THE EFFECT OF LIGHT AND TEMPERATURE ON THE BEHAVIOUR OF JUVENILE ATLANTIC SALMON (Salmo salar L.)

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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.

Neil Fraser
January 1994

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ABSTRACT

The overall aim of this thesis was to investigate behaviour exhibited by juvenile Atlantic salmon at certain key times in their life, that might predominantly be controlled by either light or temperature. Two key times chosen were: movements away from the redd and the first winter. The overall result was a series of studies in controlled environments on a variety of behaviour patterns which are known to occur in the natural environment.

Salmonids move away from the redd predominantly at night-time. Light level would therefore appear to be the controlling factor releasing activity. However, the exact relationship between light level and alevin activity is not known and so the first part of the thesis centred around this behaviour. To begin with a series of artificial redds were used to monitor salmon alevin movements under various night-time incident light levels. A single redd was subjected to a single light level only on alternate nights. In all six experimental redds were run during the three years. Combining the results together gave a significant negative correlation between the numbers of salmon alevins moving away from a redd on a light night and light level. This behaviour was interpreted as a negative photokinesis since the frequency of movement was dependent on the intensity of the stimulation.

There were two possible functional explanations as to why alevins may react in this way to light level. Firstly, the reaction could have been a simple photoresponse which has evolved to ensure that alevins only move away from the redd when they are least likely to be caught by a predator. Secondly, retinal developmental differences between alevins (less developed alevins becoming temporarily disorientated and move away from the redd because the ambient night-time incident light is still below their threshold level) could have led to the observed negative photokinesis (Ali, 1961; Manteifel, 1978). To investigate the exact underlying mechanism behind this behaviour, fine scale patterns of behaviour during movement were needed. Fortunately, in most of the artificial redds used in the above experiments some additional trapping and filming had been done already so these results were presented as evidence for the fine scale patterns of behaviour during movement.

A recent study on alevin movements away from the redd indicated that a large proportion of alevins might disperse through the gravel away from the redd so a series of undergravel traps were used to monitor movement of alevins in the artificial redds. The trapping results, presented in Chapter 3, revealed that there was a small proportion of alevins moving through the gravel. In addition, the filmed behaviour of

alevin movement revealed that fish were moving away from the redd at two different levels in the water column; close to the substrate and in midwater. Filmed alevin movements were also temporally clumped and the peak dispersal time was in the first half of the night which is in agreement with other studies. In both cases alevins were moving in close association with the gravel which suggested that they are able to control the timing and method of movement away from the redd by using the gravel as an orienting factor and a medium for movement. This goes against the traditional view that movements away from the redd are purely the result of displacement due to a temporary disorientation (Bardonnet et al., 1993). Therefore, it was concluded that alevins are able to control their movement away from the redd by means of visual and tactile stimuli.

The overwintering behaviour studied centred around the diurnal-nocturnal shift in behaviour which was recently found for stream resident trout in Norway. In this thesis the sheltering behaviour, during the day and the night, of individuals and groups of salmon subjected to manipulated water temperatures was monitored. This showed that there was an increasing tendency for fish to remain in refuges (without access to food) during the day as water temperature dropped below 10°C. However, they would emerge with the onset of darkness, and so the proportion of the daily active period occurring in darkness increased markedly as temperature decreased. This was matched by changes in feeding patterns. Total daily food intake in salmonids (as with all poikilotherms) declines at low temperatures, but this decline was far greater in daytime intake than in food obtained by night, so that the proportion of the daily total that was obtained at night increased to almost 100% in both experiments. Thus at 'summer' temperatures feeding rates were higher during the day than at night while this was reversed at 'winter' temperatures. This was a consequence of the tendency of fish to retreat into refuges by day but re-emerge at night as the temperature dropped. The social behaviour of the fish kept in a group changed with light intensity: fish were more aggressive at higher temperatures, but at any given temperature aggression rates per fish were on average six times higher by day than by night. By day the fish kept in a group tended to be well spaced, with some individuals defending territories whilst at night fish were often within a few centimetres of one another. The results of the two experiments indicate that overwintering nocturnalism exhibited by salmonids occurs independently of season and it appears to be the first demonstration of a temperature controlled inversion of daily activity patterns. A possible functional explanation for this shift in foraging pattern may well to reduce predation risk in winter since salmon are relatively more vulnerable to endothermic predators when temperatures are cold due to their much slower escape responses (Chapter 6).

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CHAPTER 1 INTRODUCTION

1.1 INTRODUCTION

In the natural environment two important physical changes that most animals respond to are light and temperature. Many species change their behaviour under different light conditions (e.g. nocturnal activity as opposed to diurnal activity) and similarly under different temperature conditions (e.g. thermoregulatory behaviour in reptiles) and in some cases the two effects interact (e.g. in hot climates many small animals are nocturnal so as to avoid activity during the heat of the day). Such effects are most marked in poikilotherms, such as fish.

In temperate waters light and temperature have a simple daily relationship in which the highest temperature normally occurs around dusk, and the lowest temperature close to dawn. However, on an annual time scale temperature and light interact in a more complex way but still in a regular manner (See Section 1.2,1.3). This means that fish experience predictable environmental changes to which they can adjust their behaviour either on a daily or annual timescale. The objective of this thesis is to investigate some of the behaviours exhibited by one freshwater fish species which may be predominantly controlled by either light or temperature.

1.2 THE IMPORTANCE OF TEMPERATURE FOR FRESHWATER FISHES

Temperature limits distribution, determines activity and may act as an environmental cue for poikilotherms. It can be defined simply as heat content where heat is a measure of molecular agitation. In poikilotherms, body temperature controls the rate of chemical reactions and hence various body processes, including development time (Prosser, 1973; Crisp, 1981, 1988).

Maintaining a stable body heat is important to poikilotherms and they do so either behaviourally or physiologically (Prosser, 1973). Such adaptations not only enhance heat gain in the individual but may also restrict heat loss through radiation, convection and conduction. However, for most poikilotherms body temperature will fluctuate with the surrounding ambient water temperature. Fluctuations in natural water temperatures occur both annually and daily, according to season, cloud cover, precipitation and habitat. In a shallow water habitat, temperature change is sudden and therefore water temperature is unlikely to be as important as more predictable environmental cues (e.g. photoperiod) in timing important biological events such as breeding and migration. In deeper water, where temperature is more constant and changes are more gradual, temperature may replace photoperiod as the principal timing

timing cue for changes in season (Helfman, 1986). In extreme habitats temperature may also act as a strong selective pressure for many fish species. For example, in southern Europe many young salmonids may die in isolated river pools and streams that dry up each summer due to the intense daytime heat and the lack of rain (personal observations). Similarly the same type of intense selection occurs in more northern latitudes during harsh winters when some aquatic environments freeze solid.

1.3 THE IMPORTANCE OF LIGHT FOR FRESHWATER FISHES

Natural light levels change according to movements of the earth and moon and are also modified by weather systems. Such fluctuations in ambient light level are thought to be the main method by which most animals, including fish, time both daily and annual changes in behaviour and physiology (Scott, 1979). Fish inhabiting northern latitudes experience a great variation in seasonal light levels and photoperiod. The amount of light available in each 24 hour period during different periods of the year therefore depends on latitude, cloud cover, moon phase and sun inclination.

In more northern latitudes light also has a very important seasonal influence on the behaviour of animals. Daylength changes with season and many animals use this annual cycle to time important life history events. For example, in teleost fish the timing of breeding is linked to an annual cycle where seasonal changes in photoperiod are likely to be the most important stimulus (Scott, 1979; Thorpe et al., 1989a). This is known as photoperiodism. However, in extreme environments (e.g. caves), where there maybe no natural light, other seasonal cues may be used (Saunders, 1977).

Most animal communities can be divided into species that are diurnal (active by day), nocturnal (active by night) or crepuscular (i.e. active by dawn or dusk). However, as many authors have pointed out, fish are opportunists and activity patterns may not be fixed (Helfman, 1986). For example, juvenile Atlantic salmon (Salmo salar) are generally thought to be diurnal visual foragers but there are many times in their freshwater life when they are predominantly nocturnal (Thorpe et al., 1988; Hoar, 1954, 1958).

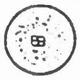
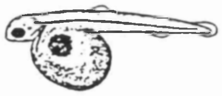
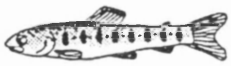
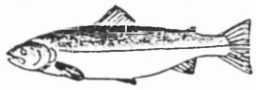
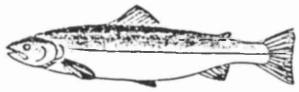
1.4 THE STUDY SPECIES

The species used in this study is the Atlantic salmon (Salmo salar), a cold water anadromous fish belonging to the family Salmonidae. Like many other anadromous salmonids, at a certain stage in their development they migrate to the sea after a period of up to 5 years in freshwater. In their sea water phase they may grow rapidly and migrate thousands of miles before returning to freshwater, predominantly to their natal stream, to spawn. The physiological and behavioural changes undertaken by the Atlantic salmon during its life history can be seen as discrete developmental phases, see Table 1.1.

The natural range of the Atlantic salmon is in the cool temperate Northern Hemisphere. Its distribution extends from New England to Ungava Bay, Greenland and Iceland, and from Northern Portugal to the Pechora River in Northern Russia. Recent introductions into Argentina, Australia, Chile and New Zealand have increased the range of the Atlantic salmon. The behaviour of each anadromous salmonid group is unique and all the fish species in this family have complex and variable life histories: each species spends different amounts of time in freshwater and seawater, has different spawning seasons and different migratory habits. However, the one factor common to all salmonids, and to most other fishes, is the high mortality rates experienced from egg to adult (Hoar, 1958).

The adult Atlantic salmon is a commercially important species in many countries and there has been extensive research into the biology of the species. For example, young fish leave the rivers for the sea in the spring when they smolt and thousands of these fish are tagged and released as part of large mark-recapture studies in many countries (Kennedy, 1988). Similarly the factors influencing juvenile survival, i.e. from ova to smolt have been researched intensively in both the laboratory (Godin, 1982) and the field (Garcia de Leaniz et al., 1993a). These areas of research are vital in understanding the long term population dynamics of this species, but in the short term the first year in freshwater has one of the most important influences on overall recruitment (Evans & Dempson, 1986; Chadwick, 1988). This first year is when the majority of any single family will die (Bley and Moring, 1988) and so this present study concentrates on this key time. Some of the most obvious times of high mortality are during the dispersal from the redd and in the first winter (Godin, 1982, Heggenes et al., 1993; Garcia de Leaniz et al., 1993a,b,c). Any behaviour that increases an animal's chance of survival during times of high mortality should be selected for strongly. This focused the present behavioural study onto two particular key times : dispersal from the redd and survival during the first winter.

TABLE 1.1 STAGES IN THE LIFE CYCLE OF THE ATLANTIC SALMON

TERM	DEFINITION	APPEARANCE
Salmon ova	Fertilised egg of salmon. In Scottish rivers the eggs are deposited in a shallow gravel nest, known as a 'redd', by the adult fish sometime between November and December.	
Eyed ova	About four months after fertilisation the ova have reached a stage in their development where the forming eye spots of the young fish can be seen in the egg. In Scotland this stage normally lasts between 2-4 weeks.	
Hatched alevin	This stage begins with the young fish or 'alevin' hatching from its egg and ends when the alevin has nearly fully absorbed its yolk sac. The development time for this stage is between 2-4 weeks, depending on environmental conditions	
Fry	At this stage the young salmon or 'fry' is no longer dependent on it's yolk sac for nutrition and has left the safety of redd in early Spring. The vast majority of fry are thought to die soon after leaving the redd from starvation or predation. The ones that survive are generally thought of as fry until the autumn of their first year. In biological terms they are in fact first year parr or 0+ parr.	
Parr	In the first few months of stream life the fry or 0+ parr grows quickly and establishes a territory within the stream. They can be easily recognised by the 8-12 dark vertical marks on each flank (parr marks). In Scotland this stage can last up to five years in the wild (i.e. 1+, 2+, 3+, 4+) and the fork length of the fish can anywhere between 3-13cm, depending on age and growth rate.	
Smolt	The parr can undergo a transformation to survive the transition from freshwater to sea water in Springtime. Fish that do undergo this transformation are known as smolts and migrate to the sea in the Spring. Whether a fish smolts or not in any one year is dependent on it's previous life history.	
Grilse	A grilse is a one sea-winter salmon that has returned to a river sexually mature to spawn.	
Salmon	A salmon is a multi sea-winter fish that has returned to a river sexually mature to spawn.	

1.4.1 MOVEMENTS AWAY FROM THE REDD

The highest mortality in a juvenile Atlantic salmon's life is in the first few months in the stream environment and by the end of the first year it has been estimated that only 8% of alevins from a single redd have survived (Mills, 1989). The period of movement begins as soon as the alevin hatches, from the egg into the gravel nest, or redd, in early spring (Hunter, 1959; Peterman & Gatto, 1978) and extends through to the start of first feeding (Mortensen, 1977a,b). Mortality rates during these early stages of movement can be attributed mainly to starvation and predation. The most important predators are: larger salmon parr (Mills, 1964, Symons & Helland, 1978), birds (Elson, 1962; Mills, 1969), mammals (Heggenes & Borgstrøm, 1988) and other fishes (McCrimmon, 1954).

Each spring broods of juvenile Atlantic salmon in Scotland disperse from the redd area over a short space of time (around 2 weeks) and over a relatively short distance (around 120m depending on habitat quality) (Garcia de Leaniz et al., 1993a,b). This leads to high densities of alevins in the vicinity of the nest site, so an alevin's first feeding habitat is essentially the same stretch of river it hatched in. In brown trout (Salmo trutta) this behaviour is thought to lead to competition for food and space so that weaker individuals are pushed further downstream, where they are may starve and die (Elliott, 1986, 1987).

Early juvenile mortalities are thought to be density dependent (Mortensen, 1977a,b; Elliott, 1986, 1992) and this limits salmonid production within a stream to the so called 'carrying capacity' (Gee et al., 1978; Buck & Hay; 1984; Elliott, 1985a,b, 1987; Chadwick, 1988). For river management purposes 'carrying capacity' is simply a relationship between the size of the river, the availability of spawning sites and habitat quality. From the juvenile salmon's viewpoint predation and food availability are the more critical factors.

These two particularly strong selective pressures, predation and starvation, during early life may account for some of the known behavioural adaptations seen in individuals at this developmental stage. For example, initial movements of alevins away from the redd site is completed almost exclusively in the first few hours of the night (Bardonnet et al., 1993). Soon after this initial dispersal fry settle into a first feeding site, where they may remain to the end of the summer after which they move to a more permanent site where they will stay for the greater part of their freshwater life (Garcia de Leaniz, 1990). They feed mostly by day and are often seen touching the surface of a particular rock, or home stone, from where they scan the flowing stream for food items, which they subsequently intercept (Fausch, 1984). Stemming the current with their pectoral fins they can maintain position using only a few tailbeats a minute whilst remaining close to the stream bed. If they are displaced downstream of their home area they will home relatively successfully (Garcia de Leaniz, 1990). This strong site specificity indicates that voluntary movement away from a home range must occur in response to a high degree of adversity, as originally suggested by Taylor & Taylor (1977). Such severe conditions begin to occur just before their first winter.

1.4.2 THE FIRST WINTER

Juvenile Atlantic salmon are generally thought of as diurnal visual foragers; however, in winter they are not seen in the streams during the day (Stuart, 1953; Bustard and Narver, 1975; Gibson, 1978). In winter, resident fish disappear from their daytime feeding stations, possibly in response to the hostile stream conditions (Heggenes et al., 1993). Permanent and drifting ice may cover high latitude streams and temperatures remain just above freezing for much of the winter. In response to these adverse environmental conditions, resident fish leave their daytime feeding stations and take refuge in the stream bed during the day (Heggenes & Saltveit, 1990; Rimmer et al., 1983; 1984; Cunjak, 1988 a,b). At night however young salmon and trout emerge from these refuges into the stream to feed (Heggenes et al., 1993). The reasons for these diel shifts in behaviour are unknown, but it has been suggested that over wintering fish may be forced out of their refuges by the build up of stream bed ice at night (Heggenes et al., 1993).

This brief review of studies during the two most critical stages in their first year tells us three things. Firstly, many descriptive papers detail the behaviour of juvenile Atlantic salmon. Secondly, little is known about the cause and effect of many of these behaviours patterns. Thirdly, little is known about any other behavioural changes occurring at these times that may influence survival. Hence this study will investigate experimentally some of the behaviour that is most likely to be influenced by the two key abiotic factors : light and temperature.

1.5 OUTLINE OF THESIS

The strategy behind this thesis came from the practical aspects of analysing behavioural adaptations. Ideally a laboratory study of behaviour should be linked to a field study of fitness. However, having spent the seven months prior to the start of this thesis working on such a field based project I am constantly aware of the difficulties of controlling key variables in studies conducted in the wild (see Garcia de Leaniz et al., 1993a, 1993b, 1993c). Abiotic factors often pose problems; in particular the constant threat of a spate in a river can put any long term study at considerable risk. Instead I chose to work in semi-natural conditions and in fully controlled laboratory set ups. In both types of studies I have concentrated on the key times in juvenile life where behaviour may be adapted to either light or temperature. This was not to obtain a measure of how strongly selection can act, but merely to gain a clearer picture of how an animal can adjust its behaviour in a changing environment. In each chapter I investigate selected aspects of behaviour that have originally been observed in the natural environment and are thought to be influenced by either light or temperature or both. Finally to understand the observed behaviour I have discussed it in relation to the animal's physiology, morphology and overall fitness in the natural environment.

In summary the topics considered in this thesis are as follows :

The influence of night-time incident light level on the pattern of movement of juvenile Atlantic salmon alevins away from the redd (CHAPTER 2).

The timing and method of movements of juvenile Atlantic salmon alevins away from the redd (CHAPTER 3).

The changeover from a night activity to a day activity after alevin have moved away from the redd, with respect to temperature and dispersal time (CHAPTER 4).

The underlying causes of nocturnalism in winter. Changes in diel activity were examined for different water temperatures under a constant photoperiod and at different times of year (CHAPTER 5).

Fast start performances of juvenile Atlantic salmon. This integrative measure was used as a standardised measure of individual ability with respect to temperature and is discussed with reference to other underlying temperature dependent physiological processes, overwintering behaviour and overall life history strategy (CHAPTER 6).

Shifts in behaviour during winter and spring in a semi-natural habitat: a recirculating flume at the University Field Station. This provided information on a range of natural responses to biotic and abiotic factors. In particular, the temperature dependent shift to nocturnalism and the breakdown in social structure associated with smolting (see table 1.1) was studied (CHAPTER 7).

A general discussion bringing together results and ideas generated by this thesis with reference to other relevant work. In addition, the main implications for freshwater fisheries management and aquaculture are outlined. (CHAPTER 8)

CHAPTER 2

THE EFFECT OF LIGHT INTENSITY ON THE NIGHTLY MOVEMENTS OF JUVENILE ATLANTIC SALMON ALEVINS AWAY FROM THE REDD

2.1 INTRODUCTION

In northern latitudes mature Atlantic salmon spawn each winter in freshwater, usually in their natal streams, after a lengthy migration in the sea. The adults spawn in a shallow gravel nest known as a redd in which fertilised eggs are buried. The fertile eggs then develop slowly over the winter and hatch out in early spring. Hatching involves sporadic bursts of lateral movements by the alevin inside the egg. Once free from the egg casing, the alevin begins to move within the gravel. This intra-gravel movement can be categorised into three distinct developmental stages: descent, ascent and a final movement away from the redd area (Godin 1982).

1. Descent Stage : The alevins move downwards after hatching, into the gravel bed of the stream. They gain all their nutritional requirements during this stage from their yolk sac. (Duration in Scotland : 20-30 days)

2. Ascent Stage : The alevins move up towards the surface of the gravel bed over a period of approximately 1 week. Nutritional needs continue to be provided by the yolk sac.

3. Movements away from the redd area: A single brood of alevins move out of the redd area and move in the stream away from the redd over a number of nights. Supplementary feeding along with the remaining yolk provide the alevin with the nutrients for this stage (duration: 20-30 days)

After alevins have left from the redd area and have completely used up their yolk sac, they can be regarded as salmon fry. The factors influencing young salmonids during most of these three stages have been investigated thoroughly, see Table 2.1.

2.1.1 THE DESCENT STAGE

The most extensive work carried out on intra-gravel behaviour of salmonids during this descent stage suggests that gravity and the interstitial structure of a gravel bed are the most important factors controlling behaviour in the wild (Nunan & Noakes, 1985a,b, 1987). However, early work carried out on the behaviour of alevins during this early developmental stage suggested that the downward movement into the gravel is due to negative phototaxis (Stuart, 1953). Other early work suggested a passive photokinesis,

Table 2.1 Documented behaviour of salmonid alevins and natural environmental influences on development during each stage of early life

Early Life Stages	Behaviour	Abiotic Influences	Biotic Influences
Descent stage	**Photonegative** (Dill, 1977; Heard, 1964) **Negatively buoyant** (Peterson. 1977a) **Olfactory capability** (Quinn & Busack, 1985) **Quiescent** (Godin, 1982) **Photokinesis** (Woodhead, 1957) **Geotaxis** (Nunan & Noakes, 1987)	**Sediment** (Dill & Northcote, 1970) **Temperature** (Peterson et al., 1977b) **Light** (Nunan & Noakes, 1987) **Oxygen** (Fast, 1987) **Gravel size** (Dill & Northcote, 1970)	UNKNOWN
Ascent stage	**Surface seeking** (Peterson et al., 1977a) **Negatively buoyant** (Bams ,1969) **Negative thigmotaxis** (Godin, 1982) **Negative rheotaxis** (Godin, 1982) **Olfactory capability** (Quinn & Hara, 1986) **Photokinesis** (Woodhead, 1957) **Geotaxis** (Nunan & Noakes, 1987)	**Sediment** (Witzel & MacCrimmon, 1981) **Light** (Carey & Noakes, 1981) **Flow rate** (Fast, 1989) **Oxygen** (Fast, 1989) **Temperature** (Peterson et al., 1977b) **Gravel size** (Dill & Northcote, 1970)	Stoneflies (Plecoptera) (Philips & Claire, 1975) (Patten, 1962)
Movements away from the redd area	**Nocturnal** (Godin, 1982) **Feeding** (Kalleberg, 1958) **Photonegative** (Ali, 1959a) **Social behaviour (grouping)** (Gustafson - Marjannen, 1983) **Undergravel migration** (Garcia de Leaniz et al., 1993a,b,c) **Night time migration** (Ginetz & Larkin, 1976) **Olfactory capability** (Quinn & Hara, 1986) **Photokinesis** (Woodhead, 1957)	**Sediment** (MacCrimmon & Gots, 1985) **Temperature** (Thomas, 1975) **Light** (Carey & Noakes,1981; Field-Dodgson, 1988) **Oxygen** (Hamor & Garside, 1976) **Flow rate** (Nunan & Noakes, 1985b)	SalmonParr (Salmo salar) Brown trout (Salmo trutta) (Garcia de Leaniz et al., 1993a)
Parr stage 0+	**Diurnal** (Hoar, 1942) **Surface feeding** (Kalleberg, 1958) **Positive rheotaxis** (Taylor & Larkin, 1986) **Neutrally buoyant** (Saunders, 1965) **Photopositive** (Stuart, 1953) **Olfactory capability** (Rehnberg & Schreck, 1986) **Territorial** (Symons, 1973) **Escape response** (Grant & Noakes, 1987) **Camouflage** (Donnelly & Dill, 1984)	**Temperature** (Gibson, 1978) **Photoperiod** (Pinhorn & Andrews, 1965, Villarreal et al., 1988; Thorpe et al, 1989a; Thorpe & Morgan, 1978) **Oxygen** **Flow rate** (Garcia de Leaniz , 1990)	Mink (Mustela vison) (Heggenes & Borgstrøm, 1988) Sawbill ducks (Feltham & Marquiss, 1989) Herons (Ardea cinerea) Fish (McCrimmon, 1954) Eels (Anguilla anguilla) (Mills, 1969)

since the degree of alevin activity could be directly correlated with light intensity (Woodhead, 1957). However, these early experiments were carried out in laboratory tanks which did not re-create the natural redd environment, so alevin behaviour was not examined within the gravel.

In the natural environment light does not penetrate the gravel of a stream bed deep enough to influence the behaviour of alevins in the redd during the descent stage (Bardonnet & Gaudin, 1990a,b). In some situations the alevins may be accidentally displaced towards the surface by an environmental disturbance (e.g. a river spate). If alevins are displaced towards the surface at the descent stage the negative phototactic behaviour, seen by Stuart (1953), may ensure that they simply remain within the gravel.

2.1.2 THE ASCENT STAGE

After the initial descent stage alevins will start ascending through the gravel towards the surface of the streambed. This ascent behaviour is associated with a further step in development which occurs 20-30 days after hatching (Peterson & Metcalfe, 1977; Peterson et al.,1977). Throughout these first two stages alevins continue to live off their yolk sac. As this resource is depleted, they become more agile and active, and gradually move upward through the gravel (Godin, 1982; Nunan & Noakes, 1987) to the surface layers of the streambed. At this point they are ready to leave the redd. There is some debate as to how to describe the first movements away from the redd. In the past the first movement away from the redd has been called emergence and the subsequent downstream movement has been called dispersal. However, these behavioural terms are no longer valid in the light of recent evidence that a significant proportion of alevins from a single redd are capable of moving considerable distances away from the redd through the gravel over a number of nights (Garcia de Leaniz et al., 1993b). Therefore at present it is probably best to use a more general description for emergence and dispersal behaviour such as 'movements away from the redd'.

2.1.3 THE FIRST MOVEMENTS AWAY FROM THE REDD AREA

The first movements away from the redd can be triggered by either a change in the environment, such as a river spate, or a change in alevin development (specifically depletion of yolk sac which may be the driving force behind the movement away from the redd). During these first movements away from the redd many alevins die from starvation and predation (Godin, 1982; Elliot, 1985a,b) and so the behaviour of alevins plays an important part in early survival. Therefore the following two chapters look at the movements of alevins away from the redd and into the stream. In this chapter the relationship between light levels and movement were investigated and in the following companion chapter the timing and method of movement were evaluated.

Most of the information about the behaviour during this last stage has come from field studies on natural redds or planted ova. These studies have shown that the majority of alevins move away from the redd at night (Garcia de Leaniz et al., 1993a), and for any one family this stage lasts around 2 weeks and the numbers moving are approximately normally distributed with respect to time (Marty & Beall, 1989). However, on any given night the numbers moving may depend on many extrinsic factors. For example, a rise in water temperature (Godin, 1980) or flow rate (Crisp & Hurley, 1991a,b,c) will increase the daily number of alevins moving. In addition water temperatures above 14°C will trigger most alevins to move away from the redd during the day (Brännäs, 1988). Seasonal movement patterns also depend on individual behaviour (such as the undergravel migrations seen by Garcia de Leaniz et al 1993a) and developmental stage (Ali, 1959a,b; Crisp & Hurley, 1991a,b,c).

A functional and a causal explanation have been put forward as possible reasons why the majority of alevins only move at night. The functional explanation is that it is a predator avoidance strategy adopted by alevins at this stage (Godin, 1982). The causal explanation behind nocturnal movement from the redd was first put forward by Ali (1959), who estimated that the rate of retinal dark adaptation in a Pacific salmonid's eye is slower than the rate of light extinction in the natural environment i.e. at dusk. He therefore suggested that alevins may suffer from a state of partial night blindness before their eyes are fully dark adapted. Under this semi-dark adapted state alevins might lose their reference points and position in the stream, leading to downstream movement. In a follow up paper on the retina of juvenile Atlantic salmon he once again suggested the same correlation between the rate of retinal dark adaptation and downstream movement (Ali, 1961). Hence the nightly pattern of movement from the redd could be the result of the absence of visual references at night or it could be a specific behavioural response to light or it could be partly the result of both of these explanations.

2.2 GENERAL METHODS

To test which of these two explanations is more likely the movements of alevins away from artificial redds were monitored, under various night-time incident light levels. Many difficulties are involved in observing alevin movements away from natural redds, so throughout this three year study specially designed artificial redds were used. This allowed the manipulation of physical conditions while maintaining many of the properties of the natural spawning redds. The final stage of movement away from the redd can only be studied in the springtime between March & May and so in some years more than one experiment was set up. Hence, this chapter has been broken down into four sections each representing one experiment in a single year.

2.3 NIGHTLY MOVEMENTS, OF ALEVINS AWAY FROM THE REDD, AT 4.5 LUX, 1991

In the first year (1991) a simple artificial redd was used in a pilot study to see if night-time incident light level had any influence on nightly movements and so a high light level, of 4.5 lux, was used. This light level was chosen because it is well above a juvenile Atlantic salmon's threshold for light reaction (1.0 lux to 0.001 lux, Ali, 1959a,b) and it is well below daylight lux levels that are known to suppress nightly movements (> 200 lux, McDonald, 1960). However, to ensure alevin movement would not be totally suppressed the 4.5 lux level was simulated only on alternate nights.

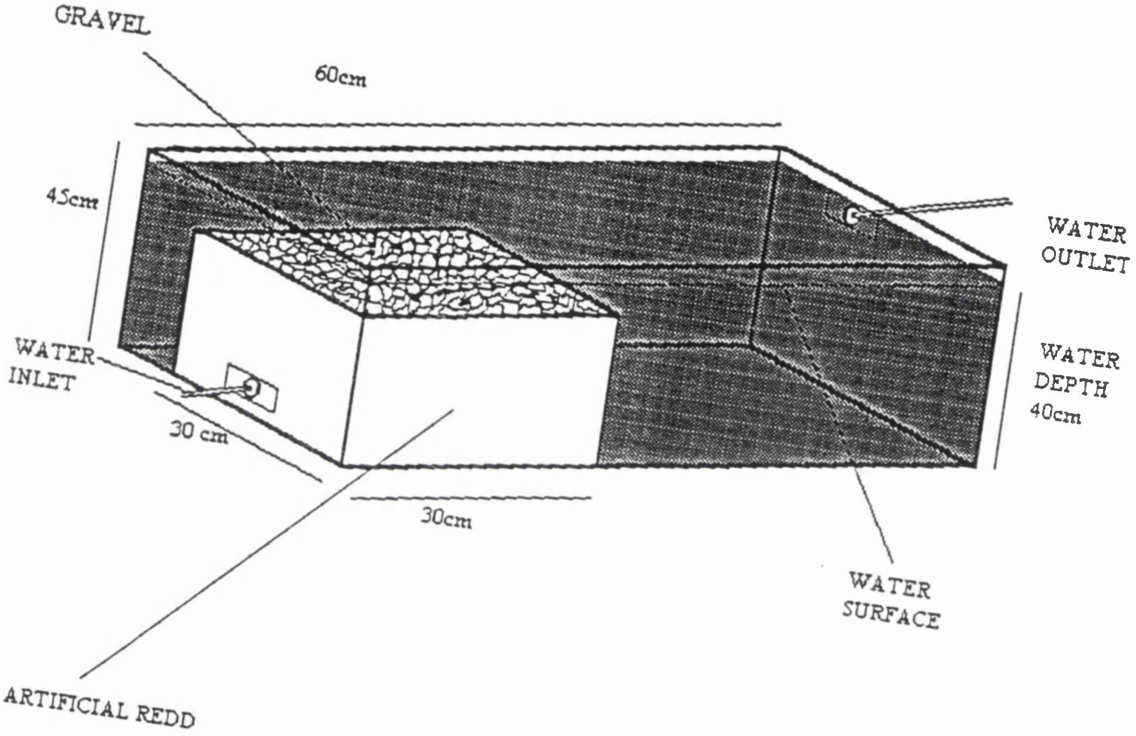
2.3.1 MATERIALS AND METHODS

Artificial redds are normally used to study the survival of alevins under different environmental conditions. Artificial redds usually consist of a plastic or wooden box filled with gravel, supplied with freshwater and covered with a specially designed perforated lid that allows alevins to move out of the redd. The perforated lid effectively prevents alevins from re-entering the redd and limits the behaviour of the alevins, so a different design of artificial redd was required. Therefore, in the first year (spring 1991) two artificial redds were constructed (Figure 2.1.). Each one consisted of a white plastic container (30cm x 30cm x 30cm) housed within a larger aquarium (60cm x 45cm x 45cm). Each plastic container was filled with gravel (mean diameter = 2.25cm +/- 0.46 (2 SE)) and was supplied with a continuous flow of freshwater, 2 litres per minute, from an inflow pipe positioned in the centre near the bottom of one of the sidewalls. As the water flowed into each container, it filtered up through the gravel, and eventually overspilled the sides of the container into the housing aquarium. The water from each housing aquarium was drained down into sump tanks where it was pumped back up into the artificial redds using Rena C40 pumps. Standpipes in the aquaria maintained the water level at 8cms above the top layer of gravel in the artificial redd. Alevins moving away from the redd dropped down to the bottom of the aquarium floor where they were captured and removed each morning. The height of the gravel in relation to the aquarium floor acted as a deterrent for re-entry into the gravel and the efficiency of this method was tested by leaving a group of 12 alevins for 24 hours inside the aquarium. At the end of the 24 hour period 9 alevins were recaptured i.e. a 75% trapping efficiency.

The young salmon used in this experiment were the mixed progeny of wild fish taken from the river Endrick. The fertilised ova were kept under ambient light and temperature conditions for the winter and spring, at the Loch Lomond Anglers hatchery at Inversnaid (Grid ref, NN395 095). Four hundred ova were taken from the hatchery as they began to 'eye up'. Two hundred ova were placed into the gravel of each trial redd on the night of the 21/3/91 using a pipe (diameter : 1cm). Ambient temperature at the

Figure 2.1.

Artificial redd 1991 : a plastic container (30cm x 30cm x 30cm) housed inside a larger aquarium (90 x 45cm). Each plastic container was filled with gravel (mean size = 2.25cm +/- 0.46 (2 SE)) and supplied with a continuous flow of freshwater, 2 litres per minute, from an inflow pipe positioned in the centre near the bottom of one of the sidewalls. Alevins moving away from the redd dropped down to the bottom of the aquarium floor where they were captured and removed each morning.


GRAVEL
60cm
45cm
WATER OUTLET
WATER INLET
WATER DEPTH 40cm
30 cm
30cm
WATER SURFACE
ARTIFICIAL REDD

hatchery was 4°C; so the artificial redds were maintained at that temperature, using a controlled temperature room, for four days after introduction of the eyed ova. The temperature was then slowly raised by 1°C in the first two weeks, to encourage development, and then by 1°C a week until a threshold of 10°C was reached. It was then held constant for the rest of the season (10°C +/- 0.07 SE). Each artificial redd was illuminated by fluorescent strip lights on a controlled photoperiod of 12 hours light / 12 hours darkness from the beginning of the experiment. The two experimental redds, A and B, experienced the same treatment: daytime light intensity averaged 64.36 +/- 4.32 SE lux, measured with a lux meter, at the water surface and a night-time incident light levels of 4.5 +/- 1.43 SE lux was set up for alternate nights using a microscope spot light controlled by a dimmer switch. Hence, the alevins in each redd experienced alternate nights of light and dark. Collection of alevins, from the bottom of the aquarium took place each morning. Every alevin was then weighed to the nearest 0.001 of a gram in a 44 x 44 mm weighing boat. Immediately after this the boat was flooded with water and a 1mm grid rule was placed over the alevin to measure its fork length and yolk sac area (Plate 1).

2.3.2 RESULTS

In experimental redd A 70.5% of the alevins survived and in experimental redd B 72% of the alevins survived. The number of alevins moving each night (Figures 2.2.A & 2.2.B) was not normally distributed with time in either experimental redd A (Kolmogorov-Smirnov test, d.f. 122, $z = 0.199$, $p < 0.001$) or in experimental redd B (Kolmogorov-Smirnov test, d.f. 121, $z = 0.135$, $p < 0.001$). In both redds many more observations lay near the centre of the graph (leptokurtic) than would be expected in a normal distribution (experimental redd kurtosis = 2.46; replicate redd kurtosis = 1.13). Furthermore in experimental redd A there was a significant shift to movement from the gravel on darker nights (Figure 2.2.A) when adjacent pairs of nights were examined (Wilcoxon paired-sample test, $n = 5$, $t = 15$, $p = 0.03$), see Table 2.2. In experimental redd B (Figure 2.2.B) there was no significant shift to movements away from the redd on dark nights when adjacent pairs of nights were examined (Wilcoxon paired-sample test, $n = 6$, $t = 13$, n.s.). No significant differences were found between the median fork length, weight and yolk sac areas of alevins moving on the same pairs of nights for either redd (Table 2.3). Two complications, the failure of a pump and a failure of a bulb, clearly caused more fish to move on the nights of the 22/5/91 and 24/5/9. This may have confounded the overall effect of night time incident light on movements away from experimental redd B (Table 2.2). Fortunately these problems did not influence survival nor did they alter development of the alevins as no significant differences were found between the two trials for fork length (t-test, $t = 0.62$, DF = 41, n.s),

Plate 1.

Weighing tray (44 x 44 mm) with alevin underneath a 1mm grid rule. Fork length and yolk sac were measured to the nearest 0.5mm using this method. Yolk sac was measured as an area, so the fry in plate has a 7 x 2.5 YS area, and a fork length of 25mm.

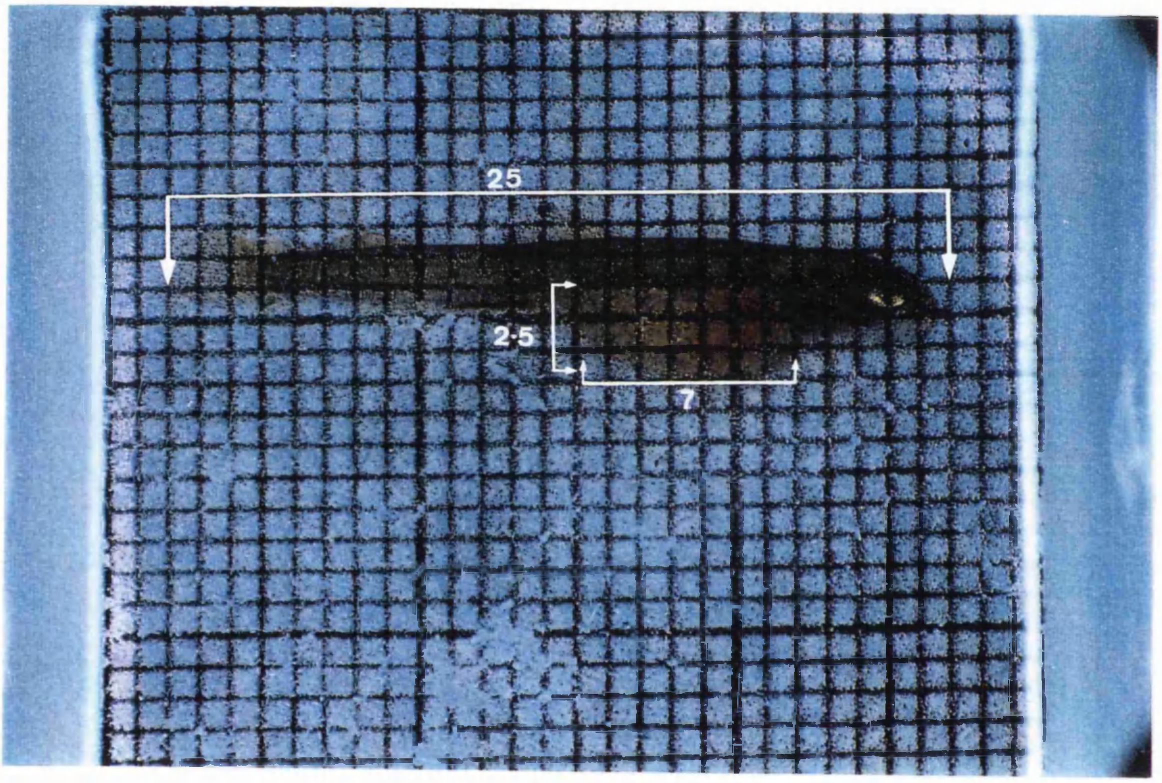

25
2·5
7

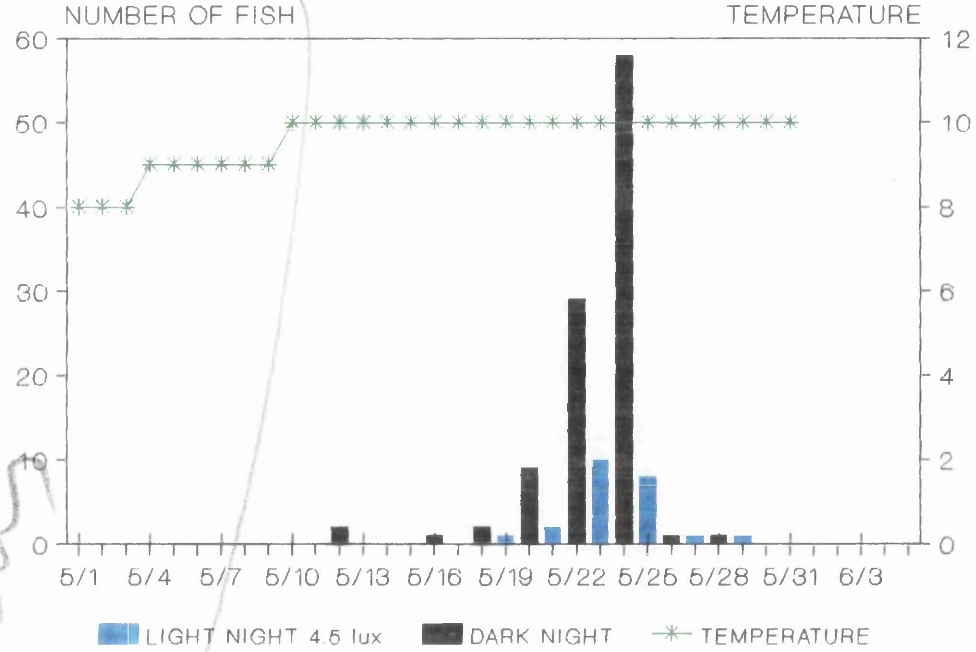
Figure 2.2A

Number of alevins moving nightly away from experimental redd A (total n = 141). Each division on the x-axis is represented as a date, the total period of movement lasted from the 12th of May to the 27th of May 1991. On alternate nights (marked in blue) the alevins were exposed to a 4.5 lux light level. Daily mean temperatures are plotted against the right hand y-axis. During the period of movement temperature was held constant at (10°C +/- 0.07 SE).

Figure 2.2B

Number of alevins moving nightly away from the experimental redd B (total n = 144). Each division on the x-axis is represented as a date, the period of movement lasted from the 6th of May to the 27th of May 1991. Daily mean temperatures are plotted against the right hand y-axis. During the period of movement temperature was held constant at (10°C +/- 0.07 SE).

EXPERIMENTAL REDD



REPLICATE REDD

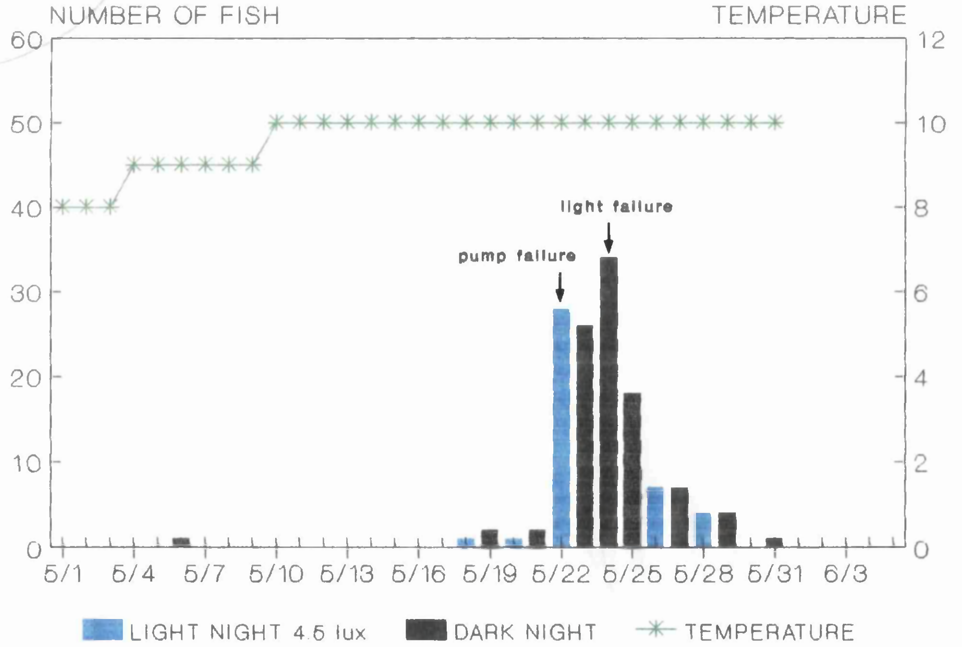


Table 2.2
The numbers of alevins moving away from the redd on light and dark nights in each artificial redd, 1991.

Artificial Redd	Variable	Light Night (4.5 Lux)	Dark Night (0 lux)	n	t	p†
Experimental Redd A	Total number	23	118	5	15	$P < 0.05$*
University 1991	Percentage	16.3%	83.7%			
Artificial Redd	**Variable**	**Light Night (4.5 Lux)**	**Dark Night (0 lux)**	**n**	**t**	**p†**
Experimental Redd B	Total number	35	109	6	13	n.s.
University 1991	Percentage	24.3%	75.7%			

p† Wilcoxon matched-pairs signed ranks test using the number of alevins moving on adjacent nights as matched pairs

Significantly more alevins moving on dark nights : * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Table 2.3.
Median size differences between alevins moving away from the redd on light and dark nights, 1991.

Artificial Redd	Variable (medians)	Light Night (4.5 Lux)	Dark Night (0 lux)	n	t	p†
Experimental Redd A	Weight (g)	0.130	0.15	4	0	n.s.
University 1991	Fork Length (mm)	27	28	4	-2	n.s.
	Yolk sac (sq mm)	1.25	1.5	4	6	n.s.
Artificial Redd	**Variable (medians)**	**Light Night (4.5 Lux)**	**Dark Night (0 lux)**	**n**	**t**	**p†**
Experimental Redd B	Weight (g)	0.15	0.15	4	2	n.s.
University 1991	Fork Length (mm)	28	28	4	0	n.s.
	Yolk sac (sq mm)	0.00	0.00	4	1	n.s.

Significantly larger midwater alevins : * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

p† Wilcoxon matched-pairs signed ranks test using median measurements of alevins on adjacent nights as matched pairs

weight (t-test, $t = .08$, DF = 45, n.s) and yolk sac area (t-test, $t = 1.5$, DF = 45, n.s).

To examine the results in more detail the relative proportion of alevins moving on a single night was calculated. This was done retrospectively using equation :

$$R_n \text{ (Relative number of alevins moving nightly)} = D_n \,/\, (T_d - T_n)$$

where D_n is the number of alevins moving on a single night, T_d is the total number of alevins that were caught and T_n is the total number of alevins that have moved away from the redd up until D_n. Hence the expression $(T_d - T_n)$ gives the remaining alevins left to move from the redd. For each night R_n was calculated and then used in a stepwise multiple regression analysis. This showed that date was the only significant predictor of the relative number of alevins moving each night away from experimental redd ($F_{1,11} = 7.83$, $r^2 = 0.416$, $p < 0.05$) and for the replicate redd ($F_{1,15} = 6.71$, $r^2 = 0.31$, $p < 0.05$).

2.3.3 DISCUSSION

The first year's pilot study proved more than anything else that it was possible to hatch out alevins and monitor movements successfully in an artificial redd at Glasgow University Zoology department. Movement away from the redd was expected earlier than the end of May and the delay in movement may have been the result of a delayed hatching time because of the low temperatures the eyed ova were kept at in the artificial redds. Alternatively the time of initial fertilisation could have been late. However, the experiment showed that movements of alevins away from a simple artificial redd system can be suppressed by a light level of 4.5 lux. A light level of 4.5 lux is well within the visual threshold of juvenile Atlantic salmon (Ali, 1959a,b) and so disorientation should not have been a cause of movement on a light night. However, the overall movement from the redd continued heedless of light level. This suggests either that some fry have not reached a stage of retinal development to see a 4.5 lux light level and are thus still moving due to disorientation or alternatively the observed movements away from the redd may be linked to some other behavioural process. To evaluate which of these possible explanations was more likely, further work was undertaken in 1992 using lower night-time incident light levels.

2.4 NIGHTLY MOVEMENTS OF ALEVINS AWAY FROM THE REDD, AT 2 LUX, 1992

On the basis of the first year results it was clear that nightly movements may be suppressed but not stopped by a 4.5 lux night-time incident light level. Further experiments were therefore set up to repeat this result under slightly different physical conditions. New artificial redds were designed to simulate a more natural environment, where fry could orientate themselves towards a current and had the option of moving through the gravel away from the redd. This latter addition to the design of the redd was made purely to investigate the recent findings on undergravel movement away from a natural redd (Garcia de Leaniz et al., 1993b) and the results are presented separately in the following companion chapter (chapter 3).

The experimental protocol in 1992 was the same as in 1991; light nights alternating with dark nights. In the second year a control redd was run, where alevins were kept in continuous darkness at night throughout the period of movement, and in contrast to the previous year all the ova selected came from a single sibling group.

2.4.1 MATERIALS AND METHODS

The new artificial redds were all made from small rectangular plastic containers, designed to simulate more natural conditions by giving alevins a surface current to orientate with as they move away from the redd (a rheotactic stimulus), a choice of migration method and an external water supply.

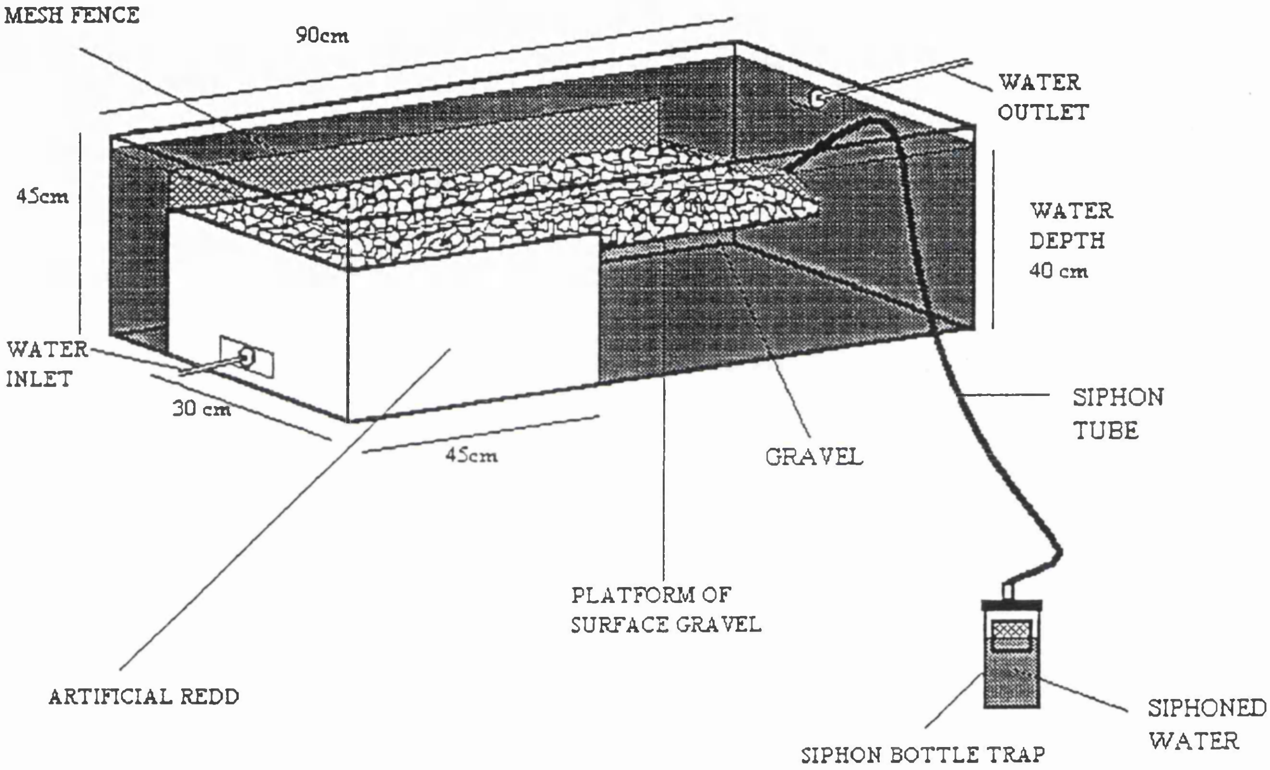
Specifications for the new redd were as follows : a plastic container (30cm x 45cm) was housed inside a larger aquarium (90cm x 45cm). Each container was modified to allow fish to move either through a platform of surface gravel (see Section 3.3 for results) or downstream in the water column (Figure 2.3). A fine mesh netlon fence prevented any alevins from passing through the system without being caught and from re-entering the redd area after migration.

Constant stream flow over the surface of the redd was provided by a Rena C40 water pumps; current velocity profiles were taken at 5cm transects over the redd using a streamflo 400 probe. The aquarium was covered with black plastic sheeting to eliminate any light penetration. A thin strip of sheeting cut away above each redd allowed for a controlled photoperiod of 8hrs dark/ 16 hrs light to be set for each tank. There was no dusk period and lights were automatically timed to go on and off.

The eyed ova used in these experiments were the progeny of a single pair of wild grilse, one sea winter salmon, (Male 73cm & Female 62.5cm) from the river Almond, stripped on the 26/11/92. The ova were kept under constant low red light and ambient water

Figure 2.3.

Artificial redd 1992 : a plastic container (30cm x 45cm) housed inside a larger aquarium (90cm x 45cm). The container was modified to allow fish to move either through a platform of surface gravel where they were caught by a siphon tube leading to a bottle trap(see Section 3.3 for results) or downstream in the water column. Trap retention efficiency was tested by leaving a group of 25 alevins for 24 hours inside the aquarium. At the end of the 24 hour period 22 alevins were recaptured i.e. a 88% trapping efficiency.


MESH FENCE
90cm
WATER OUTLET
45cm
WATER DEPTH 40 cm
WATER INLET
30 cm
45cm
GRAVEL
SIPHON TUBE
PLATFORM OF SURFACE GRAVEL
ARTIFICIAL REDD
SIPHON BOTTLE TRAP
SIPHONED WATER

temperatures at the S.O.A.F.D Almondbank hatchery, Perthshire. Four hundred eyed ova were split up into two groups of 200 and placed into two artificial redds in Glasgow University Zoology Department at night on the 2/3/91.

Eyed ova were kept at a temperature of around 4°C in the hatchery. The ambient temperature of the water around the artificial redd was around 8°C so during moving the ova were brought up to this temperature over a 6 hour period. This meant that the hatch time was slightly accelerated. The water temperature for the rest of the gravel incubation period was allowed to fluctuate naturally from outside source of water which flowed through the system at a rate of 1.5-1.6 l/min. The average current velocity over the surface of the redd was 8.3 ± 0.069 cms^{-1} at the surface and 3.2 ± 0.87 on the bottom. Both of these velocities are well below the critical levels for moving downstream alevins as found by Heggennes & Traaen(1988)

Two artificial redds were set up : one as a control and the other as the experiment. In the control no extra light was provided during night-time i.e. they were kept in total darkness each night. Combined daylight intensity for both University redds averaged 83.76 +/- 7.72 (2 SE) lux at the water surface and for the experimental redd a night time incident light intensity of 2 +/- 0.926 (2 SE) lux, was simulated on alternate nights using a 40W bulb on a dimmer switch. The alevins in the experimental redds therefore experienced alternate light and dark nights. Alevins caught from the control and the experiment were then weighed, measured and assessed for their stage of development, as described in Section 2.2.1.

2.4.2 RESULTS

In 1992 87% of the alevins in the control redd and 86.5% of the alevins in the experimental redd survived. Figures 2.4A & 2.4B show the number of alevins moving each night for each trial. The distribution of nightly alevin movements did not differ significantly from normality in the experimental redd (Kolmogorov-Smirnov test, d.f. 166, $z = 0.059$, n.s.), but did in the control where the distribution was significantly negatively skewed (Kolmogorov-Smirnov test, d.f. 173, $z = 0.069$, Skewness = -0.646, $p < 0.05$).

A Wilcoxon paired sample test was used to assess the influence of night-time incident light on numbers of alevins moving on alternate nights (Table 2.4). Taking neighbouring nights as matched pairs showed that there was no significant difference between neighbouring nights in the control (Wilcoxon paired-sample test, $N = 6$, $t = 6$, n.s.) but a significant preference for movement on darker nights was found in the experimental redd, up until the last pair of nights (Wilcoxon paired-sample test, $N = 7$, t

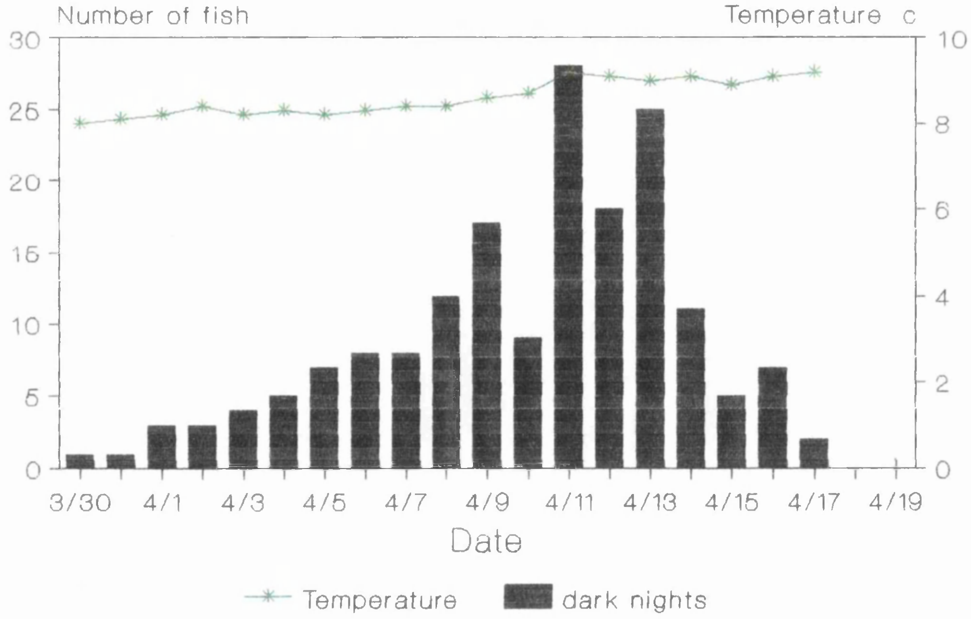
Figure 2.4.A

Number of alevins moving away nightly from the control redd (Total n = 174) at Glasgow University. Each division on the x-axis is represented as a date, the total period of movement lasted from the 30th of April to the 17th of May 1992. Daily mean temperatures are plotted against the right hand y-axis. During the period of movement the average temperature was 8.6°c +/- 0.19 (2SE).

Figure 2.4.B

Number of alevins moving nightly away from the experimental redd on light nights and dark nights (Total n = 173) at Glasgow University. On alternate nights (marked in blue) the alevins were exposed to a 2 lux light level. Each division on the x-axis is represented as a date, the total period of movement lasted from the 30th of April to the 14th of May 1992. Daily mean temperatures are plotted against the right hand y-axis. During the period of movement the average temperature was 8.55°c +/- 0.18 (2SE).

CONTROL REDD



EXPERIMENTAL REDD

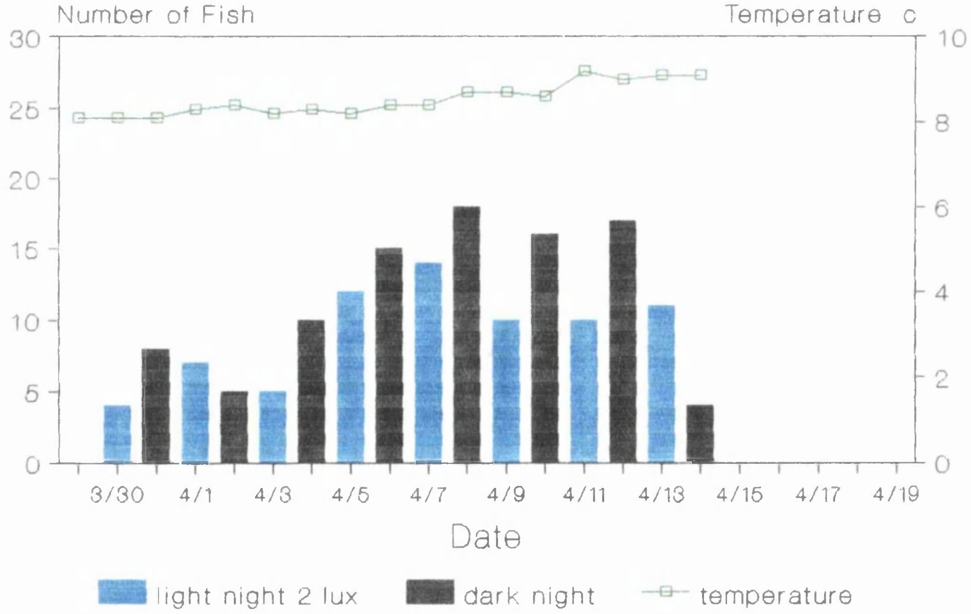


Table 2.4.

The numbers of alevins moving on light and dark nights away from the artificial redd, 1992

Artificial Redd	**Variable**	**Light Night (2 Lux)**	**Dark Night (0 lux)**	**n**	**t**	**p†**
Experimental Redd	Total number	73	100	7	27.5	$P < 0.05$*
University 1992	Percentage	42.2%	57.8%			
Artificial Redd	**Variable**	**Light Night (0 Lux)**	**Dark Night (0 lux)**	**n**	**t**	**p†**
Control Redd	Total number	99	75	6	6	n.s.
University 1992	Percentage	56.9%	43.1%			

p† Wilcoxon matched-pairs signed ranks test using the number of alevins moving on adjacent nights as matched pairs

Significantly more alevins moving on dark nights : * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Table 2.5.

Median size differences between alevins moving on light and dark nights away from the redd, 1992

Artificial Redd	**Variable (median)**	**Light Night (2 lux)**	**Dark Night (0 lux)**	**n**	**t**	**p†**
Experimental Redd	Weight (g)	0.1305	0.131	7	0	n.s.
University 1992	Fork Length (mm)	27	27	0	0	n.s.
	Yolk sac (sq mm)	7.5	5	4	-6	n.s.
Artificial Redd	**Variable (median)**	**Light Night (0 lux)**	**Dark Night (0 lux)**	**n**	**t**	**p†**
Control Redd	Weight (g)	0.131	0.132	7	10	n.s.
University 1992	Fork Length (mm)	27	27	0	0	n.s.
	Yolk sac (sq mm)	3	4	4	10	n.s.

Significantly larger midwater alevins : * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

p† Wilcoxon matched-pairs signed ranks test using median measurements of alevins on adjacent nights as matched pairs

$= 27.5$, $p < 0.05$), see Figure 2.4B. The weights, lengths and yolk sacs of alevins for the same pairs of nights did not differ in either the control or the experiment (Table 2.5).

A cross comparison of the two trials showed that fish from the control had significantly smaller yolk-sacs than fish from the experimental redd (t-test = -5.55; D.F. = 330, $p<0.001$).

The relative number of fish moving away from the redd nightly (R_n) (see Section 2.3.2) was used as the dependent variable in a stepwise multiple regression analysis, with date and water temperature as independent variables. Date was the only significant predictor of the relative numbers alevins moving in the control ($F_{1,12} = 26.27$, $r^2 = 0.686$, $p < 0.001$) and the experiment ($F_{1,7} = 44.93$, $r^2 = 0.865$, $p < 0.001$).

2.4.3 DISCUSSION

A 2 lux night-time incident light level significantly suppressed nightly alevin movements. This led to a differential pattern of movement in the experimental redd with peaks of movements on dark nights. No size differences were found between fish caught moving on a light night compared with those moving on adjacent dark nights, which suggests that there were no ontogenetic differences between fish choosing to move on different nights in the experimental redd. The developmental differences seen between the control and the experimental redd are most likely to be linked to the difference in shape between the two distributions. In the control redd more alevins moved away from the redd towards the tail end of the distribution whereas in the experiment alevin movements away from the redd were more evenly spread, leading to a flatter distribution (Kurtosis = -0.76), and so in the experiment the peak of alevin movement away from the redd was before that of the control redd. These results once again provide further evidence for a relationship between light level and nightly alevin movement.

2.5 NIGHTLY MOVEMENTS OF ALEVINS AWAY FROM THE REDD, AT 2.6 LUX, 1992

Another set of experimental redds, of the same design as Section 2.4.1, were set up in 1992 to replicate the first year study under a slightly different night-time incident light level: 2.6 lux and to provide sufficient data for an overall analysis of light level effects on nightly alevin movements.

2.5.1 MATERIALS & METHODS

The artificial redds used at the University Field Station were identical in design to those described in Section 2.4.1. Two artificial redds were set up, one as a control and the other as the experiment. In the control no extra light was provided during night-time i.e. they were kept in total darkness each night. Four hundred eyed ova, from the same sibling group used in Section 2.4, were split up into two groups of 200 and placed at night, on the 2/3/91, into two artificial redds at Glasgow University Field Station, Rowardennan.

Daylight light intensity averaged 96.34 lux +/- 4.53 (2 SE) for both redds, whilst night time light intensity for the experimental redd was 2.6 lux +/- 0.74 on alternate nights. The same experimental protocol was followed as described in Section 2.4.1. The alevins in the experimental redds therefore experienced alternate light and dark nights. Alevins caught from the control and the experiment were then weighed, measured and assessed for their stage of development, as described in Section 2.2.1.

2.5.2. RESULTS

The trials run at the University Field Station suffered a major disaster during the incubation stage. The water supply to the field station comes directly from Loch Lomond. It is significantly colder than the university water supply (T-test, $t = -8.6$, $DF = 34.27$, $P < 0.001$) averaging 7.22°C ± 0.26 (2SE). Bad weather towards the end of March stirred up the sediment in the loch which was then carried through the Field Station's water supply. Unfortunately the redds acted like a fine gravel filter separating the silt from the water. This must have reduced oxygen levels overnight in the control (Figure 2.5.A) which led to very low alevin survival rates (12%). However a slightly higher flow rate through the experimental redd during this critical time led to 83.5% of the alevins surviving in this redd (Figure 2.5.B). The numbers of alevins moving nightly from this experimental redd on each night differed significantly from a normal distribution (Kolmogorov-Smirnov test, d.f. 167, $z = 0.111$, Skewness = -0.649, Kurtosis = -0.714, $p < 0.05$). Taking adjacent pairs of nights as matched pairs showed that there was a significant preference for movement from the redd on darker nights

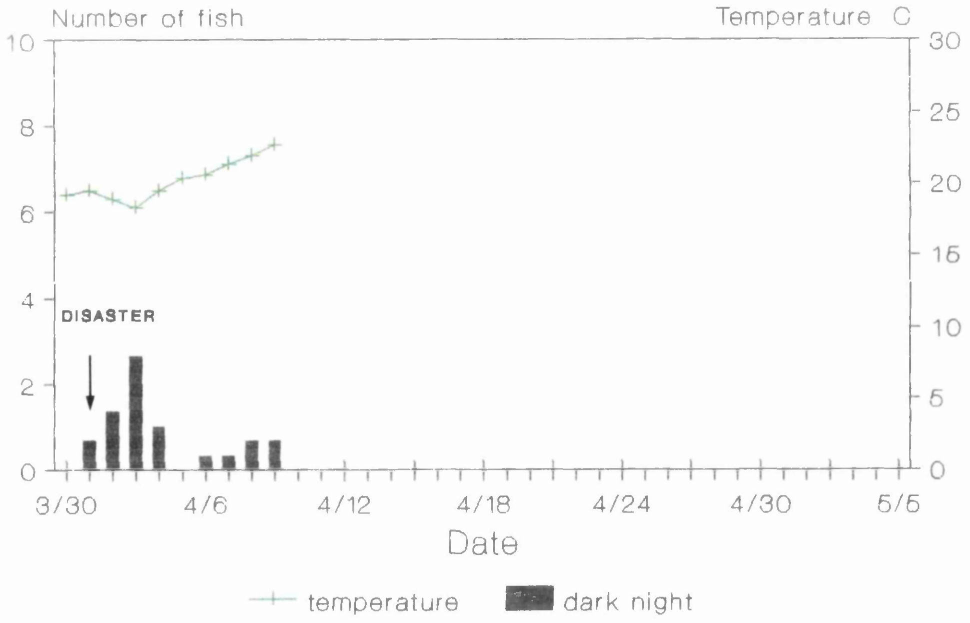
Figure 2.5.A

Number of alevins moving nightly from the control redd (Total n = 24) at the University Field Station. Each division on the x-axis is represented as a date, the total period of movement lasted from 30th of March to the 9th of April 1992. Daily mean temperatures are plotted against the right hand y-axis. The disaster indicated on the graph was an overnight build up of silt in the system.

Figure 2.5.B

Number of alevins moving nightly from the experimental redd (Total n = 173) at the University Field Station. On alternate nights (marked in blue) the alevins were exposed to a 2.6 lux light level. The total period of movement lasted from 30th of March to the 6th of May 1992. Daily mean temperatures are plotted against the right hand y-axis. During the period of movement the average temperature was 7.22°C ± 0.26 (2SE).

CONTROL REDD



EXPERIMENTAL REDD

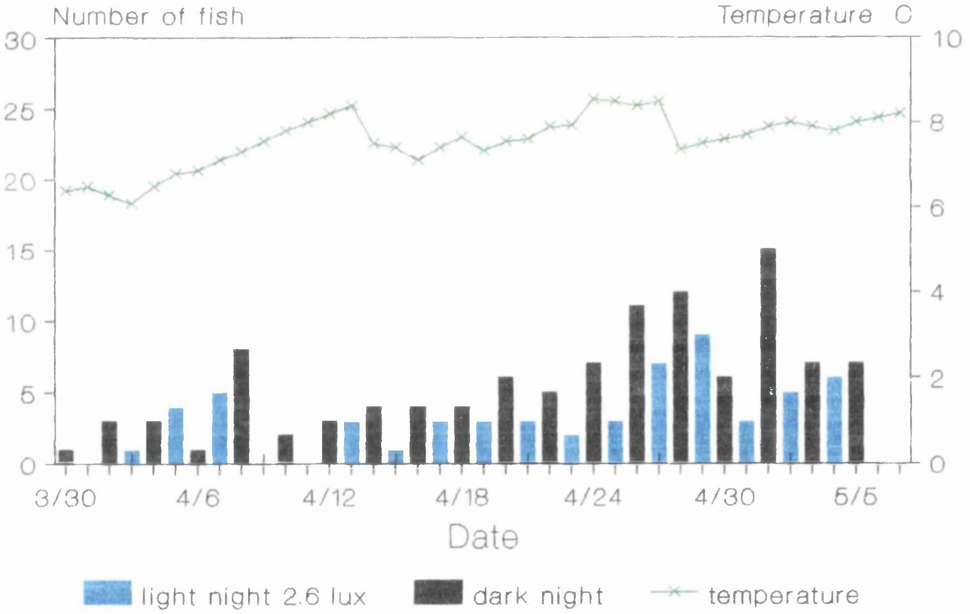


Table 2.6.

The numbers of alevins moving on light and dark nights away from each artificial redd, 1992.

Artificial Redd	**Variable**	**Light Night (2.6 Lux)**	**Dark Night (0 Lux)**	**n**	**t**	**p†**
Experimental Redd	Total number	58	115	19	132	P < 0.05*
Field Station 1992	Percentage	33.5%	66.5%			
Artificial Redd	**Variable**	**Light Night (0 Lux)**	**Dark Night (0 Lux)**			
Control Redd	Total number	10	14			
Field Station 1992	Percentage	41.6%	58.3%			

p† Wilcoxon matched-pairs signed ranks test using the number of alevins moving on adjacent nights as matched pairs

Significantly more alevins moving on dark nights : * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Table 2.7.

Median size differences between alevins moving away from the redd on light and dark nights, 1992.

Artificial Redd	**Variable (median)**	**Light Night (2.6 Lux)**	**Dark Night (0 Lux)**	**n**	**t**	**p†**
Experimental Redd	Weight (g)	0.1325	0.133	19	8	n.s.
Field Station 1992	Fork Length (mm)	27	27	19	4	n.s.
	Yolk sac (sq mm)	3.5	2	19	20	n.s.

Significantly larger midwater alevins : * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

p† Wilcoxon matched-pairs signed ranks test using median measurements of alevins on adjacent nights as matched pairs

(Wilcoxon , N = 19, P = 0.038), see Table 2.6. No significant differences were found for the fork length, wet weight and yolk sac between alevins moving on dark nights and light nights (Table 2.7). A stepwise multiple regression analysis with date and temperature as the independent variables and the relative number of fish moving (R_n) from the experiment (see Section 2.3.2) as the dependent variable showed that date was the only significant predictor of the relative numbers of alevins moving nightly ($F_{1,31} = 25.01$, $r^2 = 0.447$, $p < 0.001$).

2.5.3 DISCUSSION

In the experimental redd alevin movement on nights with a 2.6 lux night-time incident light level was significantly suppressed. No size differences were found between fish moving on a light night compared with those moving on adjacent dark nights which again does suggest that an ontogenetic difference is unlikely to be the only cause of the differential patterns of nightly movements. The extended period of movement seen in the experimental redd may have been attributable to the increase sediment load as well as to the low temperatures found at the field station in spring (Brännäs, 1988; MacCrimmon & Gots, 1985). In the control redd the increased mortality is more likely to be related to reduced oxygen levels, from the drop in flow rate, than to the increased sediment since mean alevin survival in artificial redds is uninfluenced by an increase in sediment loading (MacCