# EFFECT OF TEMPERATURE AND LIGHT ON OVERWINTERING BEHAVIOUR OF JUVENILE ATLANTIC SALMON

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Division of Environmental and Evolutionary Biology,
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University of Glasgow
December 1997

Declaration.

I declare that the work described in this thesis has been carried out by myself unless otherwise cited or acknowledged. It is entirely of my own composition and has not, in whole or in part, been submitted for any other degree.

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December 1997

# ACKNOWLEDGEMENTS

First of all I would like to say big **THANK YOU** to my supervisor Neil Metcalfe for making this study possible in the first place and for being an excellent supervisor, always ready to give advice, discuss work, correct manuscripts and listen to my ideas.

Great thanks to Felicity Huntingford and John Thorpe who helped greatly with experimental design and were always willing to discuss the project and give support throughout this study.

Special thanks to Neil Fraser and Colin Bull who worked on similar or related projects parallel to mine, for long discussions and their encouragement and great team spirit.

So many other people helped me in one way or another, either directly with the work or just by being friends and making me happy, so here's a thank you to: Colin Adams, John Armstrong, Caroline Askew, Gústaf Bollason, Victoria Braithwaite, Vivien Cameron, Chris Cutts, Sigurður M. Einarsson, David Fraser, Eva Fraser, Davið Gíslason, Janet Holmes, Erlingur Jónasson, Bjarni Jónson, Sunil Kadri, Bjarni Kristinsson, Alan McGregor, Amanda McLean, Rab McMath, Valerie Maier, Nosrat Mirsai, Ian Morgan, Ruedi Nager, Francis Neat, Alfredo Nicieza, Willie Orr, Tom Sawyer, Skúli Skúlason, Einar Svavarsson, Elaine Thorpe, Jake Veasey, Paul Walton, Peter Wilmott.

Apart from the people mentioned above I've been lucky to get to know some other superb people who all made my life here in Scotland excellent, so here is big CHEERS! to you all, especially all the postgraduates, the departmental staff and the staff at the University Field Station.

Big thanks also to my parents, Valdimar Þorsteinsson and Guðrún Sveinsdóttir who provided much support, encouragement, gave me a curiosity for the natural world and gave me my first lesson about salmon. Also thanks to my parents-in-law, Otto Julius and Verena Maier for their enthusiastic encouragement and support throughout the study.

Finally, but uppermost in my mind, my deepest thanks go to my wonderful wife Valerie Helene who supported me the whole way, was always willing to help and discuss work (even until 4 o'clock in the morning in subzero temperatures), came up with good ideas and who will be just about as relieved as I am that this has been handed in!!

# ABSTRACT

This thesis investigated the effect of light, temperature and season on several behaviours of overwintering juvenile Atlantic salmon (*Salmo salar* L). The sheltering behaviour and the nocturnal activity of the fish was examined in detail since previous work has showed that salmon become more nocturnal as temperature decreases, hiding in streambed crevices during the day. Experiments compared fish with different life history strategies; i.e. resident fish that will spend at least one more winter in fresh water and migratory fish that will leave fresh water in the coming spring.

**Chapter 2** - Observations of salmon in a semi-natural stream examined how light, temperature and time of year determine activity patterns; I also tested whether the life-history strategy of the fish affected diel activity, comparing fish that would migrate to sea the following spring with those that would be resident in fresh water for at least one additional year. The results showed that light intensity, temperature and time of year can be used to predict whether the fish hide or not: fish tended to hide at high light levels whenever the water was cold but were increasingly likely to emerge as the winter progressed.. There were significant differences between the two groups of fish; the putative migrants sheltered more than the resident group in winter, but this trend was reversed in the spring. Reducing the risk of predation in winter may be one of the reasons for this seasonal change in behaviour.

**Chapter 3** - Traditionally, behavioural studies on juvenile Atlantic salmon have been conducted during the day in summer. It is known that salmon become nocturnal in winter but very little is known about their behaviour at that time. Furthermore, comparisons between winter and spring are scarce. Therefore, observations in a semi-natural stream were carried out during the day and night, from February to June, comparing diel and seasonal differences in behaviour between the two life-history strategies. The results showed a general trend for more activity in spring than in winter. There were differences in relative feeding rate between the life-history strategies; the migratory fish foraged mostly during the day while the resident fish did more foraging at night. Overall the migratory fish made fewer feeding attempts over the winter which is surprising since they grow faster over that period. This suggests differences in foraging efficiency which could be the underlying mechanism for the separation into these two life-history strategies.

**Chapter 4** - The function of hiding in daytime refuges in winter has been 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 by juvenile salmon of refuges that offered different degrees of concealment or shelter. The fish clearly preferred refuges that allowed them to hide (i. e. locations that 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.

**Chapter 5** - Since the food density (drift in the water column) is correlated with water velocity, the fish should normally choose feeding station in fast flowing water in order to get as much food as possible. However at low light levels the detection range is reduced so the fish will not be able to detect fast-moving items early enough to intercept them before they have been carried away; fish should therefore prefer slower currents on darker nights. Tests were carried out in tapered sections of a stream tank, each of which had a velocity gradient from a mean of 5 cm/s at the upstream end to 45 cm/s at the downstream end. A single fish was placed in each section, and a single record made of the position (and hence velocity) at which it held station under four different night-time light levels (0.00, 0.3, 1.0, 5.0 lx). The results showed that fish selected slower flowing water as the night-time light intensity decreased.

**Chapter 6** - The area defended by fish should vary in relation to light level and this variation in territory size should lead to greater aggregations in better foraging areas on dark nights than on bright. Replicate groups of 8 salmon were placed in tanks modified to produce areas of variable flow rates and food supply. Distribution, aggression and feeding rates of the fish were measured in 5 min video samples recorded at even intervals throughout the night and at 4 different light levels (0.00, 0.01, 0.50, 1.00 lx). The results show that aggression rate, increased with light level. Furthermore, fish aggregated more on darker nights, the minimum distance between fish increasing in relation to light intensity.

**Chapter 7** -. One hypothesis for why salmon become nocturnal only at cold temperatures is that because of a reduced energy demand they can obtain enough food by feeding only at night. This hypothesis assumes that the fish prefer to feed in darkness, sheltered from predators, but are forced to forage during the day at

higher temperatures when their energy demand increases. Data from an experiment where fish were provided with food in a darkened shelter supports this hypothesis. The shelter-fed group emerged during the day but to a lesser degree than controls, and grew more over the experimental period, indicating that the growth rate of fish under natural conditions may be suppressed because of their tendency to hide.

**Chapter 8** - Most salmonids (and in fact many other freshwater fish species in the northern hemisphere) have been reported to show some kind of sheltering behaviour over the winter. Previous work has shown that temperatures around 6-8 °C trigger the onset of this sheltering behaviour. However, fishes from colder environments would be expected to respond differently to temperature than fish from warmer environments. A comparison between two high-latitude populations of both juvenile Atlantic salmon and Arctic charr showed population differences in sheltering responses, indicating local adaptations to changes in temperature.

**Chapter 9** - This general discussion brings together concepts and findings from the previous chapters into an overall framework. It also emphasises the applied significance of the work.

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# **CHAPTER 1 - GENERAL INTRODUCTION**

## 1. 1 INTRODUCTION

Two very important variables in the natural environment to which most organisms respond behaviourally are light and temperature. These variables are not independent of each other since they generally originate from the sun, and their interaction creates the seasons. The magnitude of changes in temperature, light and the interaction between them depends on latitude. As latitude increases these variables become less constant and seasonal differences in light and temperature become more pronounced (this is discussed more fully in chapter 8; see Fig. 8. 1).

It is probably fair to say that in combination, temperature and light are the single most important environmental 'zeitgeber' (the signal which entrains a biological rhythm; Ali *et al.* 1992) for organisms. All animals will have a range of temperatures which they can tolerate; this range will set limits on their distribution. However, within this range animals may respond to certain temperatures by becoming more or less active. Many animals may respond to the presence of daylight in a similar way, either becoming more active (diurnal) or less active (nocturnal). Season also causes similar effects, as some animals may hibernate during winter or aestivate during the summer. These patterns can be regulated by rhythms that are merely entrained by light (or more rarely temperature), or they can be the primary controlling mechanism e.g. where animals simply become more active because they are warmer. Rhythms are synchronised with the alternation of day and night (circadian), with the tides (circatidal), the lunar cycle (circalunar) and the annual season (circannual; e.g. Gerkema 1992) and the resulting rhythmic behaviour is one of the basic properties of living systems (Müller 1978; see also Thorpe 1978; Ali 1992). The objective of this thesis is to investigate how temperature and light, especially cold temperatures and low light, affect behavioural patterns in the Atlantic salmon (see appendix 1 for scientific names). In this chapter I introduce the basic concepts of light, temperature and seasonal effects on the behaviour of animals, and then summarise the biology of the salmon. I then give an overview of the content of the thesis.

## 1. 2 EFFECT OF TEMPERATURE ON BEHAVIOUR

In extreme habitats, temperatures may act as a strong selective pressure for many species. For example, strong sunlight can on occasion cause temperatures in isolated rock-pools during low tide to become lethal to fish and invertebrates. Similarly the same type of intense selection occurs during unusually harsh winters when some aquatic environments freeze solid.

Animals can be classified as being *ectotherms* (cold-blooded or *poikilothermic* in older texts) or *endotherms* (warm-blooded or *homeothermic* in older texts; Schmidt-Nielsen 1990; Davenport 1992). The main difference is that while the body temperature of ectotherms is influenced by the surrounding temperature the endotherms maintain a high body temperature by internal heat production. Both endothermic and ectothermic animals often exhibit a range of behavioural responses which are effective in maintaining body temperature (thermoregulatory behaviours), for instance they may shiver when cold or sweat when hot. In order to survive in the coldest environment on earth, emperor penguins huddle together in their thousands to minimise heat loss (Schmidt-Nielsen 1990). Since endotherm animals produce their own heat, they usually have a wider range of temperatures which they can tolerate and may therefore not respond to fluctuations of a few degrees. The metabolic rate of ectotherm animals however, is dependent on temperature and so, as a consequence is their whole activity. This is due to both the direct metabolic effect on physiological capacity and the indirect effect on nutritional needs: a low temperature creates a low energy demand, which in turn can result in lower foraging activity.

## 1. 3 EFFECT OF LIGHT ON BEHAVIOUR

Light can have many different effects on animal behaviour. Light is sensed by eyes or equivalent visual receptors, and vision is very important for most animals. For example, vision provides the most accurate source of spatial information that an animal can gain about the world (Wehner 1997). The diel activity of an animal is normally synchronised with the alternation of light and dark in the 24-h period (Müller 1978), and light is generally thought to be the main factor in controlling circadian rhythms (see Manteifel *et al.* 1978; Boujard & Leatherland 1992). Most animals can be categorised as being nocturnal (active by night), diurnal (active by day), crepuscular (active at dawn or dusk) or arhythmic (no diel peaks in activity throughout 24 h). There are several different reasons why an animal might choose a certain time of the day to be active and forage. Visual receptors require some light to function, and so the amount of light will of course be important for animals that use vision to forage. We might expect all visual foragers to be diurnal, although some have eyes especially adapted for low light levels (e.g. owls; Burton 1973). Animals that rely on echolocation are potentially less constrained in their diel activity patterns, but factors other than their own ability to forage may still cause them to adopt particular circadian rhythms. The nocturnal activity of bats (Mammalia, Chiroptera) has been explained as a response to their being particularly susceptible to predation by diurnal avian predators (Rydell & Speakman 1993). Another explanation is that insectivorous bats may be prevented from entering the diurnal niche by competition from aerial insectivorous birds (Thomas *et al.* 1991). Prey of many visual predators have been shown to take more risks in terms of potential predation at lower light levels when presumably it is more difficult for the predators to locate their prey. These include European rabbits that forage closer to cover during daytime at high light levels than during the night (Moreno *et al.* 1996), scorpions (Skutelsky 1996), heteromyid rodents (Longland & Price 1991) and gerbils (Kotler *et al.* 1991) that all forage less or become less active under full moon compared to new moon conditions.

## 1. 4 EFFECT OF SEASON ON BEHAVIOUR

Natural light levels change according to the rotation of the earth around the sun, this rotation also modifies weather systems and therefore the temperature. These annual changes, or seasons, are more pronounced at high latitudes, with almost no annual variation in temperature and light levels at the equator. The tilt of the earth's axis is such that, in winter, no direct sunlight reaches the polar regions for periods of weeks or months (see Fig. 8. 1). The winter period is typified by low temperatures and short days while the summer is relatively warm with long days.

Animals respond behaviourally in many ways to the different seasons. Since the winter season at high latitudes is typically associated with high levels of mortality due to food shortage and freezing, many species leave such regions at the onset of winter and migrate to more hospitable areas. Because of the temporal reliability of the photoperiod, it plays an overwhelming role (if only as a zeitgeber) in the control of bird migration (Berthold 1975). The reasons for migration are rarely simple, but in many cases there are direct or indirect benefits in term of movement to favourable thermal environments (Davenport 1992). Another common response to the onset of winter is hibernation. Many endothermic animals spend the winter in a state of torpor or hibernation where body temperature and metabolic rate are both reduced in order to conserve energy (Schmidt-Nielsen 1990). The onset of hibernation is influenced by the photoperiod and is associated with endocrine cycles (rhythms) and not necessarily low temperatures or lack of food. The arousal (return to normal body temperature), however, is induced by high temperatures (Schmidt-Nielsen 1990)

## 1. 5 BIOLOGY OF THE ATLANTIC SALMON

The species used in this study is the Atlantic salmon, an anadromous, teleost fish in the family Salmonidae. The natural range of the Atlantic salmon is the north Atlantic ocean with the freshwater stages living in streams and rivers on both sides of the Atlantic. Its distribution extends northwards to Iceland and Greenland and southwards to northern Portugal and Connecticut (Jones 1959; Jónsson 1983).

The Atlantic salmon is an example of a species with a highly plastic life-history strategy (Thorpe 1994). Like all salmonids, this species spawns in fresh water, usually in flowing waters. The eggs are buried in the substrate gravel in pockets called redds. Spawning occurs in the autumn in the northern parts of its geographical range, but later in the winter in the south where incubation times for the eggs are shorter. The eggs remain in the gravel and the embryos hatch in early spring (Jones 1959; Jónsson 1983). After hatching the embryos remain in the gravel until they have absorbed their yolk sac and then (usually in mid spring, when food abundance is increasing, depending on temperature) they emerge as juveniles from the gravel and start to forage. Their diet consists mostly of invertebrates (small crustaceans and insect larvae/pupae) suspended in the water column and drifting with the current. The usual foraging position of juvenile salmon is to hold position just a few millimetres off the bottom and dart forwards to intercept the prey items as they are carried past by the current (Kalleberg 1958; Wankowski 1981; Dill & Fraser 1984; Metcalfe *et al.* 1988). Salmon use their vision to locate their prey (Fraser & Metcalfe 1997) and have traditionally been considered diurnal foragers (Hoar 1942; Higgins & Talbot 1985; Sagar & Glova 1988; Thorpe *et al.* 1988).

After spending at least one year in their river, some of the juveniles undertake physiological and behavioural change (termed smolting) which prepares them for a seaward migration. During the smolting process the juveniles lose their characteristic markings and adopt silvery flanks (Hoar 1976) in preparation for a pelagic mode of life. Whilst in the productive marine environment they grow and mature, and after at least one year re-enter their natal rivers to spawn and complete the life cycle. Many adults die after spawning. The survivors return to sea and may repeat the spawning migration in subsequent years. This, however, is only a very simplified version of the life-history of Atlantic salmon, there are other possible pathways (for example some males might mature in their first year), and the duration for each stage in the life-cycle is variable (see Metcalfe 1993; Thorpe 1986, 1990, 1994 for reviews).

During the first autumn of life, an initially unimodal size distribution in sibling populations may become increasingly bimodal until by late winter two distinct modes are distinguishable. This pattern has been observed both in hatchery controlled conditions (Thorpe 1977; Thorpe & Morgan 1978; Bailey *et al.* 1980; Thorpe *et al.* 1980, 1982; Saunders *et al.* 1982; Higgins & Talbot 1985; Metcalfe *et al.* 1988; Metcalfe & Thorpe 1992a) and in the wild in fast growing populations (Baglinière & Maisse 1985; Heggenes & Metcalfe 1991; Nicieza *et al.* 1991). This phenomenon results from a brief growth spurt in those individuals destined to make up the upper mode (the upper modal group) of the size distribution during September, whilst those destined to form the lower mode (the lower modal group) of the distribution are reducing their growth (Kristinsson *et al.* 1985; Metcalfe *et al.* 1988). Although the developmental pathway appears to be partially genetically determined (Thorpe & Morgan 1980; Bailey *et al.* 1980), all individuals initially appear capable of entering the upper modal group but whether they do so appears to be determined by a physiological decision taken around midsummer (Wright *et al.* 1990) based on the size achieved by this time and the prevailing environmental conditions (Thorpe 1989). The proportions in each mode can be altered by changing the opportunity for early growth, as represented by increases in temperature and the number of hours of daylight in mid-late summer (Kristinsson *et al.* 1985; Adams & Thorpe 1989a, b; Thorpe *et al.* 1989).

The proportions in each mode remain relatively constant throughout the course of their first winter (Bailey *et al.* 1980; Thorpe *et al.* 1980), during which time the upper modal group fish undergo the physiological changes that allow downstream smolt migration the following spring, whereas the lower modal group fish delay the process for at least one more year, staying as residents in freshwater during this time. During winter the upper modal group exhibit higher rates of metabolism, growth and food intake than the lower modal group (Higgins 1985; Higgins & Talbot 1985; Metcalfe *et al.* 1986, 1988) in order to maximise their body size in preparation for smolting (in Pacific salmon, small smolts have been shown to suffer higher mortality rates; Hager & Noble 1976; Bilton *et al.* 1982). The lower modal group fish voluntarily reduce food intake in late summer (Metcalfe *et al.* 1986) and enter a state of natural anorexia during the autumn (Metcalfe & Thorpe 1992a; Bull *et al.* 1996). The reduction in appetite occurs more rapidly than would be expected due to the autumnal decline in temperature and its timing is, to some extent, under the influence of photoperiod change (Thorpe 1986). As a result, these fish cease growth over winter even in environmental conditions where growth would normally occur (Elliott 1997). Appetite is then restored the following spring (Simpson *et al.* 1996).

In late autumn, juvenile salmon also exhibit a change in micro-habitat, moving from holding station in the current during the day, to hiding in stream-bed refuges (see e.g. Gibson 1978; Gardiner & Geddes 1980; Rimmer *et al.* 1983, 1984; Cunjak 1988). However, the fish emerge from these refuges under the cover of darkness (Fraser *et al.* 1993, 1995) to feed (Heggenes *et al.* 1993; Fraser & Metcalfe 1997). Fish stay concealed for most of the day whilst water temperatures remain low (Gibson 1978; Fraser *et al.* 1993). Thus the same individual can be either a diurnal or a nocturnal forager depending on the environmental temperature. However, the determinants and consequences of this diel activity shift have not been investigated.

## 1. 6 AIMS AND OBJECTIVES

This thesis concentrates upon the behavioural ecology of salmon during their first winter, especially their responses to temperature and light. This is of commercial importance, since salmon are of great value for both the aquaculture industry and angling related tourism (thus, could provide us with information that might save on food costs or improve anglers catch). However, a separate (and perhaps more interesting) justification for the study is the fact that this flexibility in mode of foraging is highly unusual, and provides a unique opportunity to test the functional significance of diurnal and nocturnal activity patterns in terms of environmental effects on foraging efficiency within the same species.

In chapter 2, I examine whether light intensity, temperature and season affect the sheltering behaviour of salmon in an artificial stream and the possible differences between the size modal groups that form prior to the first winter in sibling populations. The effect of temperature and light on time budgets and foraging in this same environment is compared between the modal groups in chapter 3. I then look at the underlying mechanisms for the sheltering behaviour and test whether it is due to the fish trying to hide from predators or merely resting by examining shelter preferences in chapter 4. The effect of light intensity at night on the choice of feeding station is examined in chapter 5. Chapter 6 then tests the effect of light intensity during the night on aggressiveness and territoriality in salmon. In chapter 7, I examine the effect on behaviour and growth of giving fish access to food while inside a darkened shelter. Possible differences between populations and species (Atlantic salmon and Arctic charr), in the degree of sheltering at different temperatures is examined in chapter 8. And finally chapter 9 is a general discussion, bringing together results and ideas generated by this thesis.

# CHAPTER 2 - SEASONAL CHANGES IN SHELTERING: EFFECT OF LIGHT AND TEMPERATURE ON DIEL ACTIVITY IN JUVENILE SALMON

## 2. 1 INTRODUCTION

The effect of light on rhythms and diel cycles in fish has been well described (see Thorpe 1978; Ali 1992), but the effect of temperature on their behavioural rhythms has received less attention. Since fish are ectotherms they become less active as temperatures falls, but it has generally been assumed that their behavioural rhythms stay the same. Changes of temperature are a less reliable indicator of time than are changes of light intensity, and temperature is influenced by light (the night is colder than the day, winter colder than summer).

The overwintering behaviour of juvenile salmonid fish has received considerable attention, mostly because the winter is a period of high mortality (Maciolek & Needham 1952; Needham & Jones 1959; Smith & Griffith 1994). Studies have shown dramatic seasonal changes in the behaviour of salmonids, which seem to be controlled more by temperature than by daylength (Chapman & Bjornn 1969; Bustard & Narver 1975a; Rimmer *et al.* 1983; Heggenes *et al.* 1993; Fraser *et al.* 1993, 1995). In the summer, salmonids forage during the day (Rimmer *et al.* 1983), but in winter they seek refuges and are found buried in the gravel bed of their home river or hiding amongst vegetation (Rimmer *et al.* 1983, 1984; Cunjak 1988). Night-time observations in winter have shown however, that these fish emerge from their daytime sheltering places; it has therefore been suggested that they switch from being predominantly diurnal in the summer to being nocturnal in the winter (Chapman

& Bjornn 1969; Fraser *et al.* 1993; Griffith & Smith 1993; Heggenes *et al.* 1993; Riehle & Griffith 1993).

In this study I examine in more detail how light and temperature interact to affect the behaviour of juvenile Atlantic salmon. In addition, I compared the behaviour of fish adopting different life-history strategies. Under good growing conditions populations of juvenile Atlantic salmon develop from a normal to a bimodal size distribution in their first autumn (1 year from fertilisation). This bimodality is connected to the physiological decision about when the fish will undertake the seaward smolt migration. In the labratory the fish that form the upper modal group maintain some growth over the winter, smolt and go to sea in the following spring, whereas the smaller fish that form the lower modal group almost or completely cease growing over winter and spend at least another year in the river. This kind of pattern has been observed both in hatchery controlled conditions (Thorpe 1977; Higgins & Talbot 1985; Metcalfe *et al.* 1988; Metcalfe & Thorpe 1992a) and in the wild (Baglinière *et al.* 1985; Heggenes & Metcalfe 1991; Nicieza *et al.* 1991). Several studies have shown differences in overwintering behaviour between these two groups. Lower modal group fish show a loss of appetite in the autumn and winter when the segregation between the two modal groups begins, whereas feeding intensity increases from August to October in upper modal group fish (Higgins & Talbot 1985; Metcalfe *et al.* 1988; Metcalfe & Thorpe 1992a; Bull *et al.* 1996).

Although the pattern of overwinter food intake and growth is so different in the two modal groups, there have been no detailed comparisons of their diel patterns of feeding activity and refuge use. Therefore this study addresses the following questions:

1. How do temperature, light intensity and the time of year interact to determine the activity patterns and use of refuges by juvenile Atlantic salmon?
2. Do these behaviour patterns differ between upper and lower modal group fish?

## 2. 1 MATERIALS AND METHODS

On 20 January 1994, 20 lower modal group (fork length X ±SE=74.4±1.29mm, weight X ±SE=4.00±0.21g) and 20 upper modal group (fork length X ±SE=100.9±1.64mm, weight X ±SE=10.86±0.56g) under-yearling Atlantic salmon were anaesthetised in benzocaine for under 5 min. during which time they were individually marked with small subcutaneous injections of alcian blue dye. The fish were offspring of wild sea-run salmon caught in the river Almond, Perthshire, Scotland and had been reared in hatchery conditions prior to the experiment. I then placed them in an outdoor artificial stream at the University Field Station, Rowardennan, Loch Lomondside, Scotland. The stream is in the form of a continuous, approximately oval shaped loop with straight sides. The channel (depth 60 cm, width 60 cm) has an inside wall made from glass panels and an opaque outside wall made from meshed fibreglass. This arrangement allows a clear side view of the stream from a darkened observation area inside the oval. In part of one of the straight sections is a variable speed impeller that pumps the water in one direction; mesh screens isolate this section, so creating distinct 'upstream' and 'downstream' ends and giving a total usable stream length of approximately 14 m. The surface velocity in the stream was 0.12-0.16 m/s depending on the depth. There was a constant turnover of fresh water pumped from Loch Lomond into the channel, keeping water quality high and temperatures at ambient. I marked the outer sides of the channel at 15-cm intervals with permanent ink, to produce 115 numbered sections, number 1 being furthest upstream. The roof of the channel was covered by metal mesh to prevent the fish from jumping out and predators from entering. The channel was landscaped with gravel into a series of pool and riffle areas; water depth ranged from 10 to 55 cm. The gravel used for the stream bed was rather fine (5-20 mm diameter) to deter the fish from hiding in streambed cavities. I embedded 42 shelters (made of 1 litre, opaque plastic bottles cut lengthways in half to create a cavity measuring 17 x 8.5 x 4.25 cm) into the gravel so that the open side was against the glass observation walls. This allowed me to see and identify any fish inside them. These were provided in excess and were regularly spaced around the channel.

A small amount of food (Fulmar pelleted salmon food, BOCM Pauls Ltd, Renfrew, U.K.) just sufficient to avoid the accumulation of waste, was dispensed by an electronic feeder every 30 min throughout the 24 h into a hopper, and was then carried by a flow of water along separate tubes to four locations in the tank, so as to produce as even a distribution of food as possible. In addition the inflowing water from Loch Lomond already contained zooplankton. The tank was cleaned only when algae or fungi had built up to the point that it impaired visibility; the fish were not touched during cleaning, nor was the water level altered.

In April (when most of the upper modal group fish had begun to show external signs of smolting, i.e. silver coloration, darkened edges to fins) I put a trap at the downstream end of the stream, so that they could 'migrate' and leave the stream if they chose to do so. The trap was checked every day. I set the criteria that on the first occasion that a fish was trapped it was placed back in the main part of the stream tank, while on the second occasion it was deemed to have migrated and so it was removed. No fish, however, met the criteria for removal. Although the upper modal group fish were not displaced downstream from the stream channel they showed all the other changes symptomatic of smolting, and would probably have 'migrated' had the water velocity been higher.

I made scan sample observations throughout the day and night, with an attempt to cover as many different light levels as possible. During the night or day at least 1 h elapsed between successive observations, but at dawn and dusk this was reduced to a minimum of 20 min since light levels changed rapidly at these times. I made observations at night using a small torch to read the marks of each fish; this did not disturb the fish if used only briefly (see Heggenes *et al.* 1993). All fish using shelters were identified on every scan, but it was not always possible to locate all the fish that had left shelters. I analysed the data using the number of observations rather than the number of individual fish as the sampling unit. This leads to a slight risk of pseudoreplication, but this was considered to be minimal given the strength of the effect of environmental conditions on behaviour revealed by the analyses (e.g. the percentage of fish in shelter varied systematically between 0 and 100%, see below).

I also measured both the water temperature and the light intensity at the time of each observation. Temperature was measured with a digital thermometer permanently placed in the stream, in addition to a Grant SQ2-4U Squirrel meter/logger which recorded the temperature in the stream at 1-h intervals. Preliminary records showed no variation in water temperature between eight different places in the stream, and so I took only a single reading thereafter. Salmon have a spectral sensitivity very similar to that of humans (Ali 1961), and so I measured light intensity using a Skye Instruments SKL 300 photometer (luxmeter), range 0.01-2000 lx. I measured the light intensity as the mean of two recordings made just above the water surface in each of the bends. The intensity experienced by the fish would have been only slightly lower (owing to the shallow water depth), and they would have observed the same relative changes in light intensity.

Individual fish were briefly removed from the stream tank and re-marked and returned if their marks became faint. Only one fish (lower modal group) died prior to 1 May; thereafter six fish (all upper modal group) died before the termination of the experiment on 10 June, mostly from fungal infections.

I repeated the experiment the next winter/spring with the following differences: the second experiment started 18 December 1994 and ended 5 June 1995 (although only data from 1 January 1995 are included here), only 15 instead of 20 fish of each modal group were used; and the stream landscape consisted of only one long riffle (6 m long) with pools at both ends. In the 1995 experiment one lower modal group fish died in April and six upper modal group fish died in May - June.

