, 1993, 1995). In cold water, the swimming ability of the fish is reduced, due to a lowered metabolic rate, thus, they are less able to accelerate (Webb, 1978; Johnson *et al.*, 1996) and so escape from predators. Therefore, it could be adaptive for the fish to hide and minimize exposure to potential predators during the day, when the predation risk is highest (Fraser & Metcalfe, 1997). The fish therefore accept a lower predation risk at night (Fraser *et al.*, 1993). The fish are better able to escape from predators (and also need to eat more), and so extend their foraging into the day, when feeding is more efficient.

The sheltering hypotheses are mostly based on the premise that fish will attempt to reduce their energy expenditure by seeking refuge from the current (Rimmer *et al.*, 1984; Pickering & Pottinger, 1988; Heggenes *et al.*, 1993). It is suggested that the fish should shelter whenever they do not need to feed. In winter they can obtain all the energy they require at night, but at higher temperatures the metabolic rate is higher and therefore the fish need more energy and must feed both by day and by night. This idea assumes that the fish, given the choice, prefer to feed in darkness. An alternative reason for seeking shelter is that the fish are attempting to avoid displacement by floods or ice (Hartmann, 1965). The fish are less able to withstand high flows at cold temperatures (Rimmer *et al.*, 1985; Graham *et al.*, 1996; Heggenes *et al.* (1993), suggest that the risk of being trapped by anchor ice is greater at night, so prompting the fish to move out of their streambed refuges at this time. Another hypothesis in this category is that the fish are sheltering from the light at cold temperatures (Bustard & Narver, 1975; Cunjak, 1988; Hartman, 1963; Rimmer & Paim, 1990). It is known that the ratio of porphyropsin to rhodopsin in the retina of salmonid fishes is higher in winter than in summer, suggesting that the fish have better night time vision at low temperatures (Allen *et al.*, 1973, 1982); this could mean that normal daylight is too strong for the fish in winter. However, this is a proximate mechanism rather than functional explanation, and so should be treated separately.

In order to test between the hiding and sheltering categories of hypothesis, it is necessary to vary the attributes of the potential refuges, so that they do not provide both concealment and shelter simultaneously. This paper reports on such a test. Wintering juvenile Atlantic salmon were offered refuges that provided differing amounts of both visual concealment and shelter from the current; by assessing selection it was possible to test which attributes were most important to the fish.

MATERIALS AND METHODS

This experiment took place at the University Field Station, Rowardennan, Scotland, in a small fibreglass stream tank which was divided by mesh screens into six replicate sections, each 100 cm long by 60 cm wide (Fig. 1). A pump created a continuous flow in the tank while ambient temperature were maintained by a constant input of fresh loch water (drawn from Loch Lomond) into the tank; an overflow kept water depth at 0·4 m.
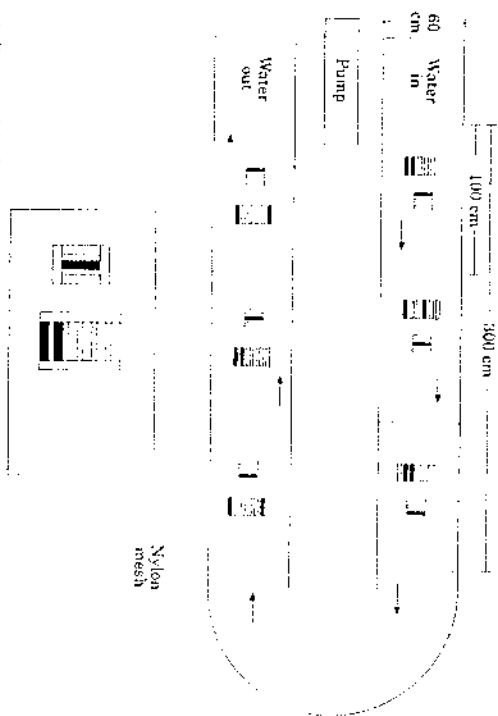
Fig. 1. Diagram of the flume. Nylon mesh divided the flume into six equally sized sections, each with a set of nine different refuges. Arrows indicate direction of flow. Enlarged insert shows a set of three refuges aligned perpendicular (receiving half flow) and a set of six refuges aligned parallel to the current. Half of the parallel refuges were closed at the upstream end (receiving no flow) while the rest had nylon mesh at the upstream end (receiving full flow).

The tank was inside a hut but the photoperiod was kept at simulated ambient; the water temperatures during the experiment (February and March 1995) averaged $4.9 \pm 0.1°C$, while the surface water velocity was approximately 0.1 m s⁻¹.

Each section of the stream was bare except for nine refuges (one of each possible combination of three light treatments and three velocity treatments). The refuges were identical in shape (each being a 20-cm long tube of perspex with a 4 × 4-cm cross-section). Their walls were either transparent or made white or black with PVC tape (the light treatments). All had one open end, while the other end (the upstream end) was either completely sealed by transparent perspex (the 'no current' treatment or no water flow through the refuge) or by light mesh, with the refuge aligned either parallel to (full current : 0.036 m s⁻¹) or perpendicular to (half current : 0.005 m s⁻¹) the stream flow. The water currents were measured by recording the time taken for a drop of ink to be carried through the refuge.

The refuges were too small to accommodate a lightened but there was an obvious difference in light intensity between the three treatments (the white PVC tape allowing some light to penetrate, while the black was completely opaque). The refuges were fixed 1 cm apart and in a randomized sequence onto a base plate. Their open entrances could be closed simultaneously, by pulling up a flap, so trapping any fish inside and allowing recording of shelter selection.

The fish used were undervearling hatchery-reared juvenile Atlantic salmon (the offspring of a pair of sea-run adults from the River Almond, in Perthshire, Scotland). The fish were <65 mm fork length and therefore not likely to smolt (migrate to sea) in the coming spring (Thorpe, 1977). Prior to testing they were kept in an outdoor holding tank, to which they were returned once tested, after having been given an identification mark (a small injection of alcian blue on the tail) to prevent re-use.

The experimental protocol consisted of placing a single fish in each section of the stream and allowing it at least 24 h to acclimate. A single record of shelter selection was
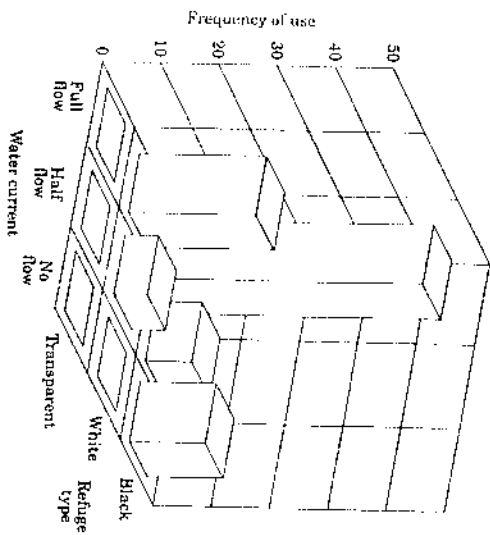
then made by closing the refuge entrances, lifting the refuges from the stream section and recording which was occupied. All fish were then moved into a new section and the procedure repeated (with a further 24 h before the next recording of shelter selection). The observations were made between 1100 and 1500 hours. This was repeated until each of the six fish had been tested in each of the six stream sections; these fish were then replaced by new ones. Therefore, each fish was tested a maximum of six times, each time in a different randomized arrangement of the nine shelters so that preferences would not be biased by spatial location. In two out of five cases the fish were not tested six times, since they seemed to avoid using the shelters after they had been tried a few times.

Fig. 2. Frequency of use of three refuge types under three flow conditions.

RESULTS

In total, 139 observations were obtained from 28 fish. On 45 occasions the fish was not inside any of the refuges; these cases were omitted from the analyses. A χ^2 test showed clearly a non-random distribution of fish between the refuge types ($\chi^2 = 17.98$, d.f. = 8, $P<0.001$). The fish were never observed in transparent refuges, and they used black refuges more than twice as often as white (Fig. 2). There was also a clear preference for using refuges with a water current through them, and on over 70% of occasions the fish used the refuge with the full current. However there was no apparent discrimination between the refuges with half and no current (Fig. 2). The results are similar if only the first observation of each fish is used, i.e. there is a non-random distribution of fish between the refuge types ($\chi^2 = 39.504$, d.f. = 8, $P<0.001$) and there was a clear avoidance of transparent refuges or those with no current through them (Table I).

Even though the fish did seem to avoid the refuges in general after they had been trapped inside them a few times, they did not seem to avoid any specific

TABLE 1. Frequency of first use of different daytime refuge types by underyearling Atlantic salmon

Water current	Black refuge	White refuge	Transparent refuge	Total
Full flow	12	6	0	18
Half flow	4	3	0	7
No flow	1	2	0	3
Total	17	11	0	28

treatment. Of the fish that entered the black full-flow refuge as their first choice, 66·7% made the same choice the next time they used a refuge, compared to 8·3% of fish that used any other kind initially, returning to that kind on the next occasion ($\chi^2 = 7.88$, d.f. = 1, $p < 0.005$). Therefore, the initial preference of the fish for dark refuges (Table 1) was, if anything, strengthened by experience.

DISCUSSION

It can be assumed from the results, that the fish were hiding rather than sheltering since firstly, they never used the transparent refuge (which would provide an equal degree of shelter from the current as the opaque ones) and secondly, they showed a preference for shelters with a through-flow of water (which would presumably increase the rate of energy expenditure while resting). Gregory & Griffith (1996) reached similar conclusions when they showed that the frequency of refuge use by rainbow trout *Oncorhynchus mykiss* (Walbaum) was reduced in turbid water or when surface ice was present. Shirvell (1990) also suggested that protection from predators might override considerations such as shelter from the current in steelhead trout *O. mykiss*.

The water current through the refuges was of course much lower than the critical holding velocity of salmon (the maximum water velocity at which they can maintain its station). Graham *et al.* (1996) found that in winter the critical holding velocity varied between 0·23–0·55 m s⁻¹ for this size of fish, while the average in the full velocity treatment in this experiment was only 0·034 m s⁻¹. However, the currents in refuges in this experiment are similar to those on the bed of natural streams and so equivalent to those experienced by wild fish (Rimmer *et al.* 1985; Heggenes *et al.* 1993).

The hypothesis that the fish are attempting to shelter from ice gains little support, since they were consistently found to use the refuges during the day even when the temperatures were well above freezing. Fraser *et al.* (1993, 1995) found that, while sheltering was most pronounced below 4° C, it commenced as soon as the temperature dropped below 10° C, and so could occur in populations that never experience ice formation.

Predator avoidance is therefore the most likely cause for this hiding behaviour. Salmonids are important prey for many predators, and it has been shown that a high proportion of salmonid mortality can be caused by predation (Alexander, 1979). Other fish are not likely to be the major cause of any seasonal change in antipredator behaviour because they will experience the same reduction in

swimming ability in cold water and therefore should be no more of a threat in winter than in summer. Mammals, especially mink *Mustela vison* Screber and otter *Lutra lutra* L., are not dependent on vision to locate prey (Chanin, 1985) so even though their prey becomes nocturnal it is unlikely to affect them. However, predation by birds could be a more important reason for the fish to become nocturnal in winter. Chinook salmon *Oncorhynchus tshawytscha* (Walbaum) show less fright response to a model fish predator than to a model bird predator (Gregory, 1993). It has been estimated that up to 30% of brown trout *Salmo trutta* L. mortality is caused by predatory birds (Alexander, 1979), so creating a strong selective pressure for hiding or other antipredatory behaviour. All main avian predators on salmon, e.g. divers *Gavia* spp., sawbill ducks *Mergus* spp., herons *Ardea* spp. and kingfishers *Alcedo atthis* L., are diurnal (Cramp & Simmons, 1977; Cramp, 1985) so a nocturnal activity pattern should be effective predator avoidance. Fraser *et al.* (1993), suggested that the lowered feeding efficiency of salmon at night may be more than offset by this reduced risk of predation.

It is important to mention that even though the results of this study show that hiding, rather than sheltering, is the underlying mechanism for the behaviour it does not rule out some adaptive value of sheltering. By hiding, the energy requirement of the fish will obviously be less than that if they were actively foraging. This, combined with a lowered metabolic rate at cold temperatures means that the fish can survive without food for a relatively long time. During the winter, resident juvenile Atlantic salmon (as used in this experiment), become anorexic, eat very little and subsequently steadily deplete their fat reserves (Metcalfe & Thorpe, 1992; Bull *et al.* 1996). The amount of time that must be spent foraging (and therefore exposed to predators) can be minimized by hiding in sites where there is the greatest opportunity to conserve energy.

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