## 2. 3 RESULTS

A forward step-wise multiple regression procedure (Tabachnick & Fidell 1989) was used to determine how light intensity (ln(lx)), water temperature (°C), time of year (1 January = day 1) and the interactions between these variables influenced sheltering behaviour, with the percentage (arcsine transformed) of fish hiding in shelters as the dependent variable. There were significant differences between the modal groups in the percentage of fish hiding, so that in winter (January to the end of April) the upper modal group fish used the shelters more than the lower modal group fish (Wilcoxon signed-ranks test: 1994, $z=8.50$, $N=178$ observations, $P<0.001$; 1995, $z=5.44$, $N=54$

observations, $P<0.001$), while in the spring (May and June) the lower modal group fish used the shelters more in 1994 (Wilcoxon test; $z=2.90$, $N=45$ observations, $P<0.005$) and a similar trend was found in 1995 (Wilcoxon test; $z=1.78$, $N=19$ observations, $P<0.1$). Because of this difference between the modal groups the regression analysis was carried out separately on the two groups of fish. For the lower modal group fish, light intensity together with the interaction between time of year and temperature was the most important predictor of shelter use, explaining 75% of the variation (Table 2. 1.). Thus in general lower modal group salmon hid at higher light levels, and at colder temperatures earlier in the year. The interactions between light and both temperature and date were also significant, but explained only small amounts of the remaining variation. For upper modal group fish 70% of the variation in sheltering was explained by temperature and light alone, while the interactions between light level, temperature and date explained a further 12.6% of the variation (Table 2. 2.). Thus upper modal group fish showed a similar trend to lower modal group fish, hiding at high light levels and when the temperature was low, but becoming less likely to hide at a given temperature as the winter progressed. I tested the robustness of these relationships by applying the two regressions to an independent data set (both groups of fish from the 1995 experiment). There were highly significant correlations between the percentages of fish sheltering in 1995 and the percentages predicted by relevant 1994 regressions (Fig. 2. 1.).

Table 2. 1. Multiple regression of the effect of light intensity, temperature and date on sheltering in lower modal group fish

| Variable | Cumulative multiple $R^2$ | $t_{172}$ | $P$ | $B$ |
|---|---|---|---|---|
| Light | 0.474 | 17.159 | <0.0001 | 5.503 |
| Temp*Date | 0.750 | -8.869 | <0.0001 | -0.016 |
| Light*Temp | 0.809 | -7.367 | <0.0001 | -0.633 |
| Light*Date | 0.821 | 3.423 | <0.001 | 0.017 |
| Intercept | | 23.826 | <0.0001 | 28.467 |

Results from step-wise multiple regression predicting the percentage of lower modal group fish using refuges ($F_{4,172}$=197.80, $P$<0.0001). Date: days since 1 January; light: light intensity (log(lx)); temp: temperature (°C)

Table 2. 2. Multiple regression of the effect of light intensity, temperature and date on sheltering in upper modal group fish

| Variable | Cumulative multiple $R^2$ | $t_{172}$ | $P$ | $B$ |
|---|---|---|---|---|
| Temp | 0.328 | 4.278 | <0.0001 | 7.430 |
| Light | 0.702 | 16.948 | <0.0001 | 6.542 |
| Light*Temp | 0.776 | -7.521 | <0.0001 | -0.858 |
| Temp*Date | 0.819 | -7.153 | <0.0001 | -0.059 |
| Light*Date | 0.828 | 2.910 | <0.005 | 0.018 |
| Intercept |  | 2.727 | <0.01 | 15.805 |

Results from step-wise multiple regression predicting the percentage of upper modal group fish using refuges ($F_{4,171}$=164.17, $P$<0.0001). Date: days since 1 January; light: light intensity (log(lx)); temp: temperature (°C)

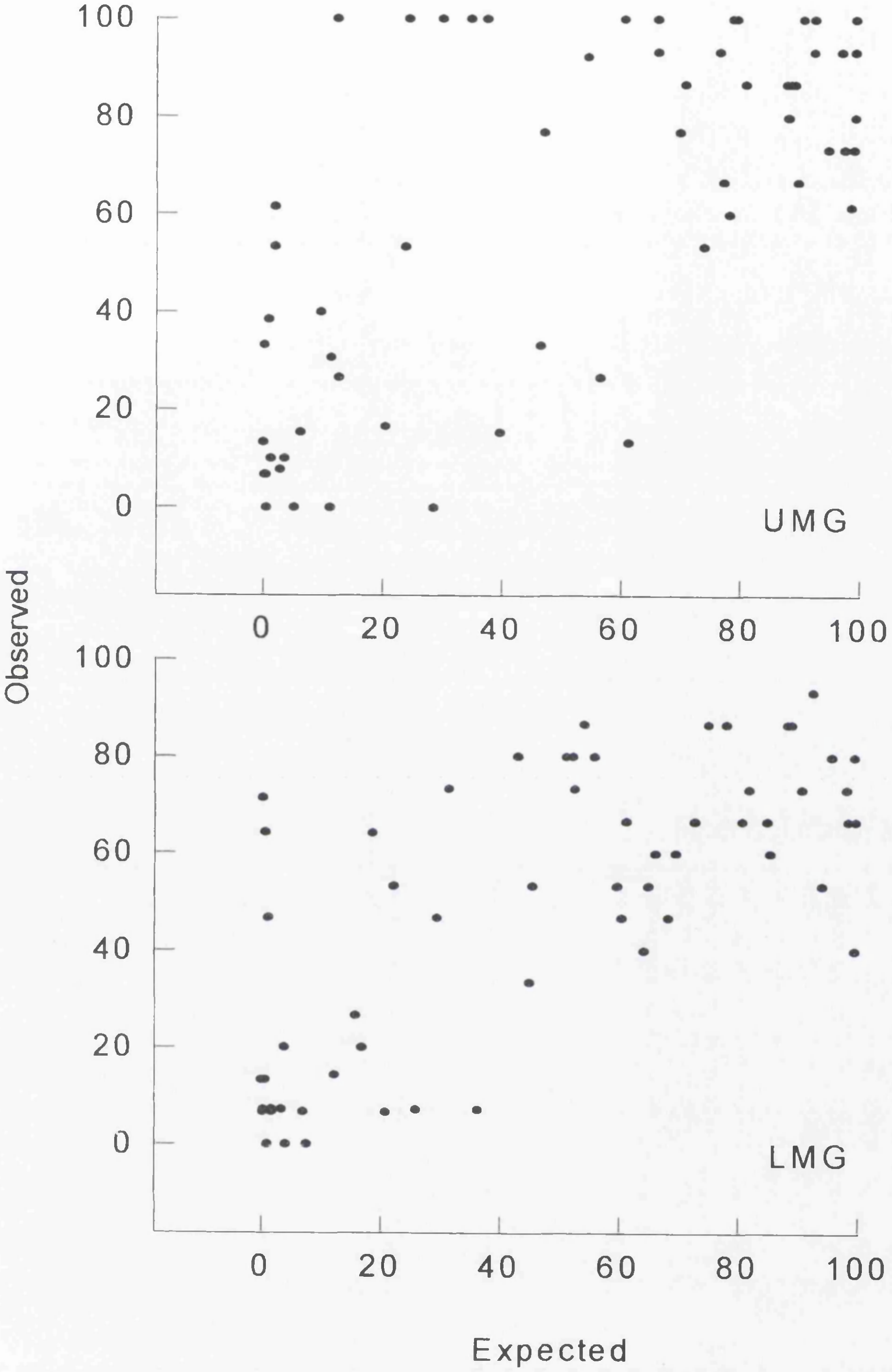

Figure 2. 1. Relationship between the observed percentage of fish hiding in the 1995 experiment and the expected percentage calculated from the multiple regression on data from 1994. (Spearman rank correlation for upper modal group (top); $r_s = 0.608$, $N = 61$ observations, $P<0.001$; for lower modal group (bottom); $r_s= 0.659$, $N = 61$, $P<0.001$).

It is possible to illustrate the effect of light intensity, time of year and the interaction between these variables by looking at the relationship between light intensity and percentage of fish hiding in shelters in winter (January-April) and in spring (May-June; Fig. 2. 2.). A highly significant positive relationship between light intensity and refuge use in winter became weaker (for the lower modal group fish) or not significant (for the upper modal group fish) in the spring. During the winter few fish hid at night, while during the day the majority of the fish were in the shelters; in the spring there was no hiding at night, while few fish still hid during the day. The difference in behaviour between winter and spring was partly (but not entirely) due to temperature changes: there was a significant negative correlation between temperature and percentage of fish hiding during the day (i.e. light more than 100 lx), but a much weaker relationship at night (light less than 1 lx; Fig. 2. 3.). At low temperatures most fish hid during the day and a few fish hid at night as well, but as the temperature increased fewer and fewer fish used the shelters. The significant interaction between temperature and date in the multiple regression indicates that fish were more likely to emerge at a given temperature as the winter progressed.

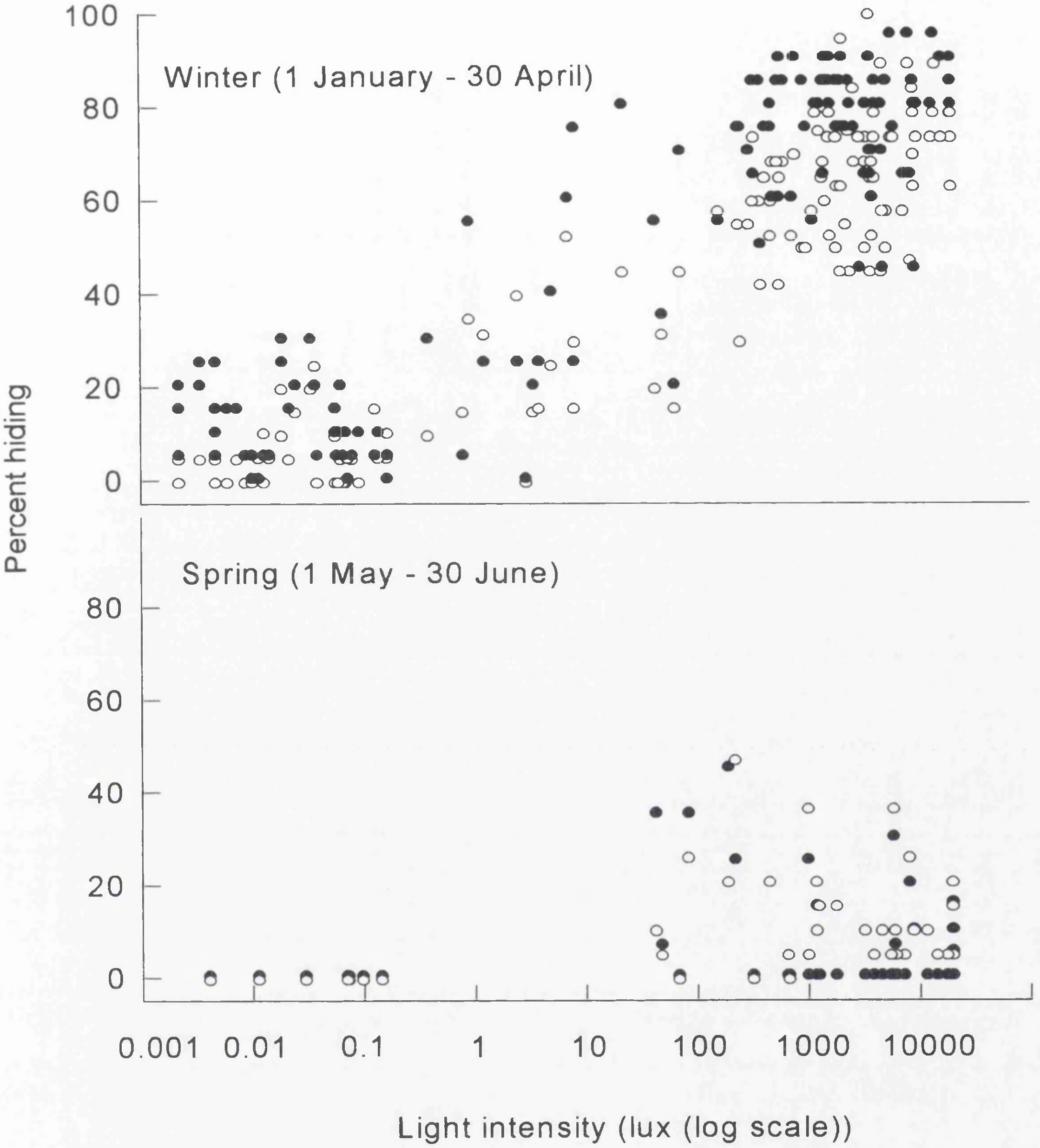

Figure 2. 2. Relationship between light intensity and percentage of fish (●: upper modal group, ○: lower modal group) hiding in the shelters provided in winter (1 January - 30 April) and spring (1 May - 30 June). Winter: Spearman rank correlation for upper modal group: $r_s$=0.787, *N*=134 observations, *P*<0.001, for lower modal group; $r_s$ =0.853, *N*=134, *P*<0.001. Spring: upper modal group: $r_s$ =0.150, *N*=43, NS; for lower modal group; $r_s$ =0.415, *N*=43, *P*<0.01). Upper and lower modal group points are displaced by 1% to avoid overlapping.

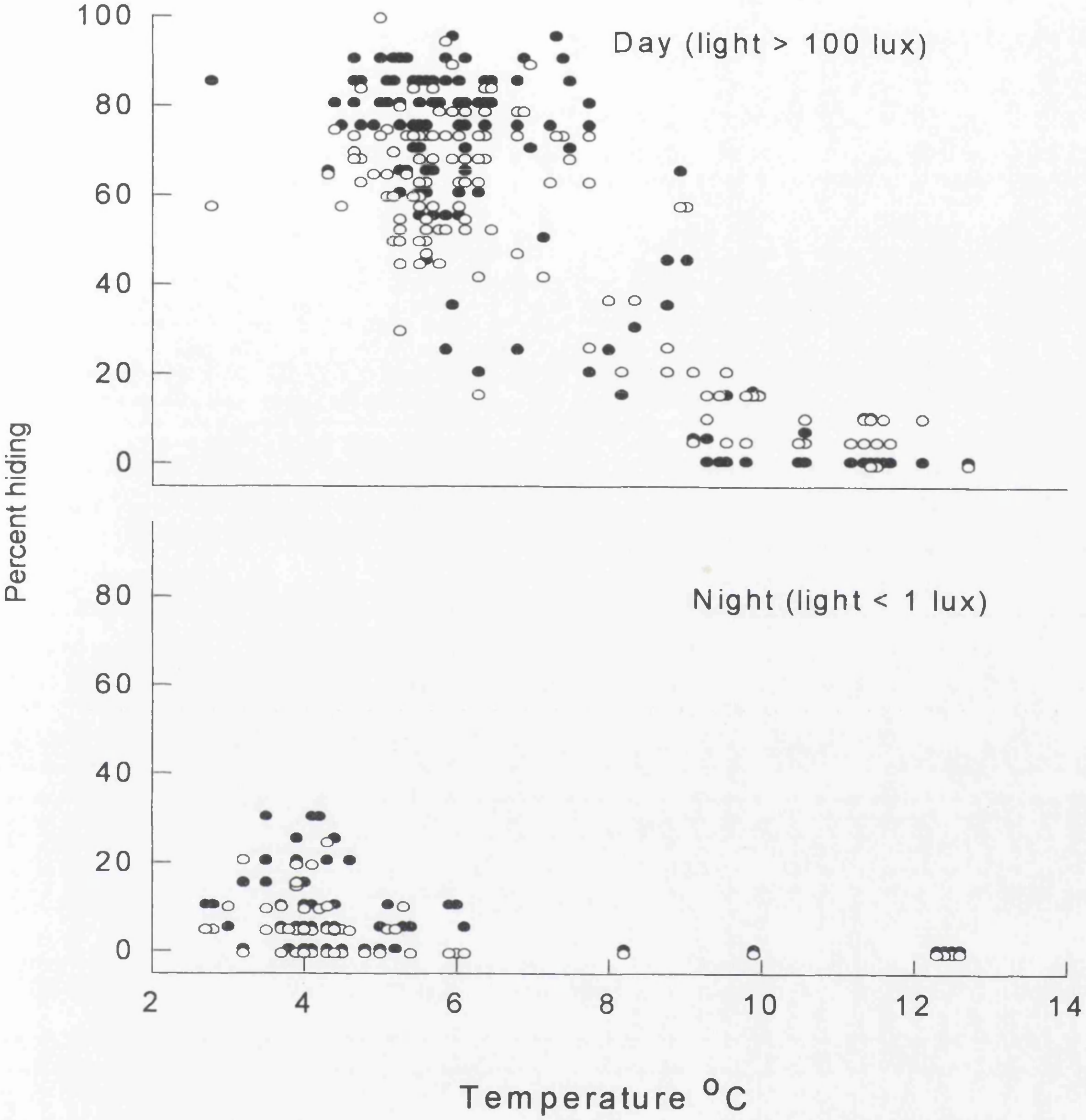

Figure 2. 3. Relationship between temperature and percentage of fish (●: upper modal group, O: lower modal group) hiding in the shelters provided during the day (light > 100 lx) and at night (light < 1 lx). Day: Spearman rank correlation for upper modal group; $r_s$ =-0.625, *N*=138 observations, *P*<0.001; lower modal group; $r_s$ =-0.543, *N*=138, *P*<0.001. Night: upper modal group; $r_s$ =-0.418, *N*=73, *P*<0.001; for lower modal group $r_s$ =-0.349, *N*=138, *P*<0.01). Upper and lower modal group points are displaced by 1% to avoid overlapping.

## 2. 4 DISCUSSION

The result that upper modal group fish tended to hide more than lower modal group fish in winter was unexpected; upper modal group fish grow more over the winter (Higgins & Talbot 1985) and therefore one would expect them to be more active and hide less. I cannot rule out the possibility that the fish were able to use crevices among the gravel as hiding places and since the lower modal group fish were smaller it would have been easier for them to exploit these refuges than for the upper modal group fish; therefore both modal groups could have been hiding to a similar extent. No fish, however, were actually observed in crevices and up to 100% were simultaneously recorded in the shelters, so the use of crevices must have been minimal. It is known that lower modal group salmon do feed over the winter even though they stop growing; however, they feed at a much lower rate than the maximum that is physiologically possible (Higgins & Talbot 1985; Bull *et al.* 1996). My results might indicate that since the fish spend a comparable amount of time foraging (assuming that the fish leave the shelter to forage), the lower feeding rate of lower modal group fish could mean that they are less capable of detecting food items than the upper modal group fish.

The tendency for upper modal group fish to hide less than lower modal group fish in spring is presumably due to their advanced state of smolting, when they tend to shoal prior to downstream migration (Fraser 1994). As the fish become more vulnerable to infections during the smolt period, smolting also explains the higher mortality of upper modal group fish in the spring.

During the winter (or at low temperatures) light intensity is clearly the most important stimulus for hiding. Contor & Griffith (1995) found a similar relationship between light intensity and concealment in wintering rainbow trout. They showed that trout began to emerge from their refuge only half an hour after sunset, and by manipulating light levels they were able to influence the number of fish that were visible. Turbidity of the water or surface ice, both of which decrease light intensities underwater, has also been reported to influence the proportion of fish hiding (Gregory & Griffith 1996b).

The reason for the fish changing their response to light intensity according to temperature and time of year is not fully understood. It is not immediately obvious why a visual forager such as the salmon should choose to forage at night. Fraser & Metcalfe (1997) have shown that under the best night-time conditions (full moon and a clear sky) juvenile salmon feed at only 35% of their daytime efficiency, while if the sky is overcast or there is no moon, their efficiency drops to less than 10%. 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 has better night time vision at low temperatures (Allen *et al.* 1973, 1982; Fraser *et al.* 1993), but their nocturnal foraging efficiency is still much lower than during the day. This reduced efficiency is offset to some degree by the greater density of invertebrate drift at night. However, the increase in nocturnal food availability is too small in winter (Anderson 1966; Elliott 1967a,b; Heggenes *et al.* 1993) to compensate fully for the reduced ability of the fish to detect and intercept the available food.

Why, then should salmon exhibit these temperature- and date-dependent shifts in activity rhythms? Owing to their low metabolic rate in cold water during the winter, the swimming ability of the fish is reduced, especially the speed at which they can accelerate and escape from predators (Webb 1978; Rimmer *et al.* 1985; Johnson *et al.* 1996). Therefore it has been suggested that fish should reduce their risk of predation in winter by hiding during the day, when the risk from endothermic predators (e.g. sawbill ducks, herons and kingfishers) is highest (Fraser *et al.* 1993). At higher temperatures, during summer, their metabolic rate is higher, and therefore swimming (and hence escape) ability is improved. Day time foraging is thus safer (and is also more profitable) than in winter, so that fish increasingly emerge from refuges as the temperature increases.

In addition, at low temperatures the daily energy requirement may be so low that it can be obtained by feeding only at night, so there is no need to risk feeding by day. However as temperatures increase with lengthening days, the greater demand of a higher metabolic rate cannot be met by feeding only at night. This may be the direct cause of the increasing tendency for fish to emerge from refuges later in the season.

It is quite possible that this seasonal change in diel activity and sheltering behaviour is more common than commonly thought. It has only been established for salmonids but other species have been found in the substrate of rivers in the winter. These species include minnows (Frost 1940), white sucker, mottled sculpin, blacknose, and longnose dace, (Cunjak & Power 1986a) and smallmouth bass, (Munther 1970). However, there are no reports on night-time observations of these species, so it is not know whether they become active at night in winter. This topic is covered in more detail in Chapter 8.

In summary this study shows that temperature, light intensity and the time of year interact to determine the activity patterns and use of refuges by juvenile Atlantic salmon, with light being the most important factor at low temperatures in the winter, making the fish hide during the day. However as the temperature increases the light becomes less and less important until the fish stop hiding altogether and stay active throughout the day and night. These activity patterns differ slightly between upper modal group and lower modal group fish.

# CHAPTER 3 - EFFECT OF TIME OF DAY AND TIME OF YEAR ON TIME BUDGETING IN JUVENILE ATLANTIC SALMON

## 3. 1 INTRODUCTION

Salmonids show diverse life history strategies both between and within species (Skúlason 1989; Metcalfe 1993). The Atlantic salmon is no exception, with variable life-history patterns in both the freshwater and marine stages of the life cycle (Metcalfe & Thorpe 1990; Thorpe 1994). In the first autumn (one year from fertilisation) life-history variation produces changes in the size distribution of the fish: instead of the former normal curve it becomes bimodal, with an upper modal group and lower modal group. This bimodality is connected to the life-history decision concerning age at seaward migration. The upper modal group fish grow slowly over the winter, smolt and go to the sea in the following spring, whereas the lower modal group fish almost or completely cease growing over winter and spend at least another year in the river. This kind of pattern has been observed both in hatchery controlled conditions (Thorpe 1977; Higgins & Talbot 1985; Metcalfe *et al.* 1988; Metcalfe & Thorpe 1992a) and in the wild (Heggenes & Metcalfe 1991; Nicieza *et al.* 1991).

This bimodality is of special interest because it is uncommon for siblings to express such variation in life history, suggesting it is an environmentally induced phenomenon. Furthermore, this gross variation in morphology and life history is associated with fine tuned changes in behaviour. Several studies have shown differences in feeding behaviour between the two modal groups. As the modal groups diverge (during autumn), lower modal group fish show a significantly greater loss of appetite than the upper modal group fish (Higgins & Talbot 1985; Metcalfe *et al.*

1986, 1988). Feeding in winter is reduced for all fish (Higgins & Talbot 1985), possibly due to their having a reduced metabolic rate at low temperatures (although rainbow trout have been observed to forage at temperatures as low as 0 °C (Needham & Jones 1959)), but that does not explain why there should be a difference between the modal groups.

When water temperatures start to fall in autumn, juvenile salmonids begin to disappear into the substrate (Chapman & Bjornn 1969; Gibson 1978; Rimmer *et al.* 1983). At night however the fish emerge from the streambed and become more active (Heggenes *et al.* 1993; Fraser *et al.* 1993; Griffith & Smith 1993; Riehle & Griffith 1993). This change in daytime activity has been shown to be controlled by temperature (Fraser *et al.* 1995), light intensity and time of year (see chapter 2). However, very little is known about the behaviour of the fish at night, possibly because of difficulties in observing fish in the dark. Heggenes *et al.* (1993) observed juvenile trout feeding at night and it is reasonable to assume that the greatest investment in foraging takes place during twilight hours or at night because most of the day is spent in shelter. However, it has been pointed out that the feeding efficiency of salmon is much lower at night-time light levels than during the day (Fraser & Metcalfe 1997). Thus, foraging rates during brief daytime feeding bouts might be higher than those during the extended feeding periods at night.

I therefore conducted an experiment to look at the behaviour of wintering juvenile salmon when outside of their streambed shelters. I particularly wanted to find out how foraging rates differed between day and night, and especially how the life-history strategies of the fish (upper vs. lower modal group) affected their winter foraging behaviour.

## 3. 2 MATERIALS AND METHODS

On 18 December 1994, 15 lower modal group (mean fork-length 57.3 ±0.88mm SE, mean weight 1.68±0.08g) and 15 upper modal group (mean fork-length 79.0±1.10mm, mean weight 4.60±0.21g) underyearling Atlantic salmon were anaesthetised and individually marked with small subcutaneous injections of alcian blue dye. The fish were offspring of wild sea-run salmon caught in the river Almond, and had been reared in hatchery conditions prior to the experiment. They were then placed in an outdoor artificial stream at the University Field Station, Rowardennan, Scotland. The stream is in the form of a continuous, approximately oval shaped loop with straight sides. The channel (depth 60 cm, width 60 cm) has an inside wall made from glass panels and an opaque outside wall made from meshed fibreglass. This arrangement allows a clear side view of the stream from a darkened observation area inside the oval. In part of one of the straight sections is a variable speed impeller that pumps the water in one direction; mesh screens isolate this section, so creating distinct 'upstream' and 'downstream' ends and giving a total usable stream length of approximately 14 m. The surface velocity in the stream was 0.12-0.16 m/s depending on the depth. There was a constant turnover of fresh water pumped from Loch Lomond into the channel, keeping water quality high and temperatures at ambient. The roof of the channel was covered by metal mesh to prevent the fish from jumping out and predators from entering. The channel was landscaped with gravel into a series of pool and riffle areas; water depth ranged from 10 -55 cm. The gravel used for the stream bed was rather fine (5-20 mm diameter) to deter fish from hiding in streambed cavities. I embedded 42 shelters (made of 1 litre, plastic bottles cut lengthways in half, to make a cavity measuring 17 x 8.5 x 4.25 cm) into the gravel so that the open side was against the glass observation walls. This allowed me to see and identify any fish inside them. These were provided in excess and were regularly spaced around the channel.

The inflowing water from Loch Lomond already contained zooplankton, but this was supplemented by a small amount of food (Ewos pelleted salmon food, size 2) just sufficient to avoid the accumulation of waste. This was dispensed by an electronic feeder every 30 min. throughout the 24 h into a hopper, and was then carried by a flow of water along separate tubes to four locations in the tank, so as to produce as even a distribution of food as possible. The tank was cleaned only when algae or fungi had built up to the point that it impaired visibility; the fish were not touched during cleaning, nor was the water level altered. Individual fish were briefly removed from the stream tank and re-marked and returned if their marks became faint. One lower modal group fish died in April and 6 upper modal group fish died in May - June mostly due to fungal infections.

In April (when most of the upper modal group fish had begun to show external signs of smolting, i.e. silver coloration, darkened edges to fins) I put a trap at the downstream end of the stream, so that they could 'migrate' and leave the system if they chose to do so. The trap was checked every day. I set the criteria that on the first occasion that a fish was trapped it was placed back in the main part of the stream tank, but on the second occasion it was deemed to have migrated and so was removed. All upper modal group fish were trapped at least once and 8 were trapped twice and therefore removed. The first fish was removed on 19 April 1995 and subsequent 'migrants' were removed intermittantly until the termination of the observations on 2 June 1995.

Observations on the activity patterns of the fish were made between 16 February and 2 June. Data were collected on 28 separate days and observation sessions covered both day and night periods. Focal animal observations were carried out by locating fish that were outside the refuges. A minimum period of 2 hours elapsed between successive observation of the same individual fish and wherever possible, data from both upper modal group and lower modal group fish were collected during the same observational period. During each 5 min observation of a single fish I recorded onto audio cassette recorder the occurrence and duration of mutually exclusive behaviours: attempted feeding, resting on the bottom, holding station in the water column (i.e. swimming against the current) and moving (i.e. swimming around). Attempted feeding was defined as when the fish swam directly towards something in the water column and apparently ate it (it was not usually possible to identify food items or their fate). Aggressive behaviour was never seen during these observations.

Observations at night were carried out using an image intensifier (Modulux Image Intensifier, Davon Optical Ltd. with Canon 28 mm lens) with infrared lights (470 nm) providing additional light. This allowed me to watch the fish even though the visible light level was below 0.01 lx (salmon are unable to see light in the infrared part of the spectrum (Ali 1961)), but it was not possible to recognise the individual dye marks on the fish. Therefore after each observation a small torch (emitting visible light) was used to identify the marks of each fish. The fish were very sensitive to all visible light in the observational area, their immediate reaction being to go straight onto the bottom and lie still, and in some cases to enter the shelters. Therefore a blanket was placed over my head and the image intensifier, to prevent light from the viewing screen from reflecting off my face, and no observations were made for at least 30 min after each use of the torch.

I measured both the water temperature and natural light intensity at the time of each focal observation. Temperature was measured with a digital thermometer permanently placed in the stream. Preliminary records showed no variation in water temperature between 8 different places in the stream, and so only a single reading was taken thereafter. Salmon have a spectral sensitivity very similar to that of humans (Ali 1961), and light intensity was measured using a Skye Instruments SKL 300 photometer (luxmeter), range 0.01-2000 lx. The light intensity was measured on the substrate close to the location of fish. In order to compare the activity of the fish during the day and the night, observations were classified as being during the day if the light intensity exceeded 100 lx, and during the night if the light intensity was below 0.1 lx. Similarly, winter was defined as from the start of the observations on 16 February until 30 April (average water temperatures 4.6°C ±0.16SE), while spring was from 1 May to the end of the experiment on 2 June (water temperatures increasing from 6°C to 13°C). A nine day interval between the last winter and first spring observations (Table 3. 1) helped to define this break. Feeding attempts were analysed as number of attempts per minute, the other activities were analysed as percent (arcsine transformed) of the time observed (5 min). The data were analysed by using 3-way ANOVA's examing the effect of time of year (winter or spring), time of day (night or day) and life-history pattern (upper modal group or lower modal group) on each type of behaviour. Some information may get lost in this type of analysis, therefore a seperate 2-way ANOVA's for each modal group looking at the effects of time of year and time of day were carried out. These are only mentioned when they add new information to the data.

## 3. 3 RESULTS

A total number of 113 observations were made (57 on upper modal group fish and 56 on lower modal group fish, Table 3. 1). Individual fish were observed between 1-7 times, giving an average number of 3.7 observations per fish.

The overall relative feeding rate (number of feeding attempts per minute) did not differ between winter and spring (3 way ANOVA examing effect of season, modal group and time of day; effect of season, $F_{(1, 105)}=0.0145$, $P=0.904$; Fig. 3. 1.), nor did it differ overall between the modal groups (effect of modal group, $F_{(1, 105)}=0.306$, $P=0.581$). The fish did however make more feeding attempts during the day than the night (effect of time of day, $F_{(1, 105)}=5.698$, $P<0.05$), this is more pronounced in the upper modal fish whereas the lower modal group fish did as many feeding attempts during the day as during the night (2-way ANOVA; effect of time of day; lower modal group only, $F_{(1, 53)}=0.760$, $P=0.760$; upper modal group only, $F_{(1, 53)}=20.605$, $P<0.001$). There was no difference between the modal groups in the overall seasonal variation in feeding attempts (interaction between modal group and season, $F_{(1, 105)}=0.0173$, $P=0.896$), with fish in both modal groups making as many feeding attempts in winter as in spring. However there was a significant difference between the modal groups in the time of day at which most feeding activity took place (interaction between modal group and time of day, $F_{(1, 105)}=8.383$, $P<0.005$): the lower modal group fish were feeding as actively by night as by day while the upper modal group fish fed more actively during the day than during the night (Fig. 3. 1). The relative day- and night-time feeding rates differed between winter and spring (interaction between time of day and season, $F_{(1, 105)}=7.151$, $P<0.01$) such that in winter feeding rates were overall higher by night whereas in spring they were higher by day. This is mostly due to the lower modal group fish making far more feeding attempts during the night in winter whereas they forage more during the day in spring (2-way ANOVA; interaction between time of day and season for lower modal group fish only, $F_{(1, 53)}=7.207$, $P<0.01$). The interaction between the life history strategy, season and time of day was not significant (3 way interaction between modal group, season and time of day, $F_{(1, 105)}=3.102$, $P=0.0811$).

A similar analysis was carried out on the extent to which fish spent their time resting on the bottom. The arcsine transformed percentages (used in all analyses but not in figures) of time spent on the bottom by fish out of shelter was only significantly affected by time of year (3 way ANOVA, effect of season, $F_{(1, 105)}=21.333$, $P<0.001$). Thus in the winter the fish spent more time on the bottom than in spring; indeed, fish were not seen resting on the bottom at temperatures above 7°C (Fig. 3. 2). There was no difference between the life-history strategies (effect of modal group, $F_{(1, 105)}=0.067$, $P=0.796$), nor were there differences between night and day (effect of time of day, $F_{(1, 105)}=0.001$, $P=0.972$). There were no significant interactions (interaction between modal group and season, $F_{(1, 105)}=0.067$, $P=0.796$; life-history strategy and time of day, $F_{(1, 105)}=0.041$, $P=0.842$; time of day and time of year, $F_{(1, 105)}=0.001$, $P=0.972$; 3 way interaction between modal group, season and time of day, $F_{(1, 105)}=0.040$, $P=0.841$).

The (arcsin-transformed) proportion of time the fish spent moving was affected by season, with the fish being more likely to be found swimming around in spring than in winter (Fig. 3. 3; 3 way ANOVA, the effect of season, $F_{(1, 105)}=40.579$, $P<0.001$). Overall the fish were also more likely to be found swimming around during the day than during the night (effect of time of day, $F_{(1, 105)}=10.046$, $P<0.005$), however, this is only significant for the upper modal group (2-way ANOVA; effect of time of day; upper modal group fish only, $F_{(1, 53)}=16.052$,

$P<0.001$; lower modal group fish only, $F_{(1, 53)}=0.328$, $P=0.569$). The upper modal group fish spent more time moving than did the lower modal group fish (effect of modal group, $F_{(1, 105)}=5.500$, $P<0.05$). Moreover, while the lower modal group fish moved as much as the upper modal group fish during the night, they swam around less during the day (Fig. 3. 3; interaction between modal group and time of day, $F_{(1, 105)}=5.468$, $P<0.05$). There was no difference between the modal groups in how their movement rates varied seasonally (interaction between modal group and season, $F_{(1, 105)}=0.473$, $P=0.493$), as both groups changed from being largely stationary the winter to being more mobile in the spring. There was no seasonal difference in the diel variation in movement rates (interaction between time of day and season, $F_{(1, 105)}=0.025$, $P=0.875$) nor was the 3-way interaction significant ($F_{(1, 105)}=0.238$, $P=0.627$).

The proportion of time spent holding station over the bottom was not subjected to statistical analysis since it was clearly not independent of the other main activities. However, there was a clear tendency for fish to hold station more in spring than in winter, and more at night than by day (Fig. 3. 4)

Table 3. 1. The breakdown of 5 min. focal observations of juvenile salmon out of their shelters by date, season, day and night for both upper (UMG) and lower modal group (LMG) fish.

| Date | Season | Time of day | Total number of observations | Number of observations UMG | Number of observations LMG |
|---|---|---|---|---|---|
| 16 Feb. | Winter | Night | 4 | 2 | 2 |
| | | Day | 1 | 0 | 1 |
| 17 | | Night | 1 | 0 | 1 |
| | | Day | 2 | 2 | 0 |
| 23 | | Night | 3 | 2 | 1 |
| 24 | | Night | 1 | 1 | 0 |
| 1 March | | Night | 2 | 1 | 1 |
| 6 | | Day | 3 | 2 | 1 |
| 14 | | Night | 7 | 3 | 4 |
| 15 | | Night | 4 | 3 | 1 |
| 19 | | Day | 2 | 1 | 1 |
| 30 | | Night | 2 | 0 | 2 |
| 31 | | Night | 10 | 4 | 6 |
| 4 April | | Day | 1 | 0 | 1 |
| 5 | | Night | 1 | 0 | 1 |
| 21 | | Night | 2 | 1 | 1 |
| 1 May | Spring | Day | 1 | 0 | 1 |
| 2 | | Night | 5 | 3 | 2 |
| | | Day | 3 | 2 | 1 |
| 4 | | Day | 4 | 2 | 2 |
| 5 | | Night | 5 | 2 | 3 |
| 11 | | Day | 5 | 3 | 2 |
| 12 | | Night | 4 | 2 | 2 |
| | | Day | 4 | 2 | 2 |
| 16 | | Night | 6 | 3 | 3 |
| 17 | | Day | 4 | 2 | 2 |
| 23 | | Day | 5 | 3 | 2 |
| 26 | | Night | 6 | 4 | 2 |
| | | Day | 5 | 2 | 3 |
| 30 May | | Night | 4 | 2 | 2 |
| | | Day | 1 | 1 | 0 |
| 31 | | Day | 3 | 1 | 2 |
| 1 June | | Day | 1 | 0 | 1 |
| 2 | | Day | 1 | 1 | 0 |

Table 3. 2. 3-way ANOVA examing the effect of time of year (winter or spring), time of day (night or day) and life-history pattern (upper modal group or lower modal group) on three types of behaviour.

| Behaviour | Source | *df* | *MS* | *F* | *P* |
|---|---|---|---|---|---|
| Number of feeding attempts per minute | | | | | |
| | Error | 105 | 0.759 | | |
| | Modal group (MG) | 1 | 0.233 | 0.306 | 0.581 |
| | Time of year (TY) | 1 | 0.011 | 0.014 | 0.905 |
| | Time of day (TD) | 1 | 4.325 | 5.698 | 0.019 |
| | MG × TY | 1 | 0.013 | 0.017 | 0.896 |
| | MG × TD | 1 | 6.364 | 8.383 | 0.005 |
| | TY × TD | 1 | 5.429 | 7.151 | 0.009 |
| | MG × TY × TD | 1 | 2.355 | 3.102 | 0.081 |
| Percent[1)] of time spent lying on the bottom | | | | | |
| | Error | 105 | 646.544 | | |
| | Modal group (MG) | 1 | 43.510 | 0.067 | 0.796 |
| | Time of year (TY) | 1 | 13793.04 | 21.333 | <0.001 |
| | Time of day (TD) | 1 | 0.8 | 0.001 | 0.972 |
| | MG × TY | 1 | 43.510 | 0.067 | 0.796 |
| | MG × TD | 1 | 26.01 | 0.04 | 0.841 |
| | TY × TD | 1 | 0.8 | 0.001 | 0.972 |
| | MG × TY × TD | 1 | 26.01 | 0.04 | 0.841 |
| Percent[1)] of time spent moving | | | | | |
| | Error | 105 | 109.542 | | |
| | Modal group (MG) | 1 | 602.416 | 5.499 | 0.021 |
| | Time of year (TY) | 1 | 4445.063 | 40.579 | <0.001 |
| | Time of day (TD) | 1 | 1100.450 | 10.046 | 0.002 |
| | MG × TY | 1 | 51.759 | 0.473 | 0.493 |
| | MG × TD | 1 | 598.945 | 5.468 | 0.021 |
| | TY × TD | 1 | 2.723 | 0.025 | 0.875 |
| | MG × TY × TD | 1 | 26.052 | 0.238 | 0.627 |

[1)] All percentages are arcsine transformed

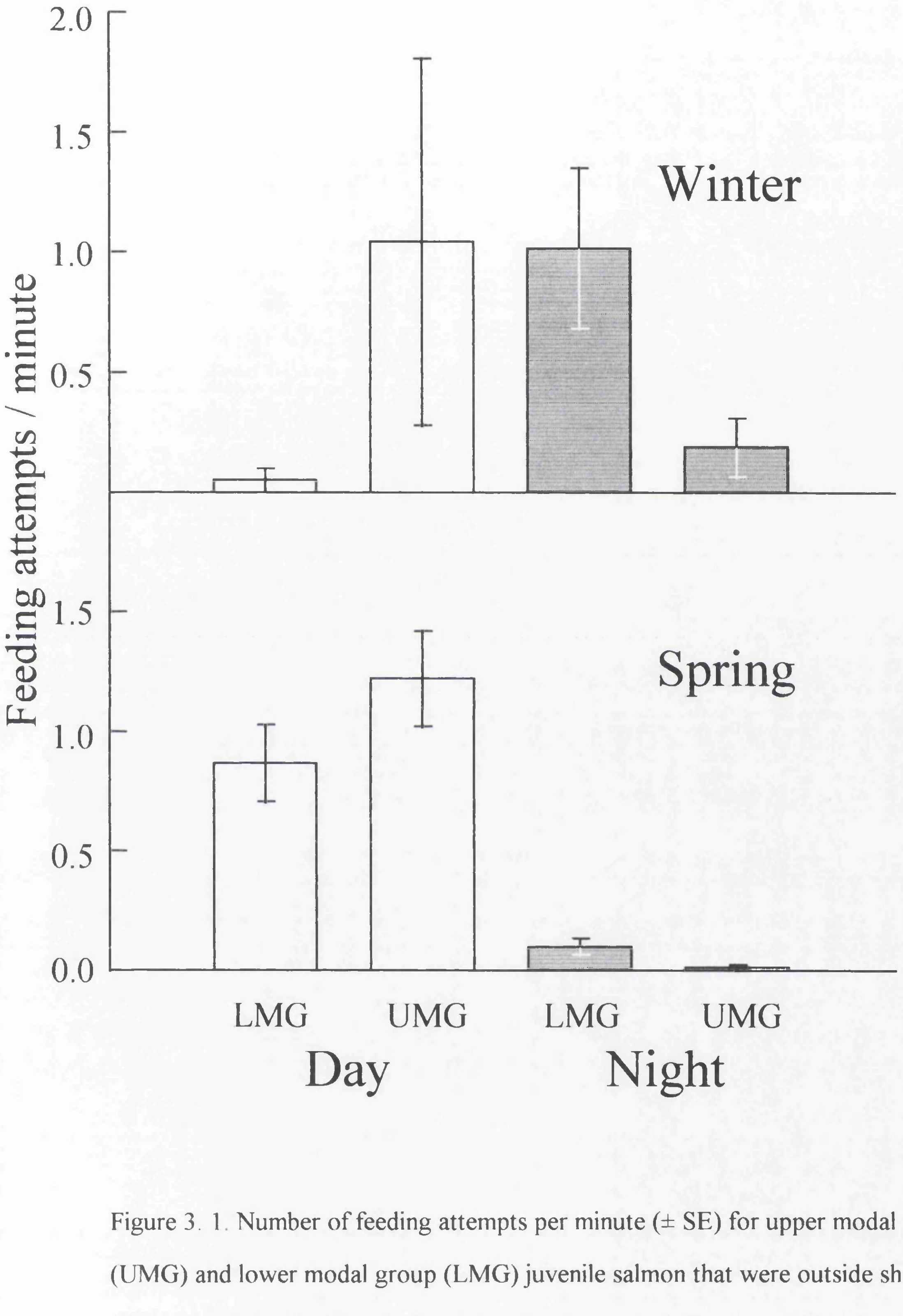

Figure 3. 1. Number of feeding attempts per minute (± SE) for upper modal group (UMG) and lower modal group (LMG) juvenile salmon that were outside shelters, during the night (dark bars), day (white bars), in winter (top graph) and in spring (lower graph).

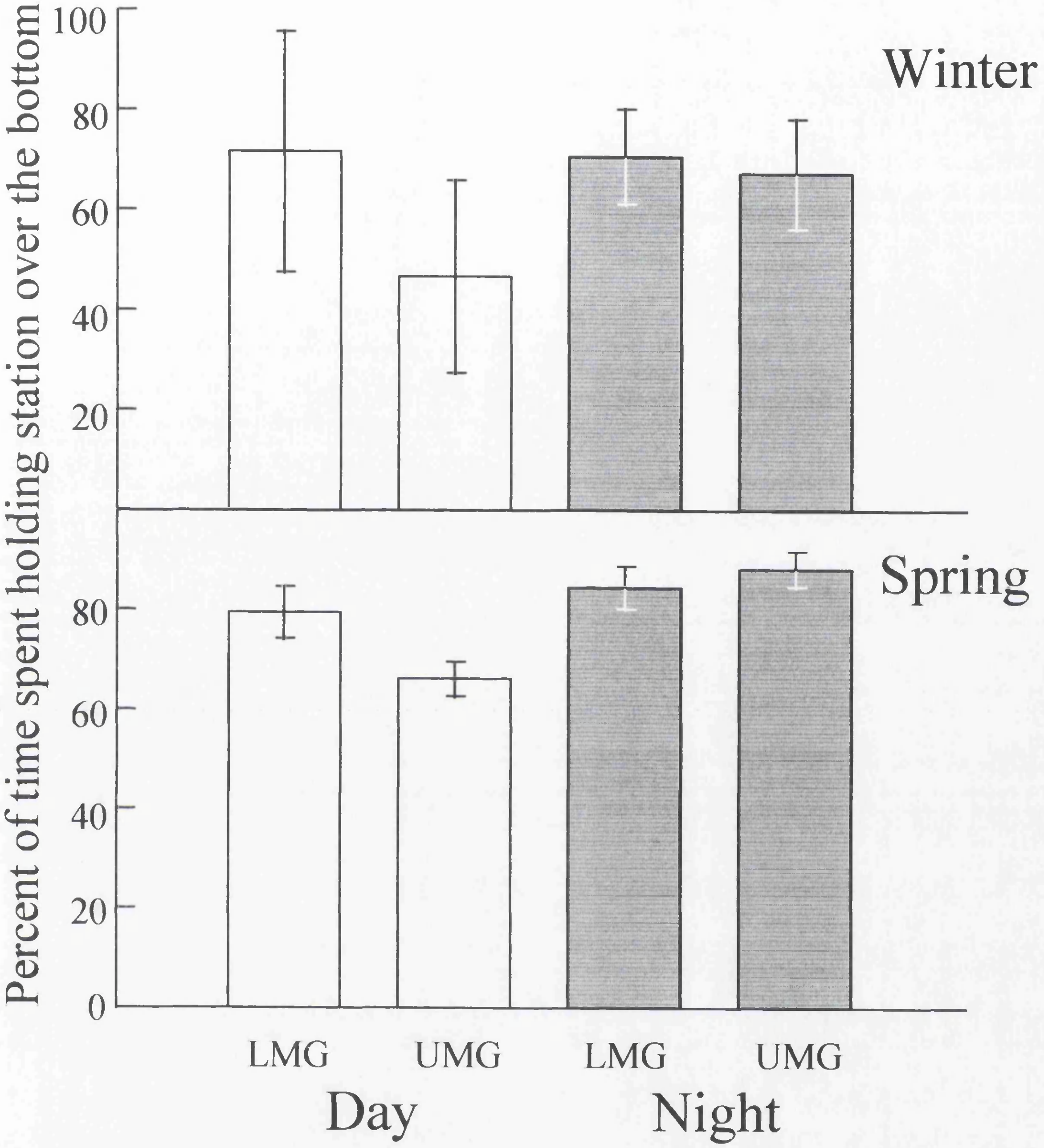

Figure 3. 2. Mean percentage of time spent lying on the bottom of the stream (± SE) for upper modal group (UMG) and lower modal group (LMG) juvenile salmon that were outside shelters, during the night (dark bars), day (white bars), in winter (top graph) and in spring (lower graph).

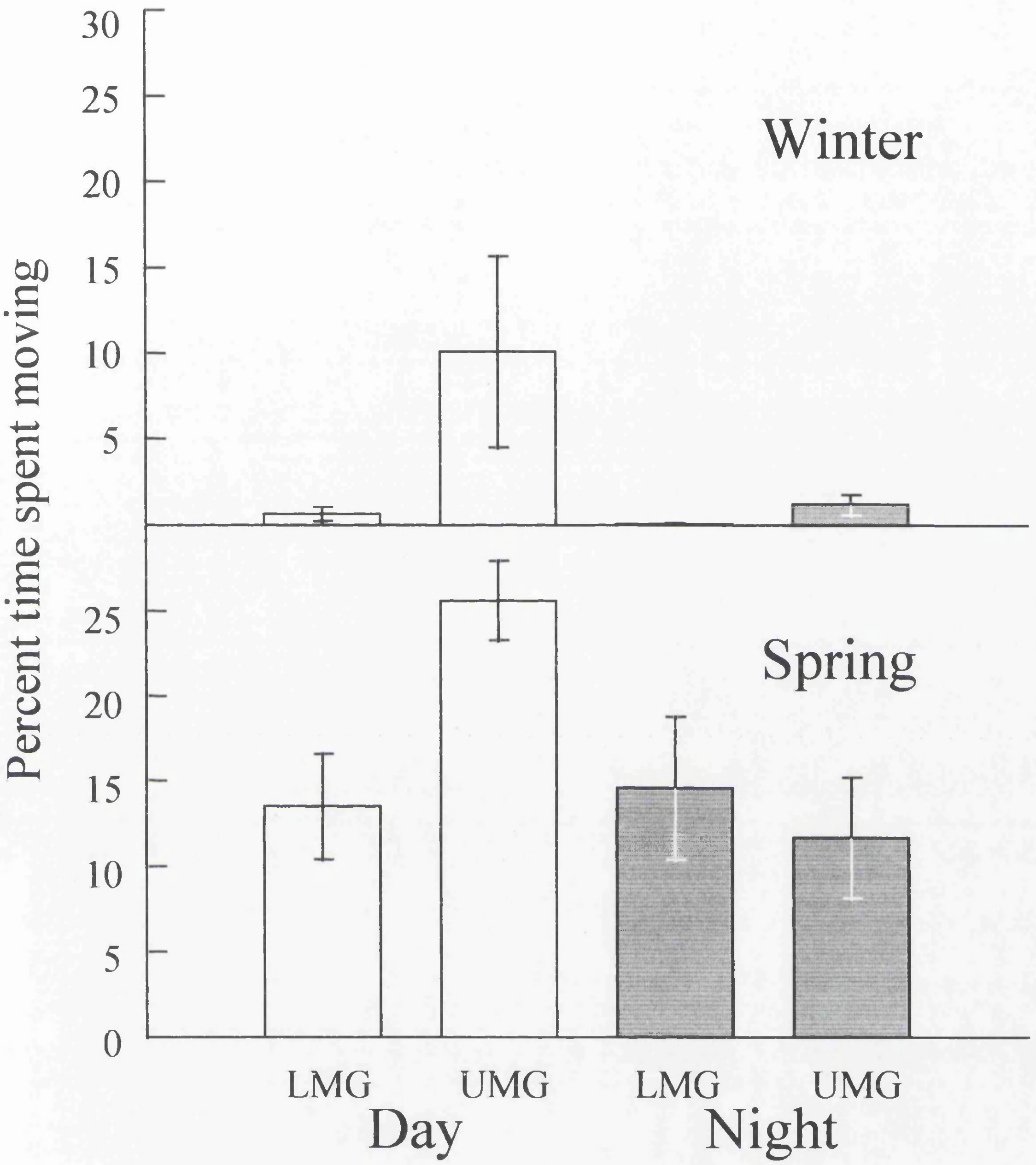

Figure 3. 3. Mean percentage of time spent moving (± SE) for upper modal group (UMG) and lower modal group (LMG) juvenile salmon that were outside shelters, during the night (dark bars), day (white bars), in winter (top graph) and in spring (lower graph).

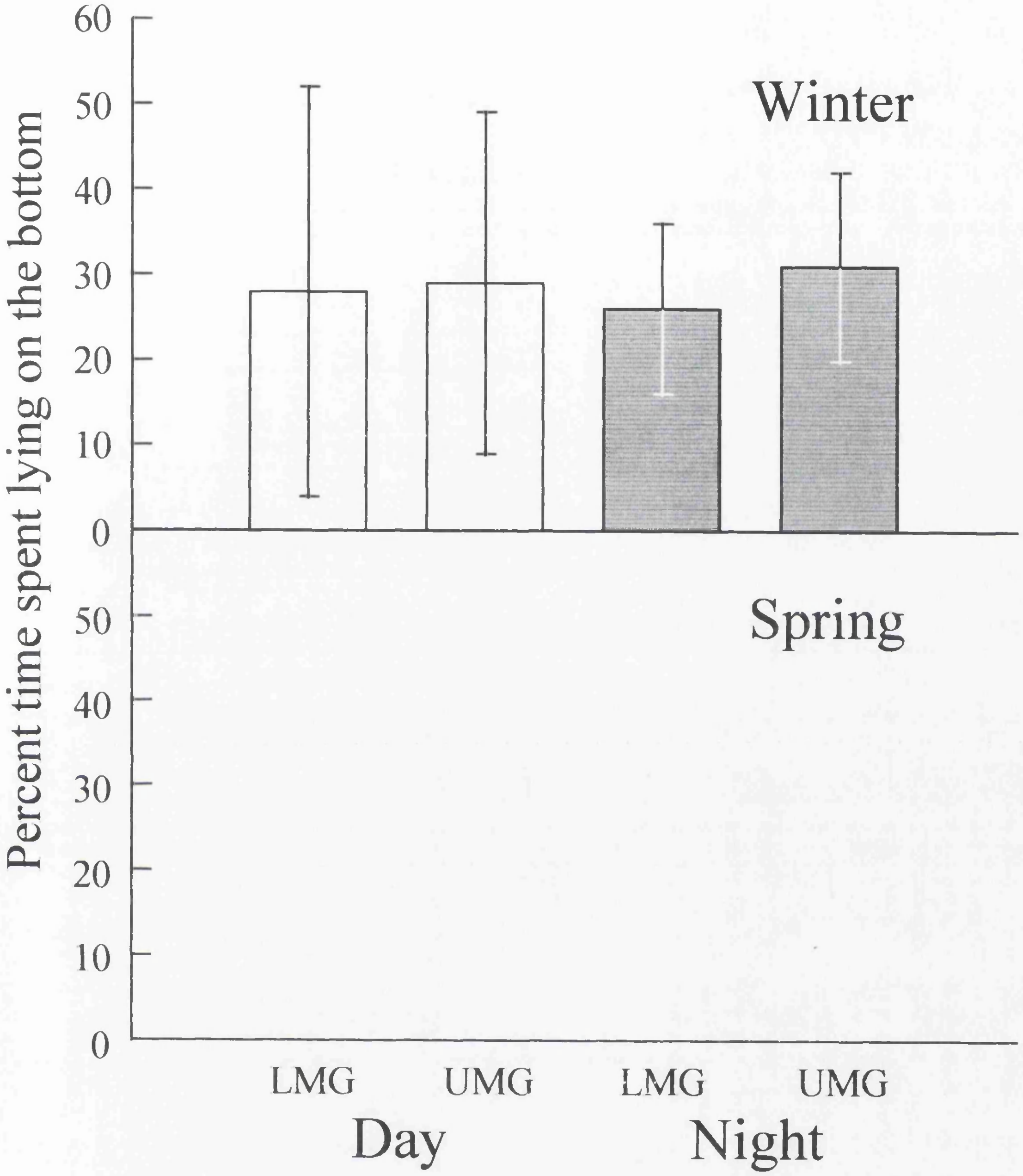

Figure 3. 4. Mean percentage of time spent holding station by swimming against the current (± SE) for upper modal group (UMG) and lower modal group (LMG) juvenile salmon that were outside shelters, during the night (dark bars), day (white bars), in winter (top graph) and in spring (lower graph).

## 3. 4 DISCUSSION

There was a general trend for the fish to become more active in spring than in winter. They stopped lying on the bottom and start to move around more instead of being stationary. This increase in activity was probably linked to temperature, which is of course not surprising since the metabolic rate of the fish increases with temperature and therefore they need more energy or food. In turn this results in them moving off the substrate since drift food density is proportional to current velocity (Elliott 1967a; Chapman & Bjornn 1969; Everest & Chapman 1972; Wankowski & Thorpe 1979; Fausch 1984; Hill & Grossmann 1993) which increases with distance off the bottom of the stream. However there was no increase in the overall number of feeding attempts per minute as the temperatures rose, but the pattern of feeding changed with the fish starting to feed more during the day when it is easier to locate prey (Fraser & Metcalfe 1997).

Since the figures for the number of feeding attempts for the two different life-history strategies during two seasons and times of day are now available, it is tempting to try to estimate the total number of feeding attempts per fish over the 24h and see how that changes seasonally. The average amount of time each modal group spent outside during winter and spring, and day or night, is calculated from figures obtained from this experiment and a similar one in 1994 (see chapter 2) on the average proportion of fish inside shelter, for each modal group, season and time of day (Table 3. 2.). Multiplying this number by the length of day or night at latitude 56° (latitude of the experiment; as given in Anon 1996) and the feeding rate while out of shelters (this chapter) then provides a rough estimate of total feeding attempts per 24h. This clearly shows that in the winter the upper modal group fish are making fewer feeding attempts than the lower modal group fish (Fig. 3. 5.) but this change in the spring when the upper modal group fish start to make more. In fact there is not a big difference between winter and spring for the lower modal group fish while the upper modal group fish make almost five times more feeding attempts in the spring than in the winter.

Although the upper modal group fish are making fewer feeding attempts per 24h over the winter than the lower modal group fish, they grow faster during that period (Higgins & Talbot 1985). However it is possible that by using the day to feed, they are more successful in locating and catching prey items. It has been shown that feeding efficiency in Atlantic salmon decreases in relation to light intensity and even under the best conditions (full moon and clear sky) their feeding efficiency at night is only approximately 35% of their daytime efficiency (Fraser & Metcalfe 1997). Therefore by feeding predominantly during the day the upper modal group fish could receive an equivalent or greater amount of food by making fewer but more successful feeding attempts than the lower modal group fish. Metcalfe *et al.* (submitted) have shown that short daytime foraging bouts have a major impact on the growth rates of wintering salmon. Therefore even though the upper modal group fish are hiding for most of the day and are active for most of the night in winter, they may not really be nocturnal foragers in terms of the relative amount of their daily intake that is obtained by night *vs.* by day.

Table 3. 3. Comparison of the proportion of time spent outside shelter by upper (UMG) and lower modal group (UMG) fish in winter and spring, night and day. Figures are calculated from observations of shelter use in 1994 and 1995 (see chapter 2)

| Modal group | Time of year | Time of day | Number of observations | Average percent of time outside shelter provided | standard error |
|---|---|---|---|---|---|
| UMG | Winter | Night | 94 | 80.22% | 2.04% |
| LMG | | | 94 | 88.86% | 1.47% |
| UMG | | Day | 148 | 27.39% | 1.80% |
| LMG | | | 148 | 39.94% | 1.67% |
| UMG | Spring | Night | 10 | 95.83% | 3.49% |
| LMG | | | 10 | 97.37% | 1.41% |
| UMG | | Day | 64 | 75.91% | 3.99% |
| LMG | | | 64 | 73.51% | 3.25% |

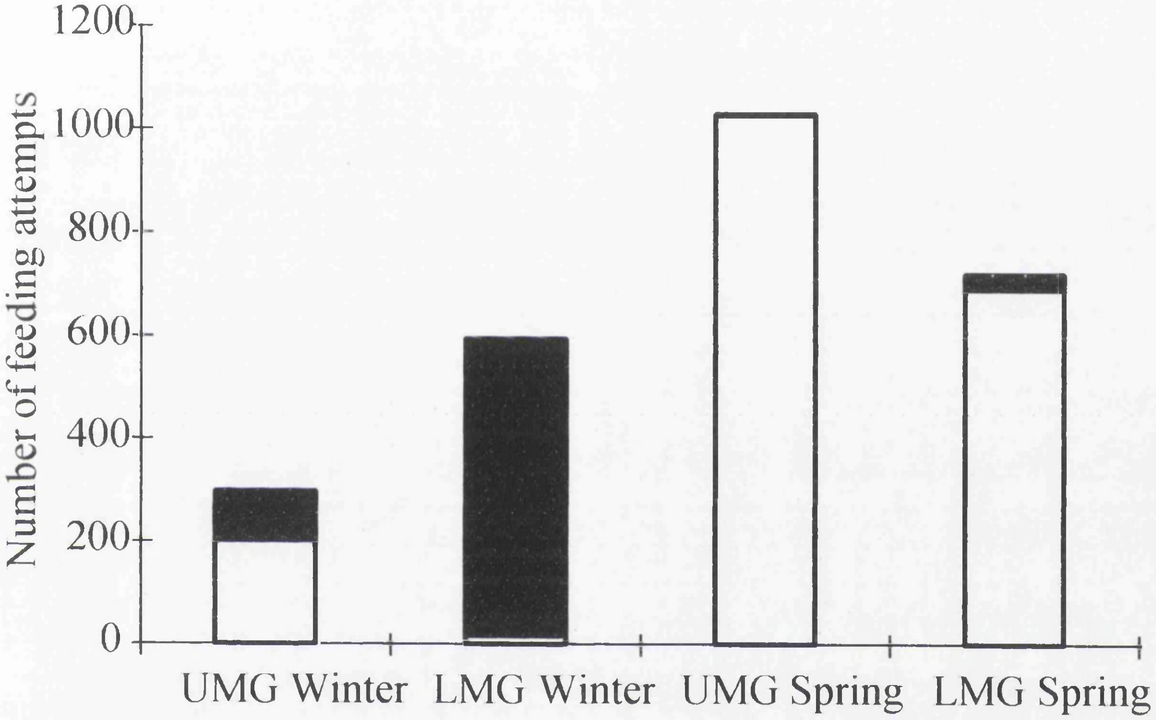

Figure 3. 5. Estimate of the average number of feeding attempts over 24h, split into those by day (white) and by night (black), during the winter and spring, for upper modal group (UMG) and lower modal group (LMG) fish.

There is some inconsistency in the literature about whether salmon are mainly crepuscular or nocturnal foragers in winter. Some early papers report that salmon are crepuscular (Hoar 1942; Kalleberg 1958; Chaston 1969), while more recent studies show that they switch to being almost exclusively nocturnal (Fraser *et al.* 1993; Heggenes *et al.* 1993). It has been shown in Arctic charr and rainbow trout that under a given set of conditions some individuals are predominantly nocturnal foragers while others forage more diurnally (Alanärä & Brännäs 1997; Brännäs & Alanärä 1997). The same has also been found in, sea bass, an unrelated marine fish (Sánchez-Vázques *et al.* 1994, 1995), but this 'dualism' is only reported for activity patterns in Atlantic salmon (Richardson & McCleave 1974; Varanelli & McCleave 1974), without any information on foraging patterns. The dualism in foraging activity that is revealed by this experiment suggests that during the summer, the fish that are biased towards diurnal activity will grow faster than the more nocturnal fish, due to a greater feeding efficiency by day and longer daylight hours. It is therefore tempting to suggest that one of the proximate causes of the divergence in growth rates and consequent bimodality in the size distribution of Atlantic salmon might be the existence of both predominantly diurnal and nocturnal foragers within the population. This would suggest a genetic basis for the separation. While some authors have demonstrated a genetic component to the bimodal separation (Bailey *et al.* 1980; Thorpe *et al.* 1980; Thorpe *et al.* 1983) , others have shown a more environmental basis (Adams & Thorpe 1989a, b; Thorpe *et al.* 1989; Metcalfe & Thorpe 1990). However, an important point from the studies of Alanärä & Brännäs (Alanärä & Brännäs in press; Brännäs & Alanärä 1997) is that the fish were often very marginal in their diel activity preference, being only slightly more diurnal than nocturnal or vice versa. The growth of these individuals will itself be intermediate between the extremes of a totally diurnal or totally nocturnal fish. This could generate a complete spectrum of growth rates, themselves subject to environmental conditions. This would produce environmentally-controlled life history strategies even if the alternative activity patterns were entirely genetically determined. Of course this is speculation at this stage but it would be very interesting to investigate this further by look at the feeding rates of individual fish at different times of the day in the spring and early summer of the first year of life, before the separation into the modal groups commences.

# CHAPTER 4 - SHELTER SELECTION IN JUVENILE ATLANTIC SALMON; OR WHY DO SALMON SEEK SHELTER IN WINTER?

## 4. 1 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. It has therefore been suggested that they switch from being continually 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; Riehle & 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.* in press; Chapter 2). 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., only feed at 35% of their day-time 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 1975a; Fraser *et al.* 1993, 1995). In cold water the swimming ability of the fish is reduced, due to a lowered metabolic rate. They are thus 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 minimise exposure to potential predators during the day, when the predation risk is highest (Fraser *et al.* 1993). The fish therefore accept a lower feeding efficiency at night (Fraser & Metcalfe 1997) since this is offset by reduced predation risk. At warmer temperatures, 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 (Hartman 1965). The fish are less able to withstand high flows at cold temperatures (Rimmer *et al.* 1985; Graham *et al.* 1996), so they might be forced into more sheltered micro-habitats. Moreover, 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 (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 differentiate between the hiding and sheltering categories of hypothesis, it is necessary to vary the attributes of the potential refuges, so that they do not simultaneously provide both concealment and shelter. 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.

## 4. 2 MATERIALS AND METHODS

This experiment took place in a small fibreglass stream tank at the University Field Station, Rowardennan, Scotland, which was divided by mesh screens into six replicate sections, each 100 cm long by 60 cm wide (Fig. 4. 1.). A pump created a continuous flow in the tank while ambient temperatures 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. The tank was inside a self contained unit but the photoperiod was kept at simulated ambient; the water temperatures during the experiment (February and March 1995) averaged 4.91 ± 0.11°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 3 light treatments x 3 velocity treatments). The refuges were identical in shape (each being a 20 cm-long tube of perspex with a 4 x 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', 0.003 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.

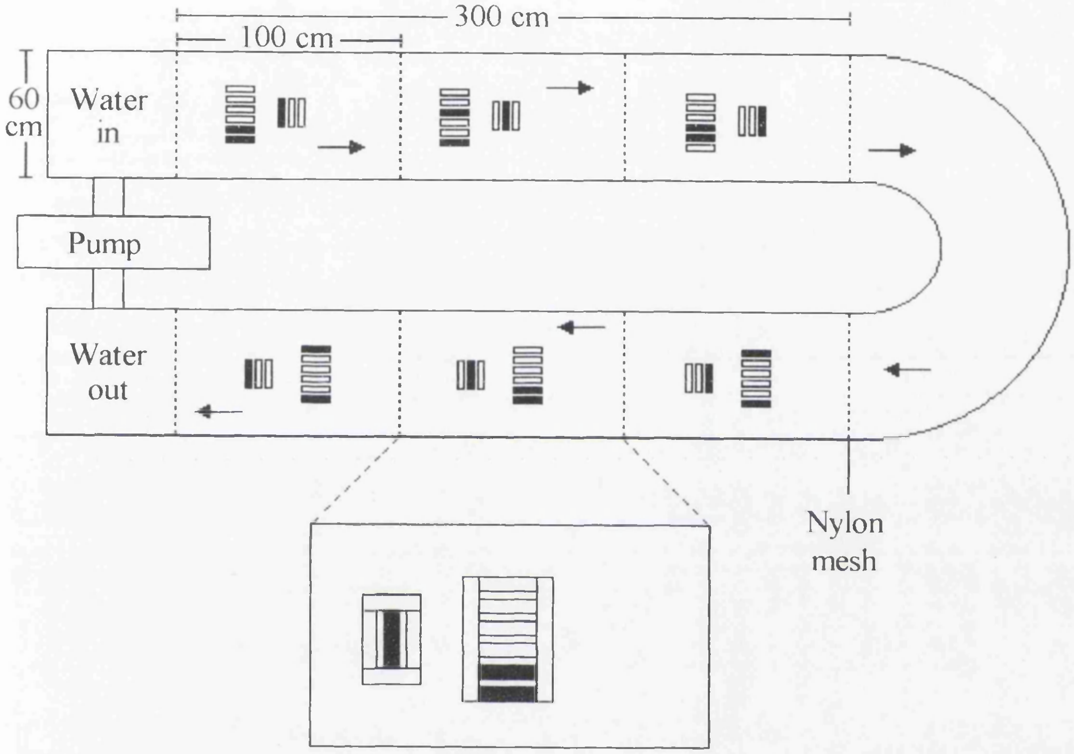

Figure 4. 1. Diagram of the flume. Nylon mesh divided the flume into six equally sized sections, each with a set of nine different refuges. Arrows indicate direction of flow. Enlarged insert shows a set of three refuges aligned perpendicular (receiving half flow) and a set of six refuges aligned parallel 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 refuges were too small to accommodate a light meter 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 randomised 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 underyearling hatchery-reared juvenile Atlantic salmon (the offspring of a pair of sea-run adults from the River Almond, in Perthshire, Scotland). The fish were less than 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 11:00 and 15:00. This was repeated until each of the 6 fish had been tested in each of the six stream sections; these fish were then replaced by new ones. Each fish was therefore tested a maximum of six times, each time in a different section with a different randomised arrangement of the 9 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.

## 4. 2 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. Chi-square test show clearly a non-random distribution of fish between the refuge types ($\chi^2$=171.98, *df*=8, *P*<0.0001). The fish were never observed in transparent refuges, and they used black refuges more than twice as often as white (Fig. 4. 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. 4. 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-square test; $\chi^2$=39.504, *df*=8, *P*<0.001) and there was a clear avoidance of transparent refuges or those with no current through them (Table 4. 1).

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 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 initially used any other kind returning to that kind on the next occasion (Chi-square test; $\chi^2$=7.88, *df*=1, *P*<0.005). Therefore the initial preference of the fish for dark refuges (Table 4. 1) was if anything strengthened by experience

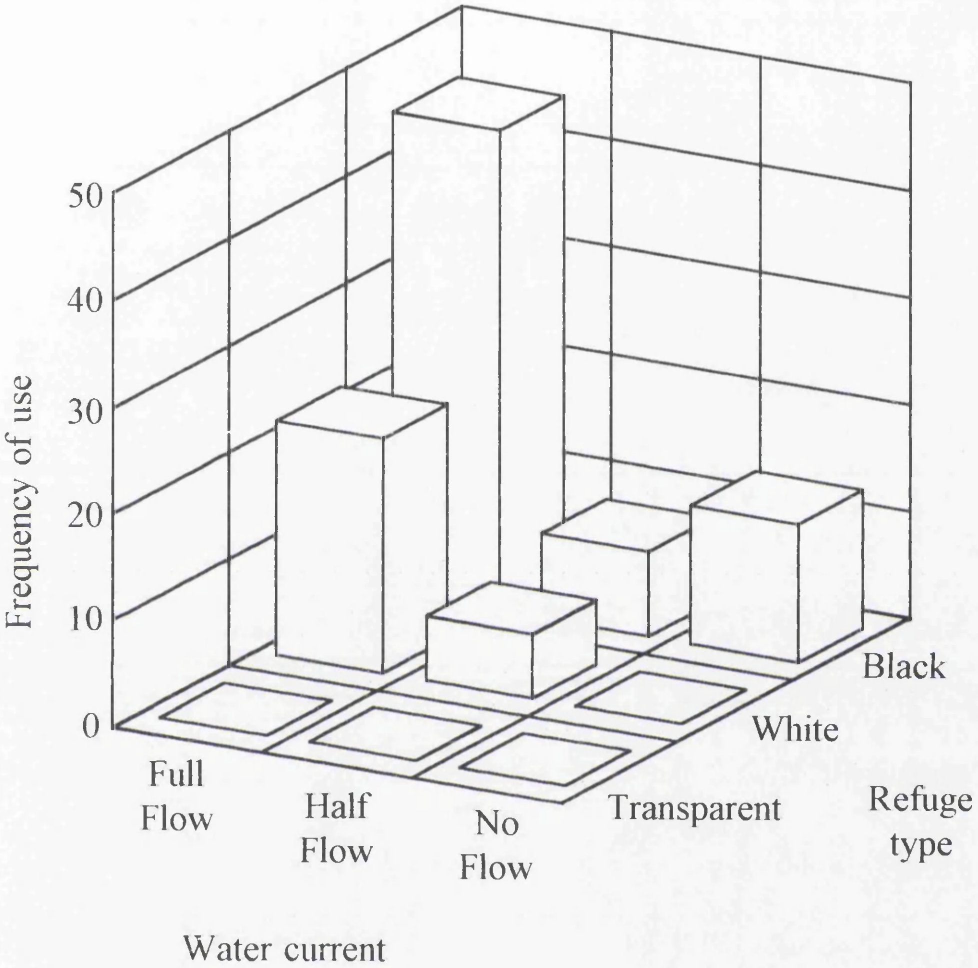

Figure 4. 2. Frequency of use of three refuge types under three flow conditions.

Table 4. 1. Frequency of first use of different daytime refuge types by underyearling Atlantic salmon (*N*=28 separate fish).

| 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 |

## 4. 4 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 (1996b) reached similar conclusions when they showed that the frequency of refuge use by rainbow trout 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.

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 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 and otter 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 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 anti-predatory behaviour. All main avian predators on salmon, e.g. divers, sawbill ducks, herons and kingfishers 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 this 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 1992a; Bull *et al.* 1996). The amount of time that must be spent foraging (and therefore exposed to predators) can be minimised by hiding in sites where there is the greatest opportunity to conserve energy.

# CHAPTER 5 - IS CHOICE OF FEEDING STATION AT NIGHT AFFECTED BY LIGHT INTENSITY: DO JUVENILE SALMON PREFER SLOWER CURRENTS ON DARKER NIGHTS?

## 5. 1 INTRODUCTION

Stream-dwelling juvenile salmonids are sit and wait predators which main foraging technique is to dart out from a vantage position to intercept prey items being carried past in the water current (Kalleberg 1958; Wankowski 1981; Bachmann 1984; Dill & Fraser 1984; Fausch 1984; Metcalfe *et al.* 1987; Godin & Rangeley 1989). The majority of the diet is thus made up of drifting invertebrates (hereafter termed 'drift') (Maitland 1965; Jenkins *et al.* 1970; Elliott 1973; Angradi & Griffith 1990). Within a stream there is a correlation between water velocity at a given point and the quantity of passing drift (Elliott 1967a; Chapman & Bjornn 1969; Everest & Chapman 1972; Wankowski & Thorpe 1979; Fausch 1984; Hill & Grossman 1993), so that fish have potentially the greatest access to food if they maintain a vantage point in the fastest flowing water available. However, the energetic costs of holding station against the flow also rise with water velocity, so that the optimal position, which maximises the net energy gain, is usually a feeding station slightly sheltered from an adjacent area of faster currents (Fausch 1984; Hughes & Dill 1990). Many juvenile Atlantic salmon therefore maintain station on or just off the bed of a stream, taking advantage of the slacker water surrounding stones and cobbles but darting out to feed in the faster water flowing overhead; velocities at the vantage point ('focal velocities') are typically only one fifth of those in the surrounding foraging zone (Morantz *et al.* 1987; Heggenes & Saltveit 1990).

However, this strategy is dependent on the fish being able to see approaching food items early enough to be able to move out and intercept them before they have been carried downstream. There will be a time window from the moment that an approaching prey item is first detected to when it is swept past the waiting fish; therefore the faster the current, the shorter the time available to the fish to recognise and move to intercept the prey item (Hughes & Dill 1990). This relationship will be affected by light intensity, since the detection distance will decrease in dim light. Juvenile salmonids can detect drifting prey items readily at light levels down to twilight (c. 1- 10 lx), but their performance declines rapidly through the range of light levels experienced at night (Brett & Groot 1963; Henderson & Northcote 1985; Fraser & Metcalfe 1997). This will result in foraging efficiency being substantially greater on moonlit than on dark nights (Fraser & Metcalfe 1997), a factor that will be most relevant at cold temperatures when these fish are predominantly nocturnal (Fraser *et al.* 1993; Heggenes *et al.* 1993; Riehle & Griffith 1993; Contor & Griffith 1995; Fraser *et al.* 1995). The most profitable feeding station may therefore change between daylight, twilight, moonlight and overcast night conditions.

I predict that fish should prefer feeding stations in fast flowing water at high light levels and slow currents at low light levels. In order to test this idea I demonstrate experimentally that the fish change their microhabitat preference as predicted in relation to changes in night-time light intensity, prefering slower flowing water on darker nights.

## 5. 2 MATERIAL AND METHODS

The experiment was carried out using a stream tank. The tank was U-shaped, with each straight arm being 4m in length with a width of 0.6m. Water was made to circulate around the tank by a pump that drew water out of the end of one arm and pumped it back in at the end of the other. Ambient temperatures were maintained by a constant flow of fresh loch water into the stream tank, while an overflow kept water depth at 0.4 m (within the preferred depth range for juvenile salmon (Heggenes 1990; Heggenes & Saltveit 1990)). The tank was constructed of fibreglass, except for the inner wall of each arm which was made of glass panels to allow behavioural observations.

The stream tank was modified to produce four replicate sections, each 1.1 m long, separated from each other by at least 1m. In each section a transparent perspex vertical baffle was placed at an angle across the tank to create a wedge-shaped compartment, wider at the upstream end. The compartment was bounded at the up- and downstream ends by a nylon mesh screen through which the water flowed along the length of the stream. The floor of the tank (on both sides of the perspex baffle) was covered with an even layer of gravel and small pebbles (c.0.5 - 2.0cm diameter), to simulate the substrate found in a real stream. The gradual narrowing of the compartment due to the slanting baffle produced a velocity gradient within each compartment without any change in water depth, nor any visible change in stream width (since the baffle was transparent); this allowed me to test the velocity preference of fish placed within a compartment independent of any preference they might have for water depth, stream width or cover.

The tank was within a light-proof hut, so that the level of illumination could be controlled. Daytime and night-time illumination were provided by separate fluorescent lights suspended above the tank; these were operated automatically by timers. A variable number of neutral density filters were used to screen the night-time lights so that they produced a range of low light intensities (see below).

The experiment was carried out on underyearling hatchery-reared salmon parr, offspring of sea-run adults caught in the River Almond. On 6 February 1996 24 were picked at random from a large stock population with the proviso that they were all from the lower modal group of the bimodal size distribution (and so would not smolt for another year; Thorpe 1977). They were then placed in a holding compartment in the bend of the stream tank. The photoperiod (simulated ambient) was then reversed so that observations of the fish under night-time levels of illumination could be made in normal working hours. The fish were then left to adjust to this regime for 12 days, during which time they were fed every other day by releasing frozen *Daphnia* or chironomid larvae into the water column.

A single fish was then placed in each of the four test compartments, and the light filters adjusted so that the night-time illumination was one of the four test levels (5.0, 1.0, 0.3 or 0.00 lx, the latter being produced by switching all lights off). The fish were then left for 24 h to settle. Observations consisted of making a single record of the focal position of each fish, scored as distance (to the nearest 10cm) from the upstream end of its compartment. They were made by illuminating each compartment in turn with a small hand-torch; preliminary observations showed that the only response of the fish to the torch was to drop directly down onto the substrate (if they were not already on it) and remain motionless (Heggenes *et al.* (1993) observed similar responses in wild fish). The observation at the first test light intensity was made a minimum of 2 h after 'dusk'. The light intensity was then altered to another of the test levels and the fish left undisturbed for at least 2 h before making the observation of fish positions at this second light intensity. This procedure was repeated on the second 'night', so that a single record of position was obtained from each fish at all four test light intensities. During these trials the fish were able to feed on low densities of planktonic drift that entered the tank in the incoming loch water, but received no additional food and so would continually have been hungry. The four test fish were then removed and replaced by four new fish from the holding compartment, and the testing procedure repeated. The order of presentation of the four test light intensities was randomised to control for any effects of learning during the two-day trial. The trials were carried out between 19 February and 7 March 1996, when the mean water temperature was 4.7 ± 0.3 °C (s.d.). At the end of the trials water velocities were measured 5 and 10 cm above the substrate across the width of each compartment every 10 cm along its length ($N = 2$-18 readings per 10 cm, depending on the width), using a Sensi Ltd. RC2 electromagnetic velocity meter. The mean velocity at the recorded position of a fish was taken to be its preferred velocity at that light intensity; measurements at 5 and 10 cm above the substrate were pooled since there was no significant difference between them.

## 5. 3 RESULTS

All fish took up feeding stations in the stream tank either in contact with, or just above, the substrate. The baffles were successful in creating an even gradient in water velocity from the upstream end of each compartment; fish therefore had to select a velocity from a continuum ranging from 5-45 cm $s^{-1}$ (Fig. 5. 1.). While there was individual variation in the current velocity preferred, there was a consistent trend for fish to move position in response to night-time light intensity (repeated measures ANOVA with the four levels of light intensity as the within-subjects factor, $F_{3,69} = 4.01$, $P = 0.021$). As predicted, there was an overall trend for fish to move into slower flowing water as light intensity decreased (Fig. 5. 2.; linear term of the orthogonal polynomal contrast, $t = 3.10$, $df = 21$, $P = 0.005$). Thus when comparing 0.00 and 5.0 lx, 18 fish were at slower velocities at the darker condition, 4 were unchanged and only 2 were in faster water.

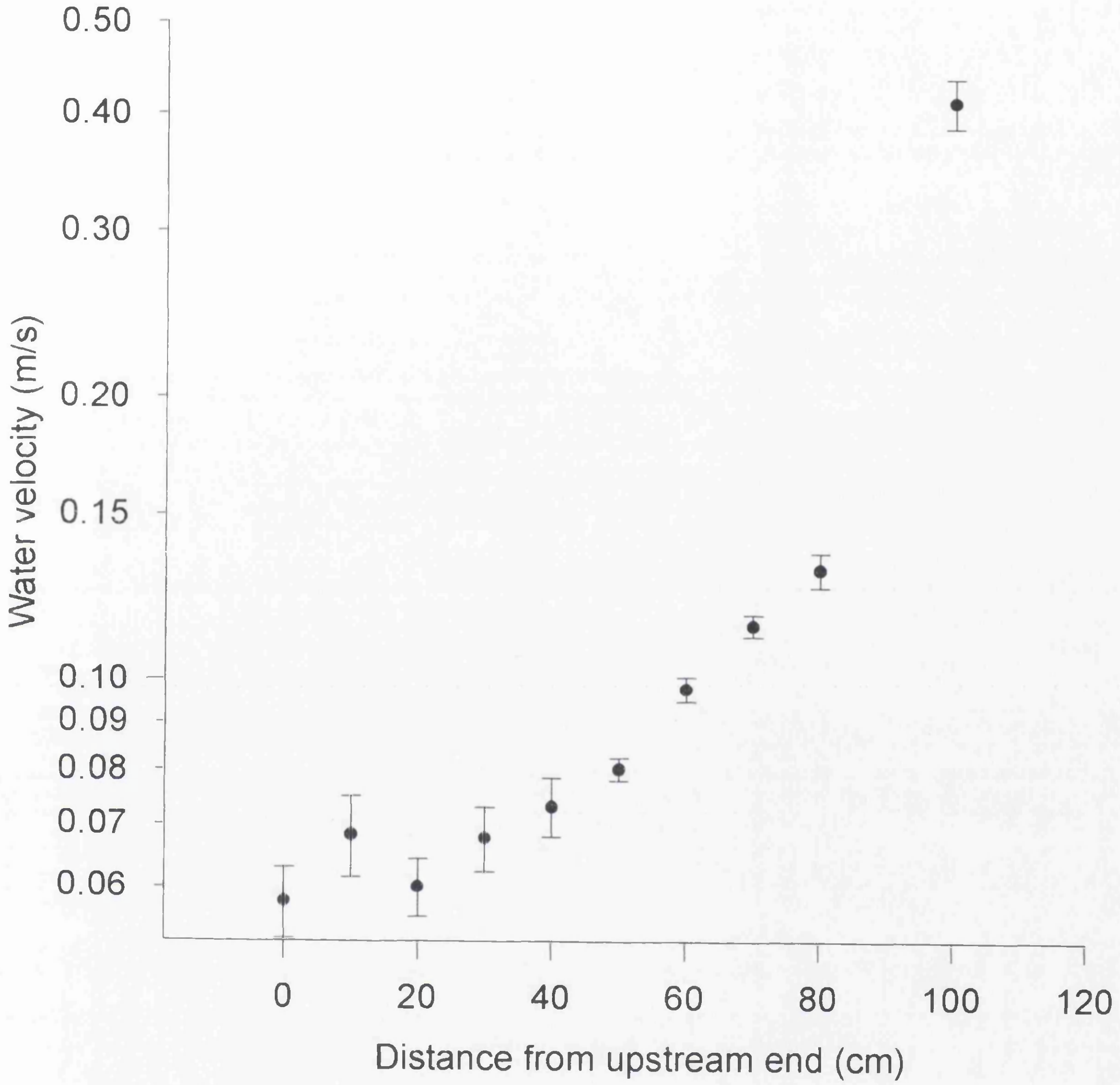

Figure 5. 1. Water velocity in relation to position in test sections of the stream tank. Data are means (± s.e.) from four replicate sections; salmon therefore had a choice of velocities from 5-40 cm $s^{-1}$ in which to hold station.

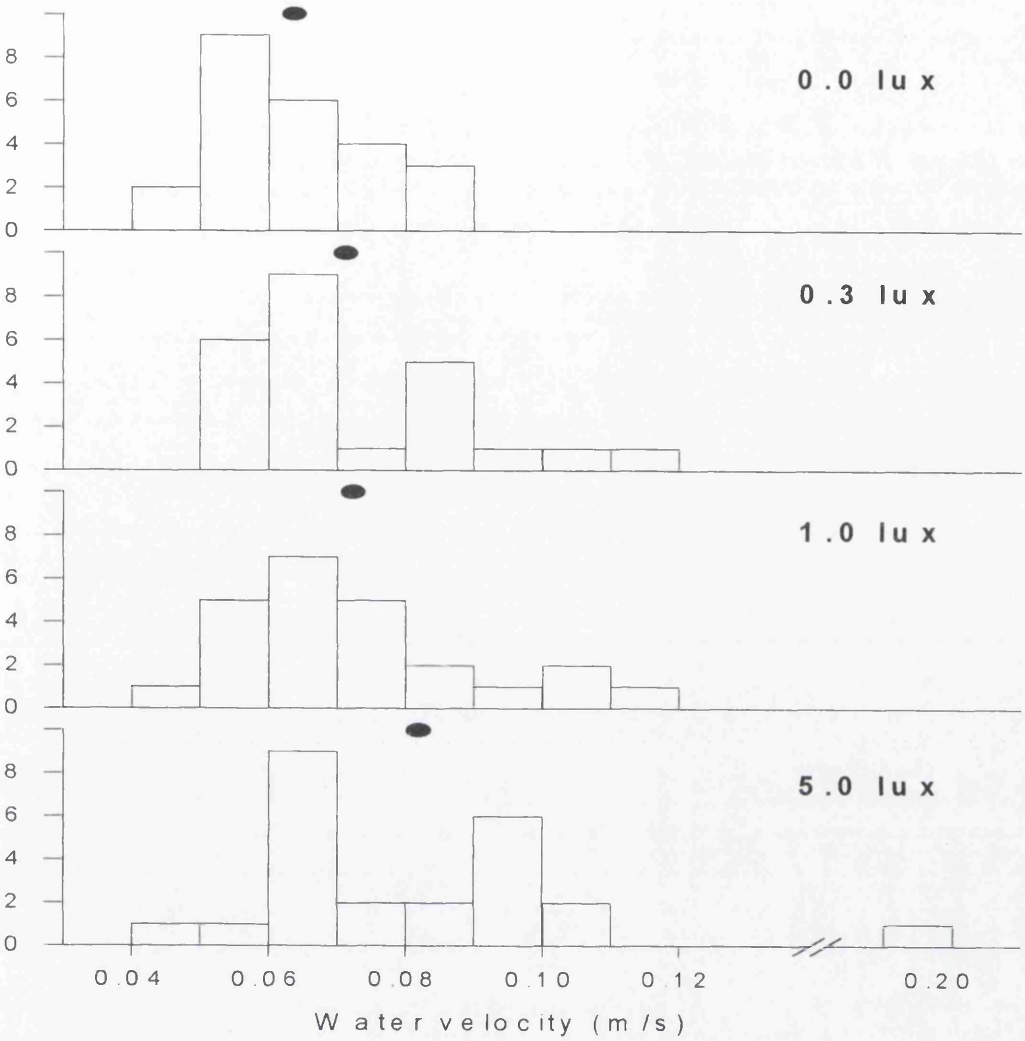

Figure 5. 2. Frequency distribution of water velocities adopted by the same 24 juvenile salmon under four different light intensities. Mean velocities are indicated by the dots; see text for statistical comparison.

## 5. 4 DISCUSSION

Several previous studies have described wild fish being in slower currents at night than during the day. Edmundson *et al.* (1968) described how individual steelhead moved up to 45m between day- and night-time stations, moving into slower flowing water near the banks at night. Heggenes *et al.* (1993) found that the majority of nocturnal feeding stations occupied by wintering brown trout were in pools or backwaters, where the water velocity within the potential feeding area was usually under 10 cm $s^{-1}$. Hill & Grossman (1993) also observed rainbow trout to be in slack water at night, but presumed these fish to be inactive and not foraging. However, my results suggest that the fish were forced to move out of their daytime foraging sites and into slower currents at dusk because the daytime sites could no longer be exploited; the fish may well have been foraging at night at a maximal rate within the constraints set by their reduced reaction distance. This study has also shown for the first time that there may be habitat shifts even between nights, since the optimal foraging position on an overcast night (when light levels will be well below 0.01 lx; Fraser & Metcalfe 1997) will be in slower flowing water than on a night with full moon. To my knowledge no-one has measured whether wild fish do indeed select different microhabitats under crepuscular, moonlit and starlit conditions. I would also predict that bankside vegetation would influence microhabitat choice, since the shade cast by overhanging trees and bushes reduces crepuscular and night-time light intensities by approximately 90 % (Fraser & Metcalfe 1997). Shade also reduces the contrast of a food item against the background, making it harder to detect. Fish should therefore select sites exposed to slower water velocities in shaded reaches of a stream.

Maximum intake rates will inevitably be reduced at lower light intensities even if fish and switch to slower flowing areas of the stream. This will constrain intake rates at night, when light levels are seldom above 0.3 lx (Fraser & Metcalfe 1997). Juvenile salmonids become increasingly nocturnal as water temperatures decrease below 10 °C (Fraser, *et al.* 1993, 1995; Riehle & Griffith 1993; Heggenes *et al.* 1993; Contor & Griffith 1995; Valdimarsson *et al.* in press; Chapter 2), and so the constraints on daily intake imposed by short detection ranges will be greatest in winter. At this time of year there is an additional factor: the maximum foraging range may be further reduced by the effect of temperature on fish acceleration (Webb 1978) and sustained swimming speed (Graham *et al.* 1996). In cold water fish will be slower to dart out and intercept passing items, and so will not be able to exploit as wide a foraging range. This is evident from the results of Hill & Grossman (1993), who found that prey capture success in rainbow trout was lower at winter compared to summer temperatures (5 vs. 15 °C), especially for prey items passing furthest from the waiting fish. Whether or not the reduction in foraging efficiency in winter actually limits daily intake rates will, however, depend on the balance between food intake and digestion rates, since the latter are also greatly reduced at low temperatures (Higgins & Talbot 1985).

The diel variation in light levels is not the only cause of changes in microhabitat choice. Suspended sediments or pollutants can reduce visibility, resulting in similar effects to a reduction in light intensity. Turbid water (for instance after heavy rain) results in reduced feeding rates as well as a switch in the diet away from drift prey in favour of benthic items (Stradmeyer & Thorpe 1987; Gregory & Northcote 1993).

# CHAPTER 6 - IS LEVEL OF NIGHT-TIME AGGRESSION AND FISH DISPERSION DEPENDENT ON LIGHT INTENSITY?

## 6. 1 INTRODUCTION

The behaviour of many animals whereby they defend an exclusive area by aggressive means results in the phenomenon of territoriality (Huntingford 1984). Two possible benefits of defending a territory are improved foraging opportunities or better chances obtain a mate. The costs are primarily the time and energy spent on territorial defence and the risk of injury from attacking intruders (see Davies & Houston 1984). In territorial species the size of the territory is of special interest because it is thought to limit population density (Wynne-Edwards 1962, 1971; Gauthier & Smith 1987; Chapman 1966; Allen 1969; Begon *et al.* 1990; Elliott 1990; but see Lack 1966), as individuals without territories may not be able to mate or obtain food. These ideas have then led to discussion as to whether animals do self-thin like plants (Begon *et al.* 1986; Elliott 1993; Grant 1993; Fréchette & Lefaivre 1995; Armstrong 1997). Three main factors will influence the economic defendability of a territory and therefore its size. These three factors are: resource quality and distribution in space (e.g. in the case of food availability and distribution an animal should defend an area that is big enough to provide all the food it needs); resource distribution in time (e.g. renewal of food: an animal should defend an area that is big enough to allow a sufficiently high rate of food replenishment); and competition for the resource (an animal can only defend an area against a certain number of competitors and must adjust the territory size according to its defendability; Davies & Houston 1984).

These factors, however, only deal with the most economically defendable area or the average size of the area in the long term, but there may also be other factors (more physical perhaps) that influence the size of area defended on a shorter time-scale. The ability to detect and recognise an intruder must be very important and if that ability is somehow reduced the size of the territory must reduce at the same rate. Similarly, territory holders should not defend areas within which food items cannot be detected. Here I predict that for a visually oriented animal, the size of territory must therefore change in accordance with visibility.

Stream-living juvenile salmonids are an ideal model to demonstrate this. They are territorial foragers that feed mainly on organisms drifting in the water current (Kalleberg 1958; Gerking 1994). These territories are defended aggressively against neighbouring intruders and territory size has been shown to depend on factors such as the size of the fish (Grant *et al.* 1989; Elliott 1990; Grant & Kramer 1990) and food abundance (Dill *et al.* 1981).

During winter many juvenile salmonids become more nocturnal, hiding in the substrate gravel during the day (Fraser *et al.* 1993; Griffith & Smith 1993, Heggenes *et al.* 1993; Riehle & Griffith 1993). Temperature, light intensity and time of year interact to trigger this switch (Fraser et al 1995; Valdimarsson *et al.* in press; see chapter 2) whose function is most likely to be avoidance of exposure to predators (Fraser *et al.* 1993; Metcalfe *et al.* submitted; Valdimarsson & Metcalfe in press; chapter 4). This is counter-intuitive since salmonids are usually considered to be visual foragers (Keenleyside 1962; Stradmeyer & Thorpe 1987) and their ability to locate prey decreases dramatically in relation to light intensity (Fraser & Metcalfe 1997). Moreover, Metcalfe *et al.* (1997; see also chapter 5) have shown that the preferred feeding micro-habitat for juvenile salmon is dependent on night-time light conditions such that during bright nights the fish forage in faster flowing areas than on dark nights. This is due to the relationship between prey detection distance and reaction time; when detection distance is impaired by low light the fish must move to slower flowing areas to have the same reaction time (i. e. the time elapsed from initial detection until the prey item passes the fish) as at higher light levels.

Since the potential foraging radius is curtailed at low light levels, then the defended areas should shrink in parallel (it is not economic to defend an area larger than the foraging area; but see Grant *et al.* 1989). The reduction in territory size at low light levels should lead to greater aggregations in better foraging areas on dark nights than on light. Territory size is difficult to measure, especially at low light levels, but an index of the size of the defended area is given by the degree of clumping of the fish and the aggression rate. In the present study I therefore looked at how the rate of aggression and nearest neighbour distance in a group of juvenile salmon varied with night-time light intensities.

## 6. 2 MATERIALS & METHODS

The experiment was carried out between 3 and 18 August 1996. The experimental tank was a 1 $m^2$ tangential flow grey fibreglass tank inside a lightproof constant temperature cabinet; this maintained water temperature at 6 °C throughout the experiment. Water was taken from Loch Lomond and let to cool down in a reservoir inside the cabinet until it reached the surrounding temperature. It was pumped into the experimental tank, entering in one corner. An opaque partition wall extending parallel to the side wall of the tank created a channel in which the water flows were strongest (Fig. 6. 1.). An automatic feeder (placed over the water inlet) dispensed food pellets into the water current every 5 min throughout the night only, uneaten food being carried into the central drain. The purpose of the arrangement of the water flow and the partition wall was to create a preferred feeding area (i. e. with faster flows and a point food source) which would induce more aggressive and territorial behaviour (Adams *et al.* 1995). Water exiting from the tank entered a sump tank and was then recirculated.

During the experiment the photoperiod was kept constant at 12L:12D, with lights off at 19:00h and lights on at 07:00h, daylight being simulated by a fluorescent strip light (450 lx). At night the tank was lit by a 400 W metal halide lamp (Thorn Kolorarc MBIF Daylight, Thorn EMI Ltd, UK) positioned 1.5 m above the tank. This lamp produces light of similar wavelengths to moon- or starlight (Fraser & Metcalfe 1997). The illumination produced by this light was varied between trials by neutral density filters. Four different light intensities were used in the experiment (0.00, 0.01, 0.50 and 1.00 lx; 0.00 lx is complete darkness while 1.00 lx is equivalent to light about 1 h after sunrise or before sunset; Fraser & Metcalfe 1997), the intensity being measured using a Skye Instruments SKL 300 photometer, range 0.01-2000 lx (Skye Instruments Ltd, Llandrindod Wells, UK). Because the lamp takes time to heat up it was left switched on constantly except for the treatment condition where the night time light intensity was 0 lx .

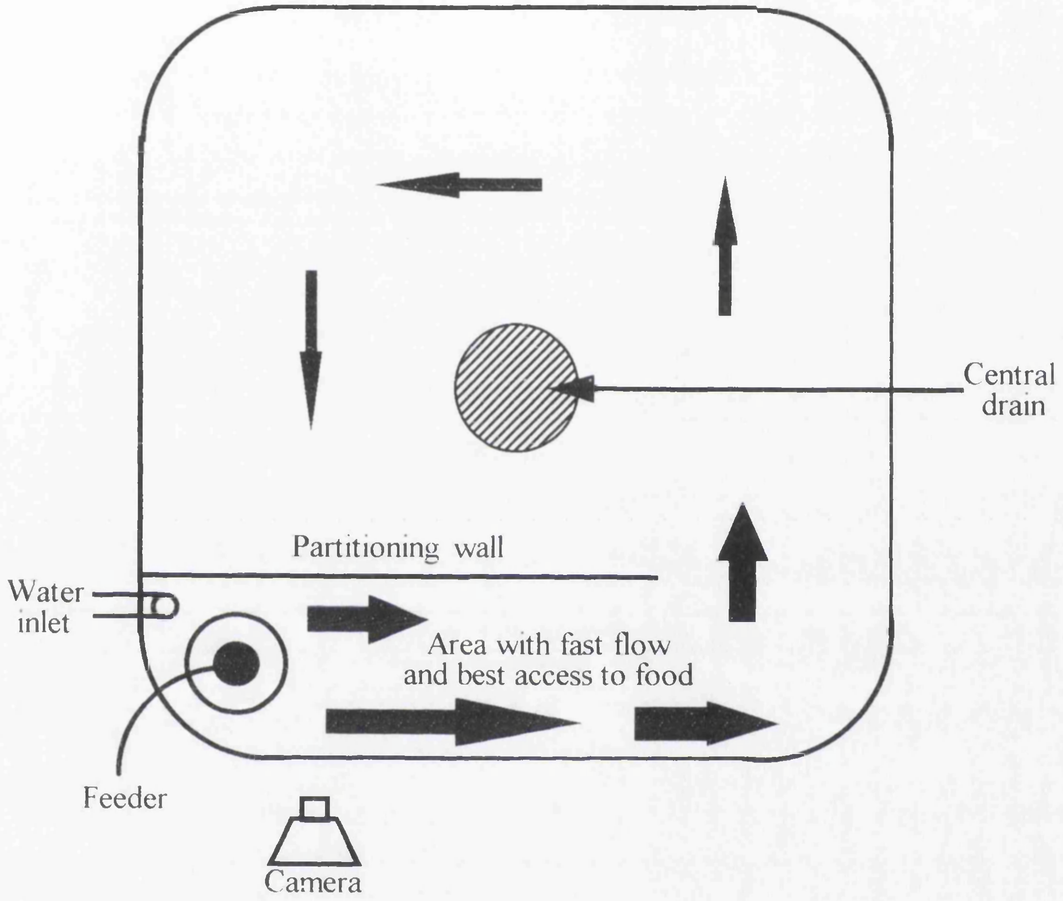

Figure 6. 1. Plan view of the experimental tank. The CCTV camera was mounted above the tank.

White PVC tape was used to cover the bottom of the tank to make it easier to see the fish during night time recording, when the tank was illuminated with infrared light (470 nm) (salmon are unable to see light in the infrared part of the spectrum (Ali 1961)). A CCTV camera with wide angle lens (4.8 mm, f 1.4) mounted above the tank was programmed to record on video tape the behaviour of the fish for 20 minutes from 18:55 h, then for ten minutes at 21:00, 23:00, 01:00, 03:00, and 05:00 h, and finally for 20 minutes from 06:50 h. The camera did not record the whole of the tank, but most of it (including all of the faster area of current) remained in view and the position of the camera was not altered between treatments.

The experimental protocol was to take 8 similar sized fish from a stock tank in which the conditions (temperature and photoperiod) were similar to that of the experimental tank. The fish were briefly (less than 2 min) anaesthetised in benzocaine, measured for forklength and then put into the experimental tank (the mean sizes of each of three groups of fish were 72.0 ±2.3 mm, 75.1 ±1.0 mm and 74.1 ±1.3 mm forklength). After the fish had settled for 24h, one of the four test night-time light intensities was picked at random, the appropriate filter was put in front of the night-time light source and the video-recorder was started. The night-time light intensity was changed every day until all four intensities (0.00, 0.01, 0.50 and 1.00 lx) had been used. The procedure was then repeated on a different group of fish, with the light intensities presented in a different order. In total 3 groups of 8 fish were tested (data on the fourth group were lost).

The tapes were analysed for two different factors: the aggression rate and the minimum nearest neighbour distance. The number of aggressive interactions observed in a 5 minute period was recorded at 6 times during each night (at 19:10, 21:00, 23:00, 01:00, 03:00 and 05:00 h). All behaviours that could be viewed as aggressive were counted; these were mainly attacks that involved burst swimming, both by the fish that made the attack and by the fish that received it. An index of nearest neighbour distance was taken as the shortest distance in mm on the video monitor (approximately one quarter of the real distance) between the two fish that were closest to each other at exactly 19:10, 21:05, 23:05, 01:05, 03:05, 05:05 and 06:55 h. The fish were watched for a few seconds before the exact time to check for the possibility of an aggressive attack at the moment of measurement; if the fish closest to each other were found to be close together because they were involved in an aggressive attack, the second nearest fish were used. These recording methods produced one value for aggression rate and one for nearest neighbour distance for each group of fish at each time of night at each four night-time light intensities.

Two-way, within subjects (repeated measures) analysis of variance was used for statistical analysis of the effect of light intensity and time of night on aggression and nearest neighbour distances. This is the most appropriate test since it omits any potential problem of pseudoreplication. However, because only 3 replicates were made it was not possible to test for sphericity and therefore it was only possible to test for overall effects and not for differences between specific light levels.

## 6. 3 RESULTS

There were clear differences in behaviour in relation to light intensity. In general the fish were less aggressive at low light-levels but, as predicted, seem to become more active and territorial at the higher light-levels. The average rate of aggressive interactions (bites, nips and chases) was lowest in complete darkness and increased as light intensity increased to 1.0 lx (two-way within subjects (repeated measures) ANOVA; effect of light level, $F_{3,15}=5.268$, $P<0.05$). On average the fish showed five times as many aggressive movements at 1.0 lux than in complete darkness (Fig. 6. 2). The time of the night was also important, as the fish were more aggressive shortly after the lights went down than later in the night (one-way within subjects (repeated measures) ANOVA; effect of time of night, $F_{5,15}=6.854$, $P<0.01$; Fig 6. 3).

The minimum distance between the fish was on average greater on bright nights than on dark nights (two-way within subjects (repeated measures) ANOVA on index of nearest neighbour distance; effect of light level, $F_{3,18}=12.959$, $P<0.005$; Fig. 6. 4). However, the minimum distances between the fish were not dependent on the time of night(one-way within subjects (repeated measures) ANOVA; effect of light level, $F_{3,15}=5.268$, $P<0.05$).

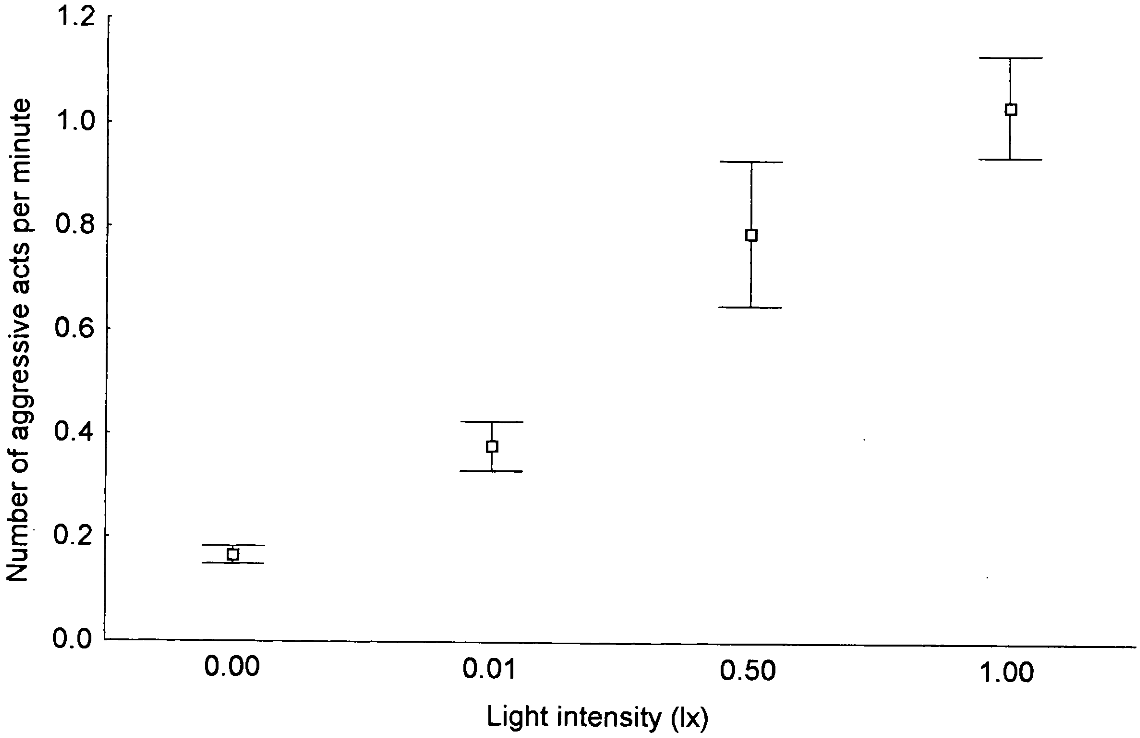

Figure 6. 2. The mean number (±SE) of aggressive acts per minute within a group of 8 juvenile salmon at 4 different night-time light levels (two-way within subjects (repeated measures) ANOVA; effect of light level, $F_{3,15}=5.268$, $P<0.05$).

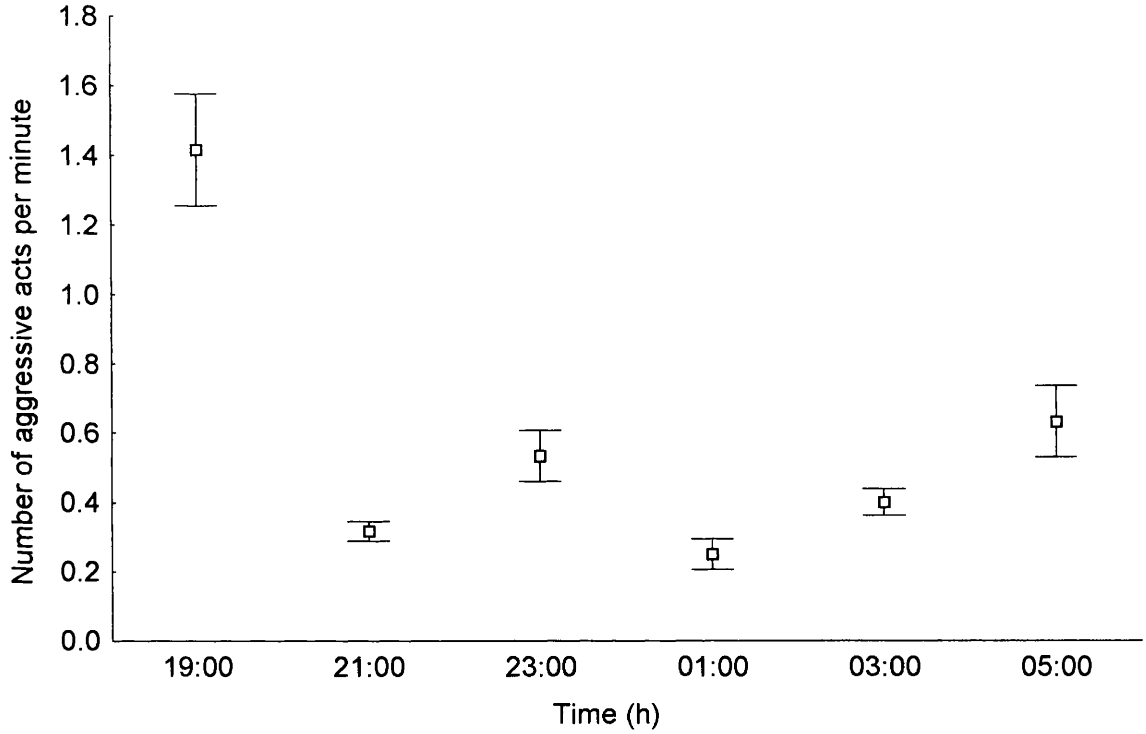

Figure 6. 3. The mean number (±SE) of aggressive acts per minute within a group of 8 juvenile salmon at six different times during the night. The 4 different light levels are pooled together (one-way within subjects (repeated measures) ANOVA; effect of time of night, $F_{5,15}$=6.854, $P$<0.01).

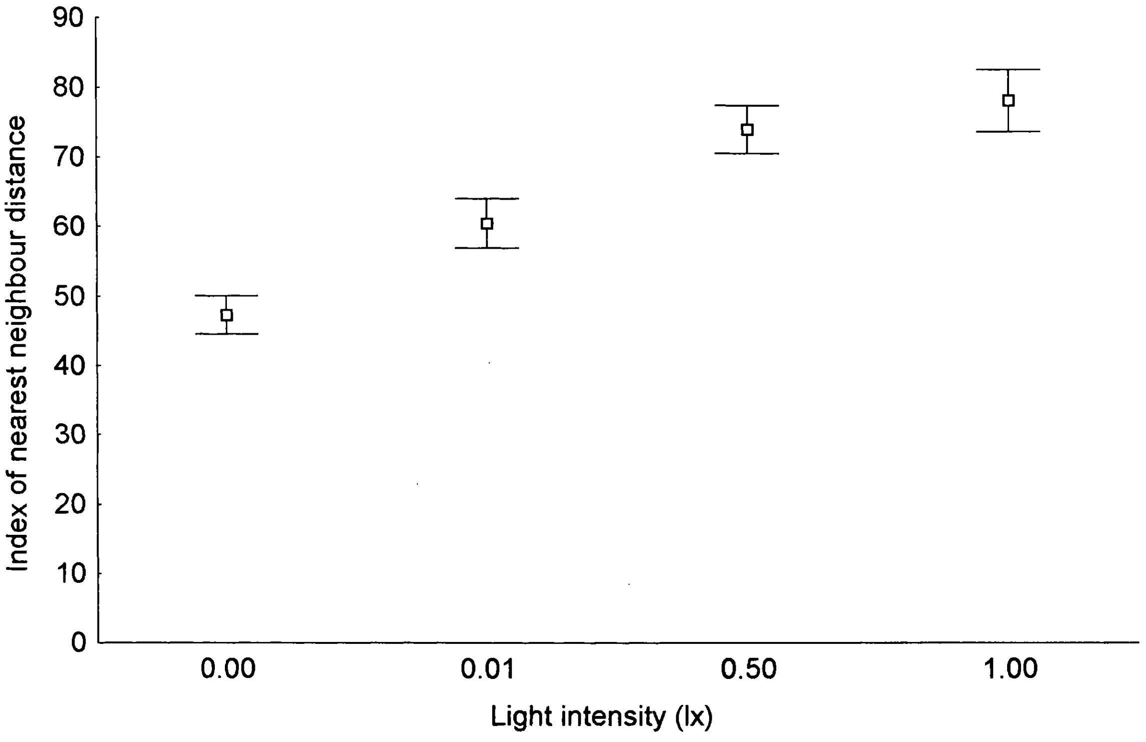

Figure 6. 4. The mean (±SE) index of nearest neighbour distance in groups of 8 juvenile salmon at 4 different night-time light levels (two-way within subjects (repeated measures) ANOVA; effect of light level, $F_{3,18}$=12.959, $P$<0.005).

## 6. 4 DISCUSSION

That the fish were more aggressive as the light intensity increased initially suggests that in order to aggressively defend a territory the fish must be able to see one another. This is further indicated by the fact that at the lower light intensities the fish were closest to each other and yet they made fewest attacks. However, it is perhaps more likely that the area defended is more dependent on how far away the fish can detect their food rather than the detection distance of conspecifics: there would be little point in spending time and energy defending an area much larger than the maximum that can be exploited for food. In order to feed, the fish are dependent on being able to see, and their feeding efficiency increases with increasing light intensities (Fraser & Metcalfe 1997); their territory size should therefore do so as well. This is not the first time where vision has been linked to territoriality or where light levels have been shown to affect aggression rates. Gregory and Griffith (1996a) showed that rainbow trout become more aggressive at dawn when light intensities increased from 1 lx upwards. Berg and Northcote (1985) showed that juvenile coho salmon reduced or ceased their territoriality following an increase in turbidity. Furthermore, when juvenile salmonids are living in areas with large boulders, where the fish cannot see each other as well due to the streambed topography, agonistic behaviour is reduced resulting in a decrease in mean territory size (Kalleberg 1958), this may help explaining the higher densities of fish in such areas (Hillman *et al.* 1987; L'Abée-Lund & Heggberget 1995; Meyer & Griffith 1997a).

Aggression is in general lower in winter than in summer (Cunjak & Power 1986b; McMahon & Hartman 1989; Fraser *et al.* 1993). Temperature is probably important in reducing aggression in winter, mostly by having an effect on metabolic rate and therefore reducing both the overall activity of the fish and the need for food (and hence the need to defend a territory). This means that salmon territories should generally be smallest when both light level and temperatures are low, and largest on a bright day in a warm river.

An important factor in determining the size of territories is food availability. Myers *et al.* (1979) identified two hypotheses for why there should be a relationship between the size of a territory and food density. First, an animal assesses the prey density and directly adjusts its territory size to include resources sufficient for its current energetic needs plus, possibly, some unspecified increment for a long-term insurance of a reliable food supply. Secondly, an animal defends an area as large as it can, but its territory size is constrained by competition. Drift abundance is usually highest during the night (Elliott 1967a,b, 1970; Forrester 1994) so therefore it could be argued that territories should get smaller at night, even without any effect of low light, since fish would only need to defend a smaller area in order to have access to the same amount of food. However, since this study only looked at the effect of night-time light intensity, with food supply kept constant, the results presented here clearly support the hypothesis that the aggressive behaviour of juvenile salmon should depend on night-time light levels independently of food supply, and further suggest that the size of territories could change between day and night.

That the fish were more aggressive at the beginning of the night than later is very likely due to the fish establishing and rearranging their social hierarchy and spatial organisation. When the light intensity starts to decrease the fish will have to rearrange and relocate their territories accordingly. Fish migrate from poorer habitats into richer which eventually results in a higher degree of aggression shortly after dusk, but stabilises when everything has been established. This should also happen at dawn when the increase in light intensity allows for bigger territories or when fish might fight for access to shelter. Kadri *et al.* (1997) found a similar pattern of higher aggression rates at the start of the day, and in a study of juvenile rainbow trout by Gregory & Griffith (1996a) the aggression rate per fish was highest about 30 minutes after sunrise. This could explain why some studies (e .g. Eriksson 1973; Varanelli & McCleave 1974) which measured the locomotor activity of salmonids suggested that these fish are crepuscular (foraging at dawn and dusk), since they recorded the greatest rate of most triggering of light beams at these times. The peaks in activity at dawn and dusk may therefore be more due to changes in preferred microhabitat (Metcalfe *et al.* 1997; chapter 5), associated increases in movement rates and aggressive interactions (this study; Gregory & Griffith 1996a; Kadri *et al.* 1997) than to peaks in feeding rates.

Some studies have suggested that mean territory size will control the population density of stream living salmonids (Chapman 1966; Allen 1969), since space is a limiting factor. While this may be important when the juveniles first start to feed (Elliott 1994), it seems less likely later on. The winter is often associated with high mortality (Maciolek & Needham 1952; Needham & Jones 1959; Baglinière *et al.* 1993; Smith & Griffith 1994), which suggests that it is a period when population regulation mechanisms would be apparent. However, since juvenile salmonids are mostly nocturnal in winter and since they appear to defend smaller territories at night (which allow nonterritorial fish access to food), this indicates that in winter it is not necessarily territory size that controls the size of the population. Instead, other factors such as the availability of suitable overwintering microhabitats (e.g. substrates that provide refuges; Hillman et al 1987; Cunjak 1988, 1996; Meyer & Griffith 1997b) and the balance between predation rate and starvation (Gardiner & Geddes 1980; Bull *et al.* 1996) may control population size at this time.

# CHAPTER 7 - ARE JUVENILE SALMON NOCTURNAL BUT FORAGE DIURNALLY IN SUMMER DUE TO A HIGH ENERGY DEMAND?

## 7. 1 INTRODUCTION

During the summer, juvenile salmonids are diurnal or even arhythmic (24h) foragers but in winter they switch to nocturnal feeding, hiding in the substrate gravel during the day (Fraser *et al.* 1993; Griffith & Smith 1993, Heggenes *et al.* 1993; Riehle & Griffith 1993). Temperature, light intensity and time of year interact to trigger this switch (Fraser et al 1995; see chapter 2) whose function is most likely to be avoidance of exposure to predators (Fraser et al 1993; Fraser & Metcalfe 1997; Metcalfe *et al.* submitted; Valdimarsson & Metcalfe in press).

That the fish become nocturnal foragers might seem odd because salmon use vision to detect and catch prey items passing by in the water current (Keenleyside 1962; Stradmeyer & Thorpe 1987). Fraser & Metcalfe (1997) have shown that juvenile Atlantic salmon are not very efficient at foraging in low light intensities and even under the brightest night-time conditions (full moon and clear skies) only 20-40% of their fish fed compared to 90% under day-time light-conditions. This suggests that switching to nocturnalism is costly for the salmon because the fish are not efficient enough to get the energy they need during the hours of darkness. This cost may be reflected in the fact that the resident salmon (those that are going to spent at least one additional year in the river) grow very slowly over winter and even lose weight (Higgins & Talbot 1985; Metcalfe *et al.* 1980; Bull *et al.* 1996). However, the cost of foraging in darkness has to be balanced against the risk of predation and it has been suggested that the lowered feeding efficiency at night is more than offset by a reduced predation risk (Fraser & Metcalfe 1997).

The reason for salmon becoming nocturnal only in winter is probably due to the temperature at that time. At low temperatures the metabolic rate of the fish is low and therefore they have a decreased energy demand. So even though salmon are inefficient nocturnal foragers they may be able to acquire enough food by only feeding at night, when the predation risk is lowest. In contrast, in summer the fish need more energy and may therefore not be able to get what they need by only feeding during the night, especially since the length of the night is shorter; this would result in the fish needing to use the day for foraging as well.

This hypothesis assumes that the fish prefer to feed in darkness and that they should shelter whenever they do not need to feed, in order to avoid exposure to predators. Fish provided with food in their shelters should not therefore need to emerge at all. In order to test this idea I set up an experiment where I compared the behaviour and growth of a group of fish who had food delivered into their shelter to that of a control group who had access to a shelter but who had to come out to feed. I predicted that the fish that were able to feed in their shelter should emerge less than the controls, especially during the day when the risks of foraging are highest; shelter-fed fish should become more nocturnal.

## 7. 2 MATERIALS AND METHODS

Forty under-yearling Atlantic salmon were selected from a stock holding tank on 27 March 1996 and anaesthetised in benzocaine for under 5 min, during which time they were measured for fork-length, weighted and given individual combination of alcian blue dye marks (with small subcutaneous injections of alcian blue dye). The fish were presumed to belong to the lower modal group (the resident salmon, see chapter 1) on the basis of their size (Thorpe 1977). They were offspring of wild sea-run salmon caught in the river Almond, Perthshire, Scotland, and had been reared in hatchery conditions prior to the experiment. The fish were then transferred to two 60 cm circular tangential flow tanks ($N = 20$ fish per tank). The addition of a removable 'false bottom' to the tanks provided a darkened refuge for the fish which they could enter through four 3 cm diameter holes in the upright section surrounding the central drain (Fig. 7. 1).

Each tank had the same type of automatic feeder, delivering approximately the same amount of food per day. A sprinkle of food was dispensed every 10 min throughout the 24h. The exact amount of food was adjusted according to how much food was left in the tank uneaten. The feeders were placed over the tanks, but the feeder for the 'shelter-fed' tank dispensed approximately half of the food into a hopper, and this food was then carried by a flow of water along a tube and released into the shelter underneath the false bottom. The remaining food in the 'shelter-fed' tank, and all of that in the control tank, fell onto the water surface and then slowly sank to the bottom and was carried down the drain in the water current. Therefore fish in the control tank could only feed by emerging from the shelter, whereas those in the shelter-fed tank could also acquire food inside the shelter.

A CCTV camera with wide angle lens (4.8 mm, f1.4) was placed facing downwards over the tanks and programmed to record onto video tape for 5 min every 3 h (00:00, 03:00, 06:00, 09:00, 12:00, 15:00, 18:00 and 21:00). An infrared light (470 nm) was used to illuminate the tanks during night (salmon are unable to see light in the infrared part of the spectrum (Ali 1961)). The tapes were analysed by counting the maximum number of fish visible (outside the shelters) during every 5 min period in each tank.

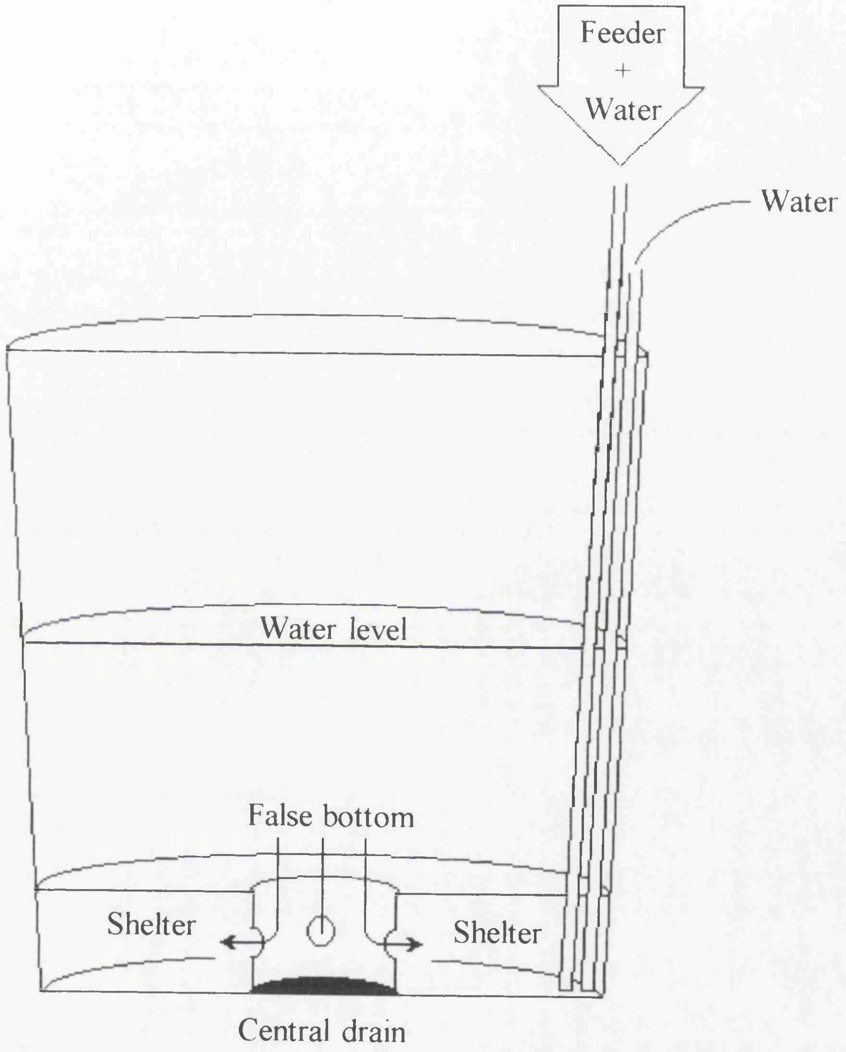

Figure 7. 1. Cross section of the tank used to house the shelter-fed group. The addition of a false bottom provided a darkened refuge into which fish could move freely at any time. The arrows show the path the fish took to get into the darkened area. The tank for the control group was identical except that there was no food pipe going into the shelter.

The experiment started on 27 March 1996 and ran until 1 July of the same year, although the data sampling was not continuous due to occasional problems with powercuts, feeders or the video system. The fish were re-weighed and measured for forklength on 19 May and 9 July for estimation of growth rates. The tanks were lit during the day by fluorescent lights on a simulated ambient photoperiod and were kept close to a window, to provide natural night time light-intensities. The water temperature was ambient and ranged from 4.8 °C at the beginning to 15 °C at the end of the experiment.

Two fish in the control tank showed external signs of smolting (silvery colour and slender body; characteristics of migrants) in the last measurement on 9 July. While it was difficult to separate the fish into the two modal groups (see chapter 1) because the small sample size did not reveal a bimodal size distribution, these fish were assumed to belong to the upper modal group. It was not possible to exclude the smolting fish from the video analysis but they are excluded from growth analyses. 12 fish died during the course of the experiment due to unknown causes, 5 in the control treatment and 7 in the other shelter-fed group. Analysis of emergence patterns is therefore based on the (arcsine transformed) percentage of fish alive at the time that were out of the shelter in each 5 min period. Observations each day (or night) are grouped together and one mean value used per day/night. To see whether differences in behaviour between the two groups were greater by day or by night, the arcsine transformed percentage of the shelter-fed group that was out was subtracted from the equivalent number from the control group for that day/night.

## 7. 3 RESULTS

There was a significant difference in the number of fish out of the refuge at night between the treatments, with fewer fish from the shelter-fed group outside (analysis of covariance; effect of treatment $F_{(1,148)}=21.509$, $P<0.001$). Overall, temperature had no significant effect on the number of fish outside (analysis of covariance; temperature as covariate, $F_{(1,148)}=0.048$, $P=0.827$) but there was an interaction between temperature and treatment group (analysis of covariance; interaction between temperature and treatment, $F_{(1,148)}=44.822$, $P<0.001$), thus the treatment groups responded differently to changes in temperature. The shelter-fed group showed a negative response to temperature so when the temperature increased the number of fish outside the shelter decreased (Pearson correlation between the percent of fish outside (arcsine transformed) and temperature; $r=-0.512$, $N=76$ days, $P<0.001$; Fig. 7. 2. b & d). However, the control group responded positively to temperature such that more fish were found outside as the temperature increased (Pearson correlation between the percent of fish outside (arcsine transformed) and temperature; $r=0.455$, $N=76$ days, $P<0.001$). At high temperatures the shelter-fed fish therefore hid in the shelter much more than the controls (Fig. 7. 2. a & c).

There was also a difference during the day between the treatment groups in the number of fish outside, and again it was the shelter-fed fish that emerged less (analysis of covariance; effect of treatment $F_{(1,166)}=11.283$, $P<0.001$). As expected, temperature had an effect on the number of fish outside (analysis of covariance; temperature as covariate, $F_{(1,166)}=6.605$, $P<0.05$), but the interaction between the treatments and temperature was also significant (analysis of covariance; interaction between temperature and treatment $F_{(1,166)}=47.743$, $P<0.001$). The response of the treatment groups to changes in the temperature was therefore different during the day as well as during the night, and again the shelter-fed group responded negatively (Pearson correlation between the percent of fish outside (arcsine transformed) and temperature; $r$=-0.306, $N$=85 days, $P$<0.005) while the controls responded positively (Pearson correlation between the percent of fish outside (arcsine transformed) and temperature; $r$=0.613, $N$=85 days, $P$<0.001). This again resulted in shelter-fed fish hiding more than controls, but only at higher temperatures.

The extent to which fish were nocturnal was quantified by using a nocturnal activity index (Fraser et al 1995):

$$\text{Nocturnal Activity Index} = 100 \times E_n / (E_n + E_d),$$

where $E_n$ is the mean number of fish exposed (i.e. out of refuges) in each 5 min film period each night, and $E_d$ is the equivalent value for each preceding day. The nocturnality index was unaffected by temperature (analysis of covariance; temperature as covariate, $F_{(1,146)}$=1.188, $P$=0.278), so even though temperature had an effect on how many fish were out day and night, it did not affect the ratio of fish outside between day and night. The treatment groups did not differ in their response to temperature (analysis of covariance; interaction between temperature and treatment, $F_{(1,145)}$=0.915, $P$=0.340), but there was a significant difference between the treatments, with the shelter-fed group being more nocturnal than the control group (analysis of covariance; effect of treatment, $F_{(1,146)}$=20.231, $P$<0.001) (Fig. 7. 3).

The difference in behaviour between the two groups was no greater during the day than during the night (analysis of covariance; effect of time of day, $F_{(1,159)}$=1.766, $P$=0.186). However, the differences were greater at higher temperatures than at lower (analysis of covariance; temperature as a covariate, $F_{(1,159)}$=116.779, $P$<0.001) but this effect was not dependent on the time of day (analysis of covariance; interaction between temperature and time of day, $F_{(1,158)}=3.600$, $P=0.060$; Fig. 7. 4).

Specific growth rates (or percent change in weight per day) of the fish were calculated according to the formula:

$$\text{Specific Growth Rate} = [\ (\ln W_t - \ln W_o\ /\ t] \times 100$$

where $W_t$ is the weight at time $t$, $W_o$ is the initial weight, and $t$ is the time, in days between weighings. There was a significant differences in growth rates between the two treatment groups ($t$-test on the specific growth rate between the treatment groups; $t=-5.02$, $df=24$, $P<0.001$; Fig. 7. 5). At the beginning of the experiment there was no significant size difference between the two treatment groups ($t$-test between the two treatment groups, weight: $t=-1.65$, $df=36$ $P=0.11$, forklength: $t=-1.16$, $df=36$, $P=0.36$; Fig. 7. 6). However, the shelter-fed group grew faster over the experimental period resulting in the development of significant size differences ($t$-test between the two treatment groups on 19 May, weight: $t=-2.62$, $df=31$ $P<0.05$, forklength: $t=-3.46$, $df=31$, $P<0.01$, and on 9 July, weight: $t=-3.81$, $df=24$ $P<0.001$, forklength: $t=-4.73$, $df=24$, $P<0.001$; Fig. 7. 6).

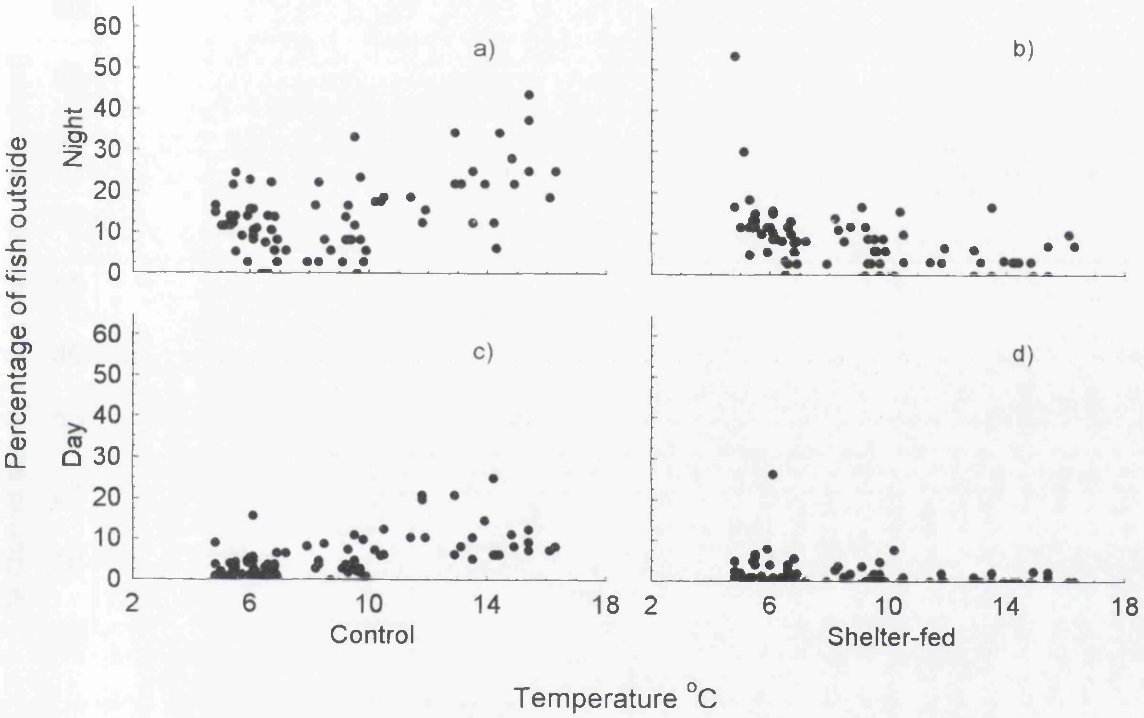

Figure 7. 2. Effect of temperature on the average percent of fish outside their shelter. a) the control group at night, b) the shelter-fed group at night, c) the control group during the day, and d) the shelter-fed group during the day.

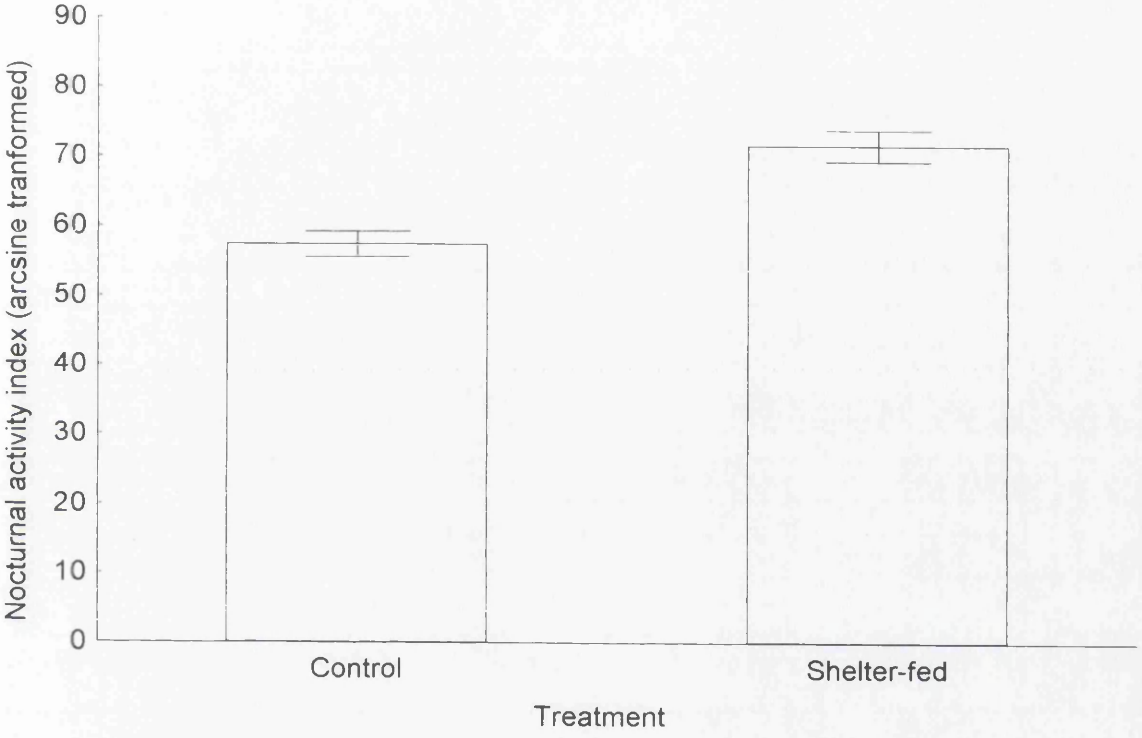

Figure 7. 3. Mean (±SE) nocturnal activity index (see text) for control (*N*=77) and shelter-fed (*N*=72) fish.

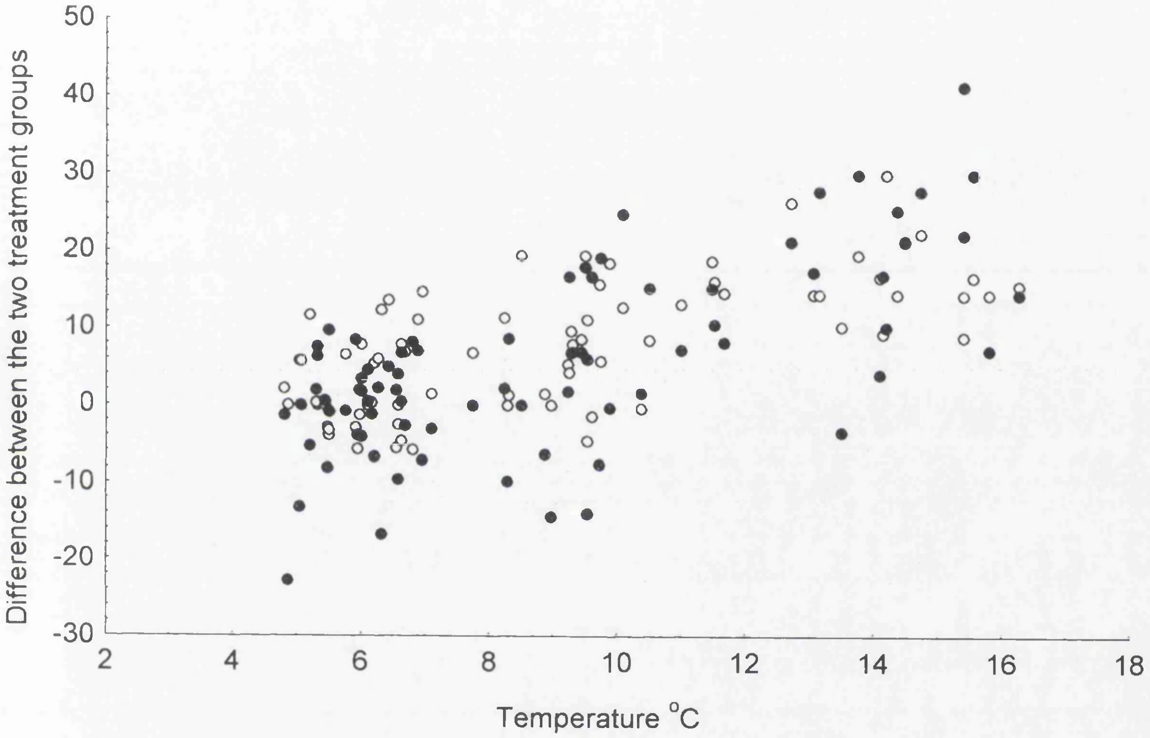

Figure 7. 4. Difference in the percentage of fish out of shelter between the two treatment groups plotted against temperature during the night (filled circles) and day (empty circles). Positive values indicate that the control fish used the shelter less than the shelter-fed fish.

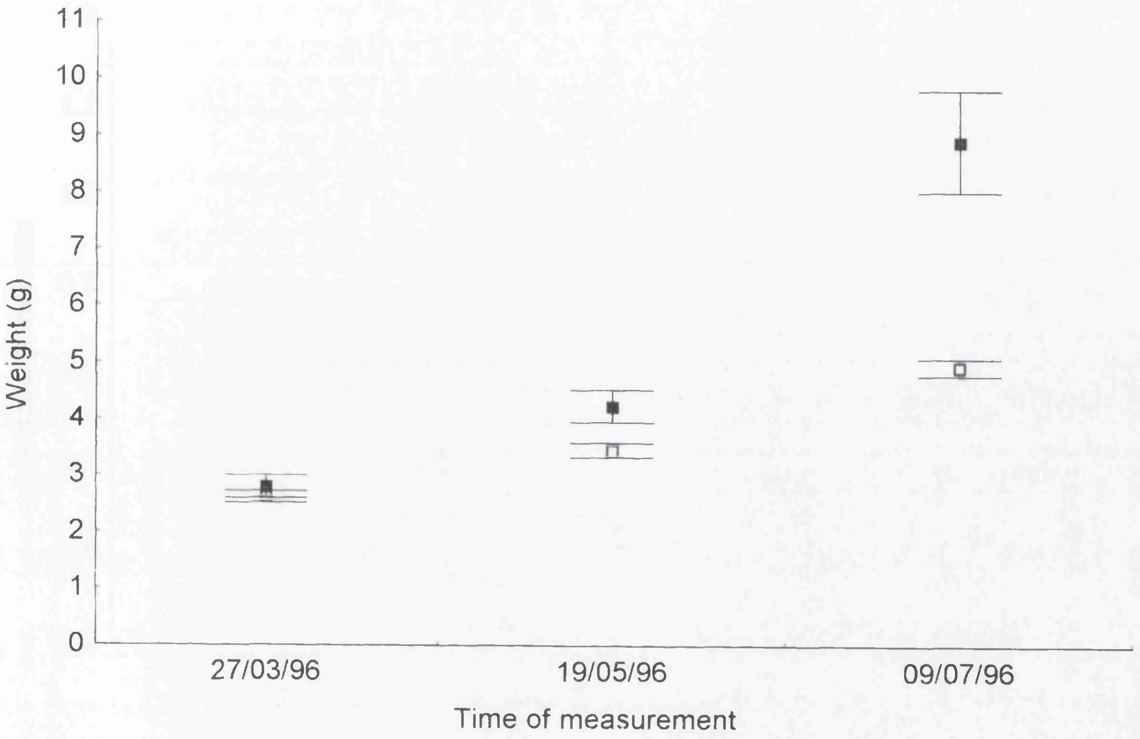

Figure 7. 5. Mean weight (±SE) for shelter-fed (closed squares) and control group (open squares) at different times of the experiment.

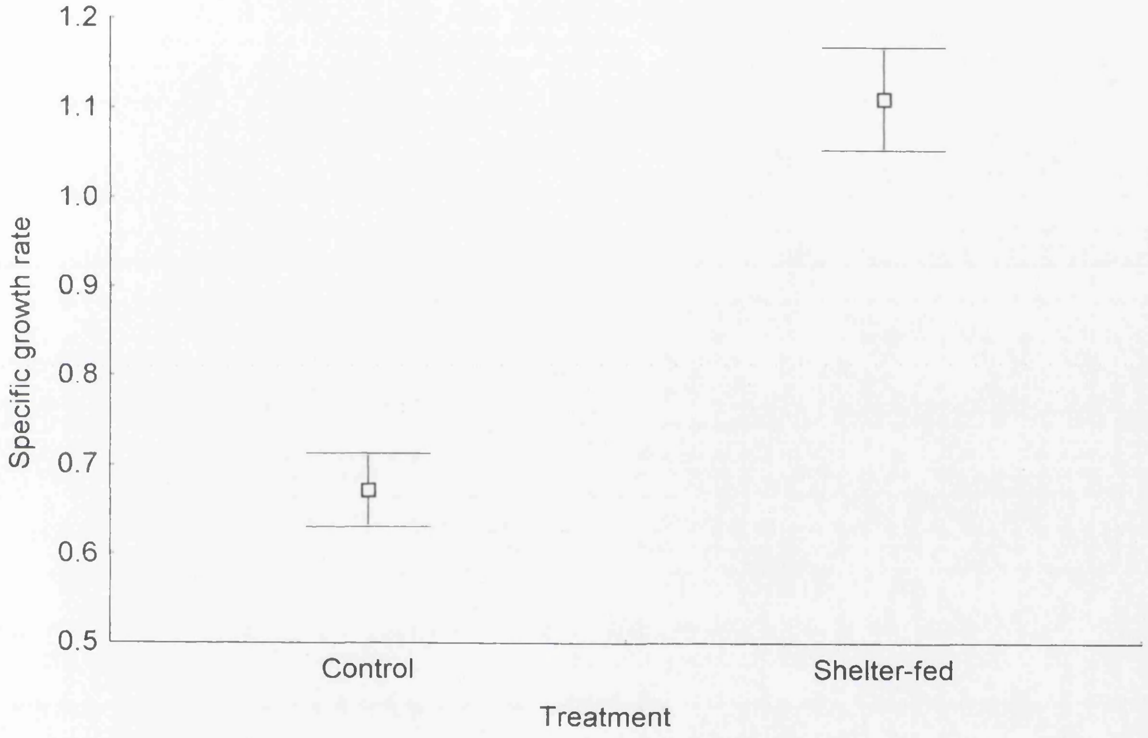

Figure 7. 6. Mean specific growth rate (% increase in weight per day) for the two treatment groups over the experimental period.

## 7. 4 DISCUSSION

That the shelter-fed group generally emerged less then the control group supports the hypothesis that fish prefer to feed in darkness, sheltered from predators, but might be forced by their higher metabolic rates to feed during the day in summer. This is not surprising since previous studies have shown that salmonids take higher risks in terms of potential predation risk when hungry (Dill & Fraser 1984; Metcalfe *et al.* 1987; Gotceitas & Godin 1993), moreover, fish previously deprived of food spent more time outside refuge than controls who were fed normally (Bull 1996). So a hungry fish should therefore emerge from its shelter and forage, even in the presence of a predator, while a satiated fish can afford to avoid predators and stay in shelter until it becomes energetically compromised.

That the shelter-fed fish came out of the shelter less as the temperature increased could be due to the time it took the fish to learn that there was no more food outside than inside; if this is true then the relationship with temperature would therefore be coincidental, being due to the fact that the ambient temperatures increased as the study progressed. The control group emerged from shelter more as the temperature rose, as has been shown in other studies (Fraser *et al.* 1995; Valdimarsson *et al.* 1997, chapter 2) and was possibly in order to meet an increasing energy demand due to their increasing metabolic rate.

Surprisingly the fish in the shelter-fed group did come out during the day, though to a lesser extent than the control group. It is possible that the food supplied into the shelter was not enough for the fish or that the emerging fish came out to forage without competition. Another possible explanation is that after the food pellets had been carried with water into the shelter they were wetter and perhaps not as appetising as the food delivered onto the surface.

One would expect that the differences in behaviour between the groups should be greater during the day when the expected risk of foraging would be highest, whereas at night there should be very little differences. However, this study does not fully support this prediction although the higher overall nocturnal activity index found in the shelter-fed group indicates that there were more difference between day and night activity levels in that group, so generally supporting the hypothesis

.

The difference between the treatment groups in growth rate was unexpected. This means that under normal circumstances the growth rate of the fish may be suppressed by hiding, and it also suggests that my prediction that in winter the fish could obtain their required energy by only feeding during the night, is wrong. A number of studies on fish have suggested that predation risk can significantly affect the growth rate (and survival) of the prey fish, by influencing the prey behaviour. For example, when exposed to model predators, fish often reduce their foraging activity and hence food intake (Dill & Fraser 1984; Metcalfe *et al.* 1987; Huntingford *et al.* 1988b; Gotceitas & Godin 1991; Dellefors & Johnsson 1995). Metcalfe *et al.* (submitted) also showed that growth in juvenile salmon was strongly correlated with the number of daytime foraging excursions (from a shelter) so that the fish which grew fastest were those that emerged most and therefore took the biggest risks. It is also well known that during the winter a large proportion of the juvenile salmon population almost stop feeding and become what has been called anorexic, probably partly because of the predation risk incurred while foraging (Metcalfe & Thorpe 1992a; Bull *et al.* 1996). These fish have therefore reduced their growth rate below the maximum, possible as a result of their trade-off between growth and predation risk. This agrees with the study by Elliott & Hurley (1997) who found that the only time when a growth model overestimated observed growth rates in juvenile salmon was during the first winter of life.

Metcalfe *et al.* (submitted) calculated that of the total number of juvenile salmon eaten by predators in winter, 89.5% were consumed by diurnal predators while nocturnal predators only counted for 10.5%. By using mean figures of 90% of the fish hiding in the day and 10% at the night, they calculated that in winter the fish were foraging for 48 mins by day versus 864 mins at night, given a photoperiod of 8L:16D. This then shows that predation risk per minute of foraging in the winter is approximately 150 times greater by day than by night ([89.5/48]/[10.5/864]=153.4). By using the same methods to calculate the predation risk in the summer (photoperiod 16L:8D) when the fish hide approximately 20% of the day and none of the night (Valdimarsson *et al.* 1997, chapter 2), so the fish are foraging for 480 mins at night and 768 mins by day, I calculated that the relative predation risk is approximately 5 times higher during the day than by night ([89.5/768]/[10.5/480]=5.3). This indicates that diurnal foraging in general is riskier than night-time foraging, but this difference is much more extreme during the winter. That the daytime predation risk is higher in winter than in the summer is in itself very interesting, however, the relative predation risk is frequency dependent since it depends on what other fish in the population are doing and is based on the fact that the foraging time is reduced by sheltering. Therefore it cannot be used to explain the sheltering behaviour. Nevertheless, if the energy requirements of a diurnal endothermic predator are relatively constant over the year, the short daylength in winter makes it riskier for the prey per unit time than during the long days of summer.

# CHAPTER 8 - POPULATION DIFFERENCES IN SHELTERING BEHAVIOUR OF ATLANTIC SALMON AND ARCTIC CHARR

## 8. 1 INTRODUCTION

Most salmonids, and in fact many other freshwater fish species in the northern hemisphere, have been reported to show some kind of sheltering behaviour during the day in winter (Table 8. 1 and 8. 2). Many of these studies have shown that the fish emerge from their shelters during the night and become active, while during the summer the fish seem to be less nocturnal or even arhythmic (no peaks in activity throughout the 24 hours). The adaptive value of this wintering behaviour is not fully understood since salmonids are usually considered to be visual foragers (Keenleyside 1962; Stradmeyer & Thorpe 1987) and therefore poor foragers at low light levels (Fraser & Metcalfe 1997). However, there are evidence that predator avoidance may be one reason for this behaviour (chapter 4; Metcalfe *et al.* submitted).

A way to understand more about the adaptive value of this behavioural pattern might be to look at the seasonal changes in daylength at very high latitudes. In mid winter it can be dark all day, while for a part of the summer there is daylight for 24 hours (Fig. 8. 1). In addition, there is often prolonged ice formation in rivers at high latitudes so the rivers are frozen over for up to 6 months with perhaps 10 cm of ice, topped by snow, which results in very low light levels in the fish's environment, even during the short day. This means that in order to obtain the (admittedly small) amount of energy necessary for the fish's survival over winter they will have to adapt to feeding at low light levels. Conversely, the fish cannot obtain their daily requirements by only feeding at low light levels during the summer since the days are much longer than the night. Thus the fish must adapt to feeding at both low and high light levels at different times of year.

It has been established that this flexibility in diel activity patterns is partly controlled by temperature (Fraser *et al.* 1993, 1995; Valdimarsson *et al.* in press; chapter 2), and the suggested temperatures for this switch in behaviour (from being nocturnally active in winter to arhythmic in summer) are around 6 - 8 °C. However, the natural environment is very diverse so there must be different threshold values for different populations: juvenile salmonids living in colder environments would be expected to emerge from shelter at lower temperatures than those of the same species in warmer waters. In order to investigate this, I compared two high-latitude populations of both Arctic charr and Atlantic salmon that differed in their natural growth environment. The salmon populations differed in the mean temperature of their home river, while the charr differed in that one population was anadromous and the other landlocked. Arctic charr have been shown to hide under cover during parts of the day (Adams *et al.* 1988; Holierhoek & Power 1995) but both of these studies were carried out during the summer and the authors did not make any link to temperature. In their natural habitat charr may live in rivers where the temperature never rises above 4 °C (Johnson 1980). This suggests that they should have a lower threshold temperature for seeking refuge, since it is difficult to see the advantage for this species in having a mechanism that drives them to hide during day, even during the short Arctic summer, when the daylength is more than 20 hours long (which would give the fish less than four hours to feed per 24 hours). I therefore compared how these four salmonid populations responded to parallel changes in temperature.

Table 8. 1. Salmonid fish that show some sheltering behaviour or bury themselves into the substrate during winter. Little or nothing is known about the nocturnal behaviour in many of these species.

| **Species** | **References** | Type of behaviour |
|---|---|---|
| Atlantic salmon (*Salmo salar*) | Smirnov *et al.* 1976 | *c)* |
| | Gibson 1978 | *b)* |
| | Gardiner & Geddes 1980 | *b)* |
| | Rimmer *et al.* 1983 | *c)* |
| | Cunjak 1988 | *c,e)* |
| | Rimmer & Paim 1990 | *g)* |
| | Heggenes & Saltveit 1990 | *c)* |
| | Fraser *et al.* 1993 | *a,e)* |
| | Fraser *et al.* 1995 | *a,e)* |
| Brown trout (*Salmo trutta*) | Needham & Jones 1959 | *d)* |
| | Eriksson 1978 | *g)* |
| | Gardiner 1984 | *c)* |
| | Cunjak & Power 1986a | *c)* |
| | Heggenes & Saltveit 1990 | *c)* |
| | Heggenes *et al.* 1993 | *a,e)* |
| | Griffith & Smith 1993 | *a)* |
| Cutthroat trout (*Oncorhyncus clarki*) | Bustard & Narver 1975b | *c,d)* |
| | Griffith & Smith 1993 | *a)* |
| Coho salmon (*Oncorhyncus kisutch*) | Hartman 1965 | *c,d)* |
| | Bustard & Narver 1975a | *b,d)* |
| | Bustard & Narver 1975b | *b,d)* |
| | Hillman *et al.* 1992 | *c,d)* |
| Steelhead/rainbow trout (*Oncorhyncus mykiss*) | Hartman 1965 | *c,d)* |
| | Needham & Jones 1959 | *d)* |
| | Bjornn 1971 | *c)* |
| | Bustard & Narver 1975a | *b,c)* |
| | Hillman *et al.* 1992 | *c,d)* |
| | Riehle & Griffith 1993 | *a)* |
| | Contor & Griffith 1995 | *a)* |
| | Gregory & Griffith 1996b | *a)* |
| Chinook salmon (*Oncorhyncus tshawytscha*) | Hillman *et al.* 1987 | *d)* |
| | Hillman *et al.* 1992 | *c,d)* |
| Brook trout (*Salvelinus fontinalis*) | Needham & Jones 1959 | *d)* |
| | Gibson 1978 | *b)* |
| | Cunjak & Power 1986a | *c)* |
| Arctic charr (*Salvelinus alpinus*) | Adams *et al.* 1988 | *f)* |
| | Holierhoek & Power 1995 | *d)* |

*a)* During winter the fish are hiding by day but emerge at night.
*b)* As the temperature decreases the fish start to hide more.
*c)* The fish hide under or between stones in winter.
*d)* The fish hide between amongst and under overhanging banks.
*e)* The authors suggests that nocturnal activity occurs in winter
f) Fewer fish seen during day than at night
g) Photonegativity

Table 8. 2. Fish other than salmonids that show some sheltering behaviour or bury themselves into the substrate during winter. Little or nothing is known about the nocturnal behaviour in many of these species.

| **Species** | **References** | Type of behaviour |
|---|---|---|
| Blacknose dace (*Rhinichthys atratulus*) | Cunjak & Power 1986a | *c)* |
| | Cunjak & Power 1986b | *c)* |
| Longnose dace (*Rhinicthys cataractae*) | Cunjak & Power 1986a | *c)* |
| | Cunjak & Power 1986b | *c)* |
| White sucker (*Catostomus commersoni*) | Cunjak & Power 1986a | *c)* |
| | Cunjak & Power 1986b | *c)* |
| Mottled sculpin (*Cottus bairdi*) | Cunjak & Power 1986a | *c)* |
| | Cunjak & Power 1986b | *c)* |
| Paiute sculpin (*Cottus beldingi)* | Needham & Jones 1959 | *f)* |
| Smallmouth bass (*Micropterus dolomieni*) | Munther 1970 | *c)* |
| Minnow (*Phoxinus phoxinus*) | Frost 1940 | *c)* |
| | Harden Jones 1956 | *b)* |
| | Huusko & Sutela 1997 | *e)* |

*a)* During winter the fish are hiding by day but emerge at night.

*b)* As the temperature decreases the fish start to hide more.

*c)* The fish hide under and between stones in winter.

*d)* The fish hide amongst vegetation and under overhanging banks.

*e)* The authors suggests that nocturnal activity occurs in winter

*f)* Fewer fish seen during day than at night

*g*) Photonegativity

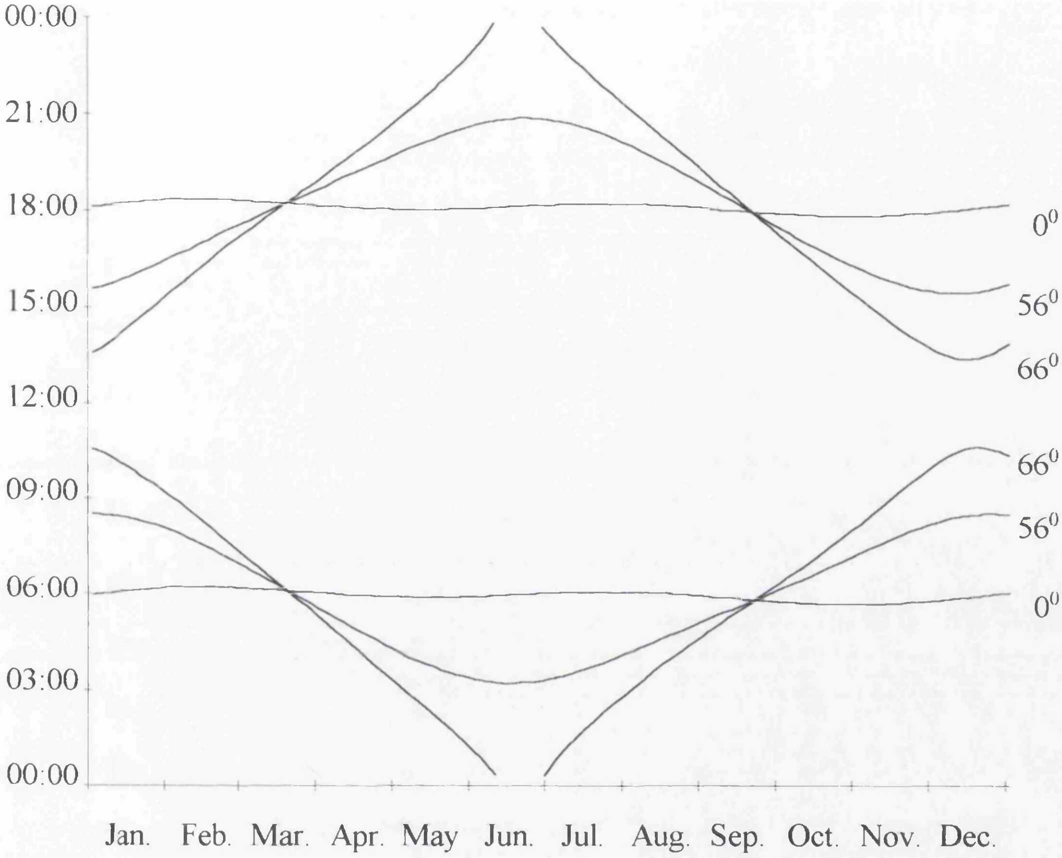

Figure 8. 1. Seasonal (*x*-axis) changes in time (*y*-axis) of sunrise and sunset at three different latitudes (data from Anonymous 1996).

## 8. 2 MATERIALS AND METHODS

Two populations of salmon and two of Arctic charr were used. The salmon populations were from rivers in NW-Iceland: the river Laxá á Ásum (S-LA) and the river Hrútafjardará (S-HR; see Fig. 8. 2.). These populations were chosen because there has been little or no human interference with their genetic structure (i.e. no releasing of fish from other rivers, see discussion) and their natal rivers differ in temperature and productivity. Both rivers are classified as wetland heath rivers (Guðjónsson 1990), but the river Laxá á Ásum is warmer and more productive since it runs from two large (11.8 and 2.92 $km^2$) lakes that in summer are relatively warm and productive (releasing plankton into the rivers; Tómasson 1989), while the Hrútafjardará catchment contains no lakes, is cold (Rist 1990) and supports very little plankton production. There are no direct measurements available of the water temperatures in the rivers, but air temperature should be a good if conservative indicator of water temperature. Mean figures for the average air temperature in the Hrútafjardará river area in July and January (for the years 1931-1960) is 8 and -4 °C respectively, while the same figures for Laxá á Ásum are 10 and -2 °C (Einarsson 1984). The average annual adult salmon catch during the years 1974-1995 was 1254 fish from the Laxá á Ásum compared to 304 in the Hrútafjardará, with a similar catch effort (Guðbergsson 1996). A simple estimation on productivity (based on the number of salmon per size of catchment area) reveals that the river Laxá á Ásum is more than 5 times as productive than the river Hrútafjardará (for the river Laxá á Ásum; 1254 fish from 294 $km^2$, or 4.3 fish per $km^2$ and for Hrútafjardará; 304 fish from 367$km^2$, or 0.83 fish per $km^2$). The two charr populations were also from NW-Iceland, one was a landlocked lake population from lake Ölvesvatn (C-OL) and the other was a mixture of anadromous stocks used for fishfarming at Hólalax (C-HO; see Fig. 8. 2). The main difference between the charr populations lies in the fact that the C-HO population migrates to the sea to grow whereas the C-OL one remains within a lake throughout its life cycle. The salmon used were hatchery-reared offspring of wild parents caught for stocking, but the C-HO and C-OL were of farmed origin, having been farmed for 6 and 3 generations respectivly.

The experiment was conducted at the Holar Agricultural College, the Icelandic research centre for the cultivation of Arctic charr, which is combined with a fish-farm and a salmon hatchery. The farm produces Arctic charr and the hatchery is responsible for stocking salmon rivers in NW-Iceland.

White, circular plastic tanks were used for the experiment. These were 56 cm high and 42 cm wide at the bottom, widening to 48 cm at the top (Fig. 8. 3). The tanks were modified as follows to create a simulated streambed refuge. The water level was maintained at 30 cm by fixing the height of a standpipe. Centered on the bottom of each tank was a 5 cm wide drain-hole, connected to the standpipe. Over the hole I fixed a 15 cm wide round plastic container, upside down with holes drilled on the sides, serving as a drain. On top of this container I put a round plastic plate, little more than 42 cm in diameter, thus fitting exactly into the tank at 11 cm above the bottom. In two places on opposite edges of the plate (now effectively a false bottom) I cut out a section (10 cm by 2 cm) to allow fish access to the darkened area underneath. I used 12 tanks in total (3 replicated tanks for each of the four populations), and in each tank I put 20 fish netted at random from a stock tank on 12 July 1995. All fish were of similar age (approximately 8 months from fertilisation) at the start of the experiment.

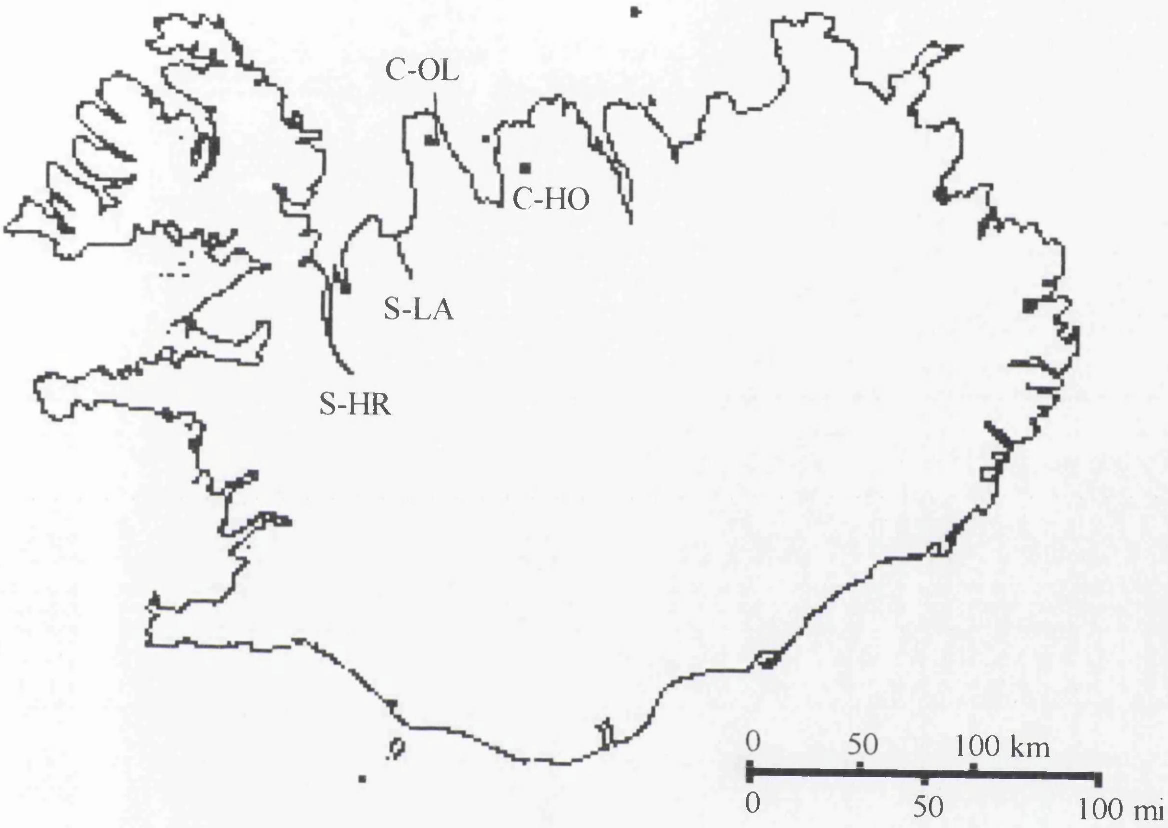

Figure 8. 2. Map of Iceland showing the location of the river Hrútafjardará (S-HR), the river Laxá á Ásum (S-LA), the lake Ölvesvatn (C-OL) and the fish farm Hólalax (C-HO) where the experiment took place.

The water flowing into the tanks was ground water taken from a borehole. The temperature of the source water is cold (4.6 °C ± 0.05 SE), but to manipulate the temperature, part of the water was heated in a heat exchanger with 70 °C geothermal water. The cold and the warm water were then mixed to the desired temperature in a funnel about 2 metres over the tanks, from which a hosepipe led to each tank. Each hosepipe was connected to a 60 cm long vertical PVC pipe, 2 cm in diameter, which stood on the bottom of the tank and had three holes at 10 cm intervals drilled into it, one underneath the false bottom. Water exiting from the holes created a circular flow in the tank both above and underneath the false bottom.

The photoperiod was artificial (9L:15D), created by putting an opaque lid onto each tank at 17:00 in the afternoon and removing these at 08:00 in the morning. The fish were handfed twice a day, after removing the lid in the morning and just before the lid was put on in late afternoon. Cleaning was done daily and consisted of lowering the drainage standpipe and flushing out approximately three quarters of the water in the tank. Once weekly I took up the false bottom and cleaned the tank thoroughly without removing the fish. The fish were allowed to acclimate to the tanks for 12 days prior to observations.

Observations were made by counting the number of fish seen on top of the false bottom during the day. The observations were made at random intervals over within the following constraints: there were always 2 or 3 observations made per day, the first was made at least 60 minutes after the lids had been taken off, at least 60 minutes elapsed between each observation, and the fish were not observed for 60 minutes after feeding. For statistical analysis the average number of fish visible from all the observations made on a given day is used. I observed the behaviour of the fish first at 5 °C (4.85 °C ±0.058) from 25 July to 3 August 1995, then the temperature was raised to 11 °C (11.1 °C ±0.078) from 4 August to 16 August and finally I dropped the temperature to 8 °C (7.77 °C ±0.095) from 17 August to 31 August.

After the experiment finished all fish were anaesthetised and weighed and 40 fish of each population were measured for forklength

The most appropriate test for statistical analysis of this form of behavioural data is repeated measures analysis of variance. However, since each population was only replicated three times this results in very low degrees of freedom, so greatly reducing the power of the test. I therefore also made comparisons within species by *t*-tests. For the statistical analysis the average number of fish outside during each day is used but in the graph it is expressed as the percentage of fish outside.

## 8. 3 RESULTS

Fewer fish hid underneath the false bottom at the high temperatures than the low temperatures (repeated measures ANOVA on the mean number of fish visible per day, with the three levels of temperatures as the within-subjects factor and the four populations as the between-subjects factor; effect of temperature $F_{(2,16)} = 5.96$, $P = 0.012$). The same analysis did not show any significant differences between the four populations (two salmon and two charr; repeated measures ANOVA, effect of population: $F_{(3,8)} = 1.46$, $P = 0.295$). However, there are clear differences between the population of each species, as revealed by separate *t*-tests based on the pooled

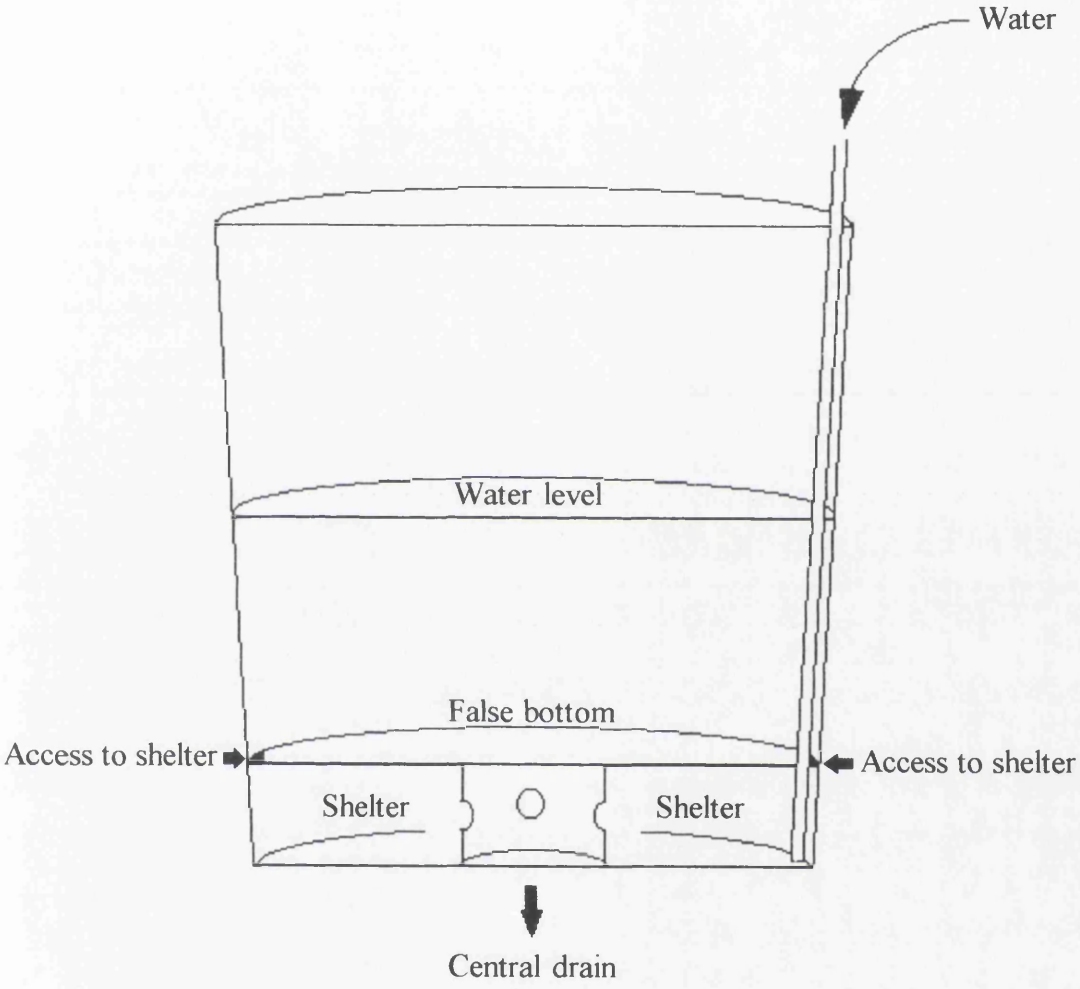

Figure 8. 3.. Cross section of the experimental tank. The addition of a false bottom provided a darkened refuge into which fish could move freely at any time.

replicates. The two salmon populations do not differ from each other at 5 °C (*t*-test between the S-LA population and the S-HR population on number of fish on the top of the false bottom, $t = 0.55$, $df = 7$, $P = 0.60$) but they do differ at both 8 °C (8 °C; $t = 23.23$, $df = 10$, $P < 0.001$), and at 11 °C ($t = 4.91$, $df = 7$, $P < 0.005$; Fig. 8. 4). The charr populations differed from each other at all temperatures (*t*-test between the C-OL and C-HO populations on number of fish on the top of the false bottom, at 5 °C; $t = -2.74$, $df = 7$, $P<0.05$, at 8 °C; $t = -16.32$, $df = 10$, $P < 0.001$, and at 11 °C; $t = -4.89$, $df = 7$, $P < 0.005$; Fig. 8. 4).

There was no significant difference in fish size between the three replicate tanks within each population (one-way ANOVA on the wet weight for each population: C-OL; $F_{(2,57)}=0.33$, $P=0.72$, C-HO; $F_{(2,56)}=1.18$, $P=0.32$, S-LA; $F_{(2,57)}=0.05$, $P=0.95$, S-HR; $F_{(2,57)}=0.33$, $P=0.72$). There was also no significant difference in wet weight between the two salmon populations (one-way ANOVA between S-LA and S-HR population wet weight; $F_{(1,118)}=1.14$, $P=0.29$). However, there was a significant difference between the two charr populations, with the C-OL population weighing more than the C-HO population (one-way ANOVA between C-OL and C-HO population wet weight; $F_{(1,117)}=55.2$, $P<0.001$; see Table 8. 3 for fish sizes).

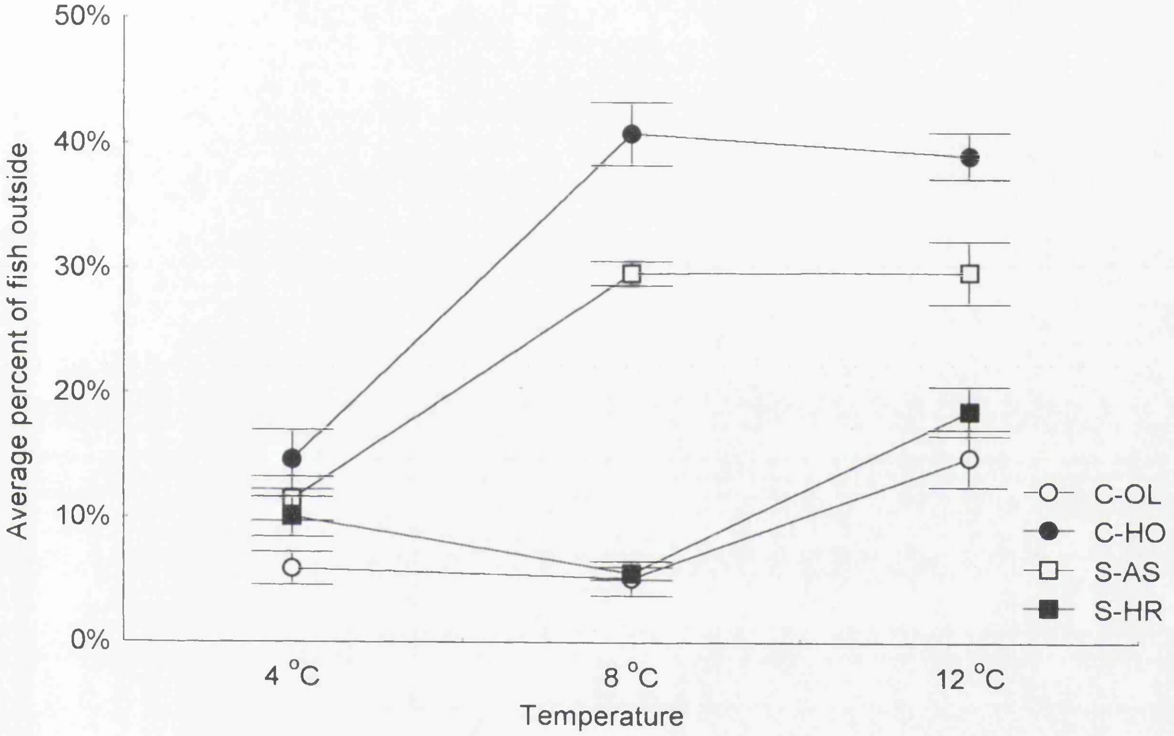

Figure 8. 4. Average percentage (±SE) of fish outside shelter at three different temperatures. Arctic charr are represented by circles (the C-OL population by open circles, the C-HO population by closed circles) and the salmon population are represented by squares (the S-LA population by closed squares and the S-HR population by closed squares).

Table 8. 3. Wet-weight (g) and forklength (cm) of the fish used in the experiment.

| Population | | Mean | N | Std.Error |
|---|---|---|---|---|
| Ölvesvatn (C-OL) | g | 4.94 | 60 | 0.223 |
| | cm | 8.08 | 40 | 0.160 |
| Hólar (C-HO) | g | 2.80 | 60 | 0.176 |
| | cm | 6.85 | 40 | 0.163 |
| Laxá á Ásum (S-LA) | g | 2.15 | 60 | 0.119 |
| | cm | 6.10 | 40 | 0.133 |
| Hrútafjarðará (S-HR) | g | 1.97 | 60 | 0.117 |
| | cm | 5.72 | 40 | 0.124 |

## 8. 4 DISCUSSION

The results show that the two salmon populations respond differently to temperature, suggesting that, as predicted, they may have different threshold values for the temperatures at which they switch between sheltering and feeding by day. However, it was the population from the warmer river (Laxá á Ásum, S-LA) that utilised main tank during daylight periods more at lower temperatures, which is the opposite trend to that predicted. So while the S-LA population switched from being predominantly nocturnal to more diurnal at temperatures between 5 - 8 °C, the population from the river Hrútafjardará did not make this switch until the temperatures exceeded 8 °C. Since the water temperature in the river Hrútafjardará probably seldom exceeds the values which the fish require to become more active by day, these fish are likely to be nocturnal for most of their juvenile life. This would be expected to result in slower growth and smolting at a later age for the S-HR fish than the S-LA fish. However, according to Guðjónsson (1990) the smolt age is similar in these two rivers, the common smolt age in Hrútafjardará being 2, 3 and 4 years compared to 3 and 4 years in Laxá á Ásum. Symons (1979) suggested that 500 days with temperatures at or above 7 °C were required to produce a 15cm smolt. However, smolt size is on average smaller both in Iceland (Gudjónsson 1978) and in some cold Norwegian rivers (Jensen and Johnsen 1986) than elsewhere, and it has been demonstrated that the shorter the growing season the more effectively each day is utilized for growing, indicating that this is an adaptation to feeding, growth and survival at lower temperatures in the coldest rivers (Jensen and Johnsen 1986). Furthermore, it has been shown that the resident salmon (fish that stay in the river for at least one additional year) tend to hide less (Valdimarsson *et al.* 1998, chapter 2) and forage more (chapter 3) but grow slower (Metcalfe & Thorpe 1992a; Bull *et al.* 1996) than the fish that will smolt in the following spring. This indicates differences in feeding efficiency so some fish may get the same amount of energy but within a shorter time than others.

The data on the charr are equally interesting, with clear differences between the two populations, and even bigger differences than for the salmon. In cultivation there are several differences between these two populations: fish from the C-OL population are faster growing (see Table 8. 3.), less aggressive and tend to mature later than the C-HO population (Adalsteinsson *et al.* 1992; Eyþórsdóttir *et al.* 1993; Skúlason unpublished data). The data suggest that the C-OL fish, which are the faster growing population, are also more nocturnal. This of course is surprising since one would expect the faster growing fish to spend less time in shelter and more time foraging. However, there are several possible explanations. The C-HO fish come from a mixture of three riverine populations from NW-Iceland while the C-OL fish are derived from a landlocked lake population. The riverine fish are probably more dependent on good summer conditions (which are connected to increasing temperatures), whereas food availability is probably not as seasonal in the lake as in the river. Therefore it is more important for the riverine population to be active at lower temperature as shown in this present study. Furthermore, it is possible that fish derived from a lake population are better foragers in darkness because of adaptations to foraging in deeper (and hence darker) water than riverine fish. Feeding performance in Atlantic salmon is reduced at low light levels (Fraser & Metcalfe 1997) and it has been suggested that salmon could grow faster by not becoming nocturnal (chapter 7). However, it has been suggested that Arctic charr are better adapted to feeding in darkness than most other salmonids (Wallace *et al.* 1988; Jørgensen & Jobling 1989, 1990), mostly because they feed on bottom invertebrates as well as drift in the water column. This might suggest that a nocturnal Arctic charr population can grow as fast as a diurnal one.

In none of the populations did the number of fish outside the refuges exceed 50%, even at the highest temperatures. This is in accordance with results from another experiment where the fish were observed in similar tanks (chapter 7, see Fig. 7. 2); juvenile salmon have also been shown in field studies to hide during the summer at high temperatures (Gries *et al.* 1997). The reasons for this could be linked to foraging and the availability of food, since if it is not profitable to be outside and forage the fish should rather hide and avoid predators and save energy.

There is an important lesson to draw from these results concerning wildlife management. In order to increase the annual salmon catch, a common method is to release juveniles or smolts into rivers and therefore get more fish to return as adults than the rivers are naturally capable of producing. There are often difficulties in obtaining enough adults from each river to make a sufficiently large broodstock so sometimes adults from a "nearby" river are used. The data presented here clearly show that populations from two rivers in the same geographical area (less than 50 km apart) can behave very differently from each other. By mixing these populations together, one might lose genetic information which could have a dramatic effect on the survival of the population, since the distinct behavioural traits that they exhibit presumably have arisen through natural selection in their own environment and so must confer a fitness advantage. Thus transplanted or 'hybrid' fish that showed an inappropriate sheltering response to temperature would be predicted to either survive or grow less well than the original native stock.

# CHAPTER 9 - GENERAL DISCUSSION

## 9. 1 INTRODUCTION

The overall aim of this thesis was to examine the effects of light, temperature and season on the behaviour of juvenile Atlantic salmon. This study has mostly focused on the sheltering behaviour of salmon in winter, their night-time behaviour in cold water and the behavioural differences that exist between resident and migratory fish. I have demonstrated that light, temperature and season interact to control the sheltering behaviour and the time budget of both the resident and the migratory salmon (chapter 2 and chapter 3). Predation risk has been suggested to be one of the underlying mechanisms for this sheltering behaviour (chapter 4). It has been demonstrated that foraging and territorial behaviour are affected by night-time light intensities, with fish preferring slower flowing water and being less aggressive on darker night, presumably because of increased difficulty of prey detection (chapter 5 and chapter 6). Allowing the fish access to food inside a darkened shelter has been shown to greatly increase their growth rate but not totally suppress their tendency to emerge at night (chapter 7). Finally this study has shown that the level of sheltering and the temperature threshold for the switch between nocturnal and arhythmic foraging can differ between populations and between species of salmonids (chapter 8).

## 9. 2 SHELTERING BEHAVIOUR

That salmon were found in this study to bury into the substrate during winter is nothing new. Many previous of salmonids had found this (see Table 8. 1 and 8. 2), but very few had shown that they re-emerged during the night and became active. It was Fraser *et al.* (1993) who showed that this behaviour was controlled by temperature and they suggested that salmon switch from being diurnal in summer to become nocturnal in winter. Subsequently, Fraser *et al.* (1995) demonstrated that this switch in behaviour could be induced during summer, by subjecting the fish to abnormally cold temperatures. However, this study has extended the previous work by proving that by sheltering, salmon are responding to at least three environmental variables, namely: light intensity, temperature and time of year, and the interaction between them (chapter 2). Furthermore, it revealed that it is incorrect to describe salmon as diurnal in summer, since a few fish were still found hiding during the day at temperatures above 10 °C but none during the night at temperatures above 8 °C (chapter 2). There is still therefore a tendency for the fish to seek shelter more during the day than the night even at warmer temperatures, so their activity schedule during summer is perhaps best described as arhythmic or weakly nocturnal (see also Gries *et al.* 1997).

By recording the locomotor activity of salmon, some studies have suggested that they are crepuscular foragers (e.g. Eriksson 1973; Richardson & McCleave 1974; Varanelli & McCleave 1974: but see also Eriksson & Alanärä 1992)). This study never directly examined the foraging rate of salmon at dawn and dusk, but since the fish use light as a main cue to trigger entry to or emergence from shelter, it is justifiable to assume that higher locomotor activity at dawn and dusk arises simply because the fish are moving between sheltering areas and foraging areas. Furthermore, since the salmon appear to modify their territory size according to light intensity (chapter 6), a higher locomotor activity would be expected because of a higher degree of aggression shortly after dawn (Kadri *et al.* 1996) and dusk (chapter 6).

Predator avoidance seems to be the most likely cause for this sheltering behaviour (chapter 4). Diurnal predators are more numerous and take a higher toll of salmon populations than nocturnal predators (Metcalfe *et al.* submitted). By making the simplifying assumption that endothermic predator populations and their daily requirements are fairly constant over the year, we can predict that the short daylength in winter results in a higher predation risk per hour of daylight. In contrast, during the long days in summer the most important predators of salmon have a longer time in which to obtain their daily requirements, therefore producing a lower predation risk for the fish per hour of daylight (chapter 7). Similar estimates of relative predation risk per unit time during the night should reveal a higher predation risk in the summer, but since nocturnal animals are not as significant predators on salmonid populations as diurnal predators, this should not be as important a selection factor. It is difficult to obtain estimates for the density of salmonid predators both in summer and winter, and to make things even more complicated, some diurnal predators on salmon may migrate in winter (e.g. Witherby *et al.* 1939; Cramp & Simmons 1997). This would obviously weaken the speculative argument presented above since it would reduce the daytime predation risk in winter. However, it is important to examine why a predator on salmonids would leave in winter while there are still fish in the rivers. Is it perhaps because the short daylength in winter is insufficient for the predator to obtain its daily requirements? Some predators will stay over the winter (Cramp & Simmons 1977; Cramp 1985) and even within species (e. g. goosander and cormorant) some individuals might leave while others might stay (Cramp & Simmons 1977; Cramp 1985). This surely should indicate greater competition for food among the predators in winter than in summer, which forces some of them to leave and look for food elsewhere.

Of course it could be argued that it is because of the fish hiding during the day in winter that the predators need to find food somewhere else. It is clear from this study (chapter 4) that the salmon are hiding from something rather than simply sheltering from the current, and previous studies have shown that the immediate response of juvenile salmonids when approached by an observer is to hide under cover (Hoar 1958; Chapman & Bjornn 1969; Grant & Noakes 1987). Assuming that salmon would respond to a predator in a similar way suggests that the hiding behaviour is a means of avoiding predators. An important factor in connection with this is the phenomenon of ice formation in winter. During harsh winter conditions, long stretches of river might freeze over, forcing endothermic predators to move elsewhere. This gives the salmon the opportunity to feed in darkness underneath the ice, free from their major predators. However, this would also increase the relative predation risk in ice free stretches of the river since predators might aggregate in such areas, forcing the salmon to either move to areas with ice-cover or hide in the substrate.

Another reason for why predator avoidance might be more important in cold water than warm is the effect of temperature on the swimming ability of the fish. As the temperature drops, the time taken for the contraction of the two main fibre types in fish locomotor muscle (red and white muscle) increases (Wardle 1980), resulting in a temperature-dependent swimming performance (Bennett 1984, 1985). It is not only the sustained swimming speed but also the burst or rapid swimming speed which is affected by temperature (Webb 1978; Fraser 1994). Prey fish rely on a short bout of burst swimming to escape from a predator's lunging attack. If the ability to escape from predators is reduced it must have a dramatic effect on the prey, which must then compensate by trying to reduce their exposure to predators.

Even though most sheltering activity happens in winter, there are still fish that shelter during the day in summer (chapter 2). Furthermore, fewer fish emerge from their shelter during the day if they are fed inside a darkened shelter (chapter 7). This could be due to the fish being nocturnal in general, but then being forced to feed during the day as well at high temperatures because of a higher metabolic demand (see chapter 7). However, the relative predation risk could also be used to explain this since it is always higher during the day than at night, so therefore if fish do not need to feed at this riskier time then they should hide.

From the literature it seems that most salmonids and in fact quite a few other freshwater species of fish show this sheltering behaviour especially in winter (Table 8. 1 and 8. 2). In most cases it is not known whether the fish emerge at night or not, but it must be likely. Since the arguments concerning temperature-dependent swimming performance and relative day vs. night-time predation risk do not only apply to salmonids it is possible that this behaviour is caused by predator avoidance in many of the other species as well. It is tempting to suggest that this behaviour is a general pattern found in most northerly distributed species of freshwater fish.

Even though predator avoidance is the most likely cause for the sheltering behaviour, there are other explanations that are not mutually exclusive (see chapter 4). In fact it is possible that this behaviour has evolved for some totally different reason (perhaps still unknown) but by chance also provides a good defence against predation. At this stage this suggestion can only be speculation perhaps worthy of investigation, although, this study strongly suggests that predator avoidance is the main cause for this behaviour.

## 9. 3 NIGHT TIME BEHAVIOUR

Very few studies have tried to look at salmon behaviour during the night. Presumably this is due to technical difficulties since the immediate response of juvenile salmon when approached by an observer is to hide (Hoar 1958; Chapman & Bjornn 1969; Grant & Noakes 1987). During daylight observers can try to conceal themselves from the fish, but at night this becomes more difficult since the observers need light to see. Even the smallest amount of light makes the fish change their behaviour (personal observations) and infrared light is quickly absorbed by water making observations in all but very shallow water impossible. In this study an image intensifier was used with additional strong infrared lights. There were no apparent changes in the behaviour of the fish when the infrared lights were switched on and the extra light made observations easier. However, it was impossible to quantify successful feeding attempts and to recognise individuals without using a torch projecting visible light. However, recent work by Metcalfe, Fraser and Burns (Burns *et al.* 1998; Metcalfe *et al.* submitted) has been carried out using a new technology (using PIT or passive integrated transponder tags). This new technique is very promising as a tool for understanding the night-time movements of fish so there is good hope for more studies in the near future.

Salmon were found to feed at surprisingly low light levels both in winter and in spring (chapter 3; Fraser & Metcalfe 1997). Their feeding efficiency is naturally not as good at low light levels, as is to be expected from a visual forager (Fraser & Metcalfe 1997) but fish were observed to forage at light levels below 0.01 lx (the minimum of the meter used to measure light intensity; personal observation). The reduced feeding efficiency at low light intensities is further exemplified by the choice of microhabitat in relation to light intensity (chapter 5). By moving into slacker water at low light intensities the fish are not getting the same amount of food as they would if they could feed in more profitable faster flowing water at higher light intensities, since the amount of drift food passing them is proportional to water velocity. Fraser and Metcalfe (1997) observed no feeding at all in complete darkness. However, complete darkness is probably very rare in the natural world, and on most nights there is some light provided by several sources such as the moon, stars, aurora borealis or even citylights reflected off clouds. If seen from underneath an insect drifting in the current will be silhouetted against this small amount of light (and may also create a faint shadow) and will therefore be easier to see. In complete darkness a drifting prey item will not make any shadow and will not stick out from the background, and therefore will be invisible. The usual foraging position of juvenile salmon is to hold position just a few millimetres off the bottom and dart forwards and upwards to intercept prey items being carried past in the current (Kalleberg 1958; Wankowski 1981; Dill & Fraser 1984; Metcalfe *et al.* 1987). During this study the fish were often seen taking this position during the night, invariably feeding on items passing above them. Only once (and then during a very bright night with a full moon) were salmon seen taking a prey item off the bottom. This method of feeding on overhead items could explain why salmon can forage at very low light levels.

In summer some fish may still hide during the day irrespective of temperature (Gries *et al.* 1997; chapter 2) but at night no fish tend to hide. It is possible that the fish that hide during summer are doing so because they have not been able to establish a territory, whereas they can find a foraging location at night since territories are smaller then (chapter 6). One must also take into account the light intensity and the microhabitat choice of the fish (chapter 5). At very low light levels the fish cannot use the more profitable but faster flowing areas, and need to feed in the slower flowing areas. This reduces the overall size of area within which a fish can feed and thus makes the territories very small and less profitable. However, it might be better to forage at a small, less profitable site than to remain in an area with a higher abundance but low availability of food, so preventing the fish from foraging at all.

In the experiments carried out in the artificial stream tanks no aggression was observed during the night, similarly, Fraser *et al.* (1993) did not observe any aggression at night at low temperatures. However, aggressive interactions were frequently observed at night in the experiment carried out on the effect of light level on territoriality in the constant temperature rooms (chapter 6). It is possible that the lack of aggression in some experiments was due to low densities of fish so that they did not need to fight for feeding areas; moreover, the experiment on territoriality and light levels deliberately used an experimental tank with a localised food source to promote competition.

## 9. 4 DIFFERENCES BETWEEN LIFE HISTORY STRATEGIES

This study has shown great differences in behaviour between the two modal groups. It was unexpected to discover that the upper modal group fish hid more than the lower modal group (chapter 2), because the upper modal group salmon grow more over the winter and therefore would be expected to be more active. For the same reasons it was also not expected that the upper modal group fish would make fewer feeding attempts per 24 h over the winter. One possible reason for this result is that the upper modal group fish are using short feeding bouts during the day when it is easier to locate prey. It has been shown that salmon will make short excursion from a refuge during the day in order to feed (Metcalfe *et al.* submitted). Another possibility, suggested by Eriksson (1973, 1975) is that the fish are doing most of their foraging at dawn and dusk. One scenario could be that upper modal group fish have enough light at dawn and dusk and therefore big enough territories (chapter 6) to exclude the lower modal group fish from feeding at these times, resulting in the lower modal group fish being forced to feed more in darkness. Since this study did not test this possibility directly this cannot be ruled out. However, both groups were observed foraging both at night and by day (albeit at different rates) and during the scan sample observations on sheltering (chapter 2) there were no indications that the fish were foraging especially actively at dawn and dusk.

It has been shown that upper modal group fish are more dominant than the lower modal fish (Huntingford *et al.* 1988a, 1990; Metcalfe *et al.* 1989) and should therefore obtain better territories. It has also been shown that territory size is positively correlated with body size (Grant *et al.* 1989; Elliott 1990; Grant & Kramer 1990), which suggests that the lower modal fish should benefit more from the tendency for fish to have smaller territories at night since smaller territories allow more fish to feed. This means that there should be a bias towards mostly lower modal group fish hiding during the day in the summer, since these are most likely to be excluded from potential feeding areas; they also have a reduced feeding demand and so may not need to continue their feeding into the day as much as upper modal group salmon.

## 9. 5 IMPLICATIONS FOR FISHERIES MANAGEMENT AND AQUACULTURE

All the experiments in this thesis were undertaken in a controlled environment, which either simulated that of the natural world or held the fish at low densities in hatchery tanks, thus were carried out in neither field nor true aquaculture conditions. However, this does not reduce the importance or reliability of the results since this thesis deals more with fundamental questions rather than specific, solvable problems. Furthermore, when the results can not be applied directly, they suggest the experiments should be repeated in conditions that more closely match that of natural streams or the fish farming industry as appropriate.

This study provides some information that could improve feeding techniques for salmon in aquaculture. This is of importance since food is probably the single biggest cost in fish farming (Bjørndal 1990). It is clear that feeding during the night is important but only if there is some available light. The results also suggest that the fish should be allowed access to some form of shelter, especially at low temperatures, and food should be delivered into that shelter. It has been suggested that food should be delivered so that it is indefensible, in order to obtain more uniform growth rates among fish in culture (Noakes & Grant 1992). Noakes and Grant (1992) then suggested that in order to achieve this one has to deliver the food in a random manner, either in space or in time. This study suggests that another way to achieve this would be to reduce the light to an intermediate level: there will be less aggression in a darkened area and the food resource is less defendable giving more fish the chance to feed.

The biggest threat to salmonid populations is probably not overfishing but rather habitat destruction. Hydroelectric dams, roads and other structures destroy migration routes and pollution of rivers from to extensive farming or overpopulated areas makes rivers uninhabitable for salmonids. Therefore habitat restoration or enhancement has become one of the most important tools for salmon conservation. However, most of our knowledge on salmonid behaviour and habitat choice, and therefore the basis behind most habitat restoration programmes, has been based on their summer activity. This study shows that overwintering behaviours are of great importance (chapter 8) and therefore should been taken into account (see also Cunjak 1994). There are two main factors that should be considered; salmon need slow flowing water because they are nocturnal foragers in winter and move to slower flowing water when their detection range is impaired at low light levels (chapter 5), and they need substrate to hide in because they avoid predators by hiding during the day (Griffith & Smith 1993; chapter 2, chapter 4). In order to restore habitat successfully both these features need to be provided.

This study also clearly showed that fish populations can differ in how much they use shelter (chapter 8). That populations respond differently to given changes in the environment is remarkable and suggests local adaptations in sheltering which are important for the survival of the fish. All manipulations with the genetic material within a population could therefore have a deleterious effect on the survival of the fish since these vital behavioural adaptations to reduce the risk from local predators might get lost in the gene pool.

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# APPENDIX

| Common name | Scientific name | Chapter |
|---|---|---|
| **Insecta:** | | |
| Scorpion | *Buthus occitanus israelis* | 1 |
| | | |
| **Pisces:** | | |
| **Salmonidae:** | | |
| Brook trout | *Salvelinus fontinalis* | 8 |
| Arctic charr | *Salvelinus alpinus* | 3,8 |
| Steelhead/rainbow trout | *Oncorhyncus mykiss* | 2-6,8 |
| Chinook salmon | *Oncorhynchus tshawytscha* | 4,8 |
| Coho salmon | *Oncorhyncus kisutch* | 6,8 |
| Cutthroat trout | *Oncorhyncus clarki* | 8 |
| Atlantic salmon | *Salmo salar* | 1-9 |
| Brown trout | *Salmo trutta* | 4,5,8 |
| **Others:** | | |
| Blacknose dace | *Rhinichthys atratulus* | 2,8 |
| Longnose dace | *Rhinicthys cataractae* | 2,8 |
| Minnow | *Phoxinus phoxinus* | 2,8 |
| Mottled sculpin | *Cottus bairdi* | 2,8 |
| Paiute sculpin | *Cottus beldingi* | 8 |
| Smallmouth bass | *Micropterus dolomieni* | 2,8 |
| Sea bass | *Dicentrarchus labrax* | 3,8 |
| White sucker | *Catostomus commersoni* | 2,8 |
| | | |
| **Aves:** | | |
| Cormorant | *Phalacrocorax carbo* | 9 |
| Divers | *Gavia* spp. | 4 |
| Emperor penguins | *Aptenodytes forsteri* | 1 |
| Goosander | *Mergus merganser* | 9 |
| Herons | *Ardea* spp. | 2,4 |
| Kingfishers | *Alcedo atthis* | 2,4 |
| Owls | *Strigidae* spp. | 1 |
| | *Tytonidae* spp. | 1 |
| Sawbill ducks | *Mergus* spp. | 2,4 |
| | | |
| **Mammalia:** | | |
| Bats | *Chiroptera* spp. | 1 |
| European rabbits | *Oryctolagus cuniculus* | 1 |
| Gerbill | *Gerbillus allenbyi* | 1 |
| Gerbill | *Gerbillu. pyramidum* | 1 |
| Mink | *Mustela vison* | 4 |
| Otter | *Lutra lutra* | 4 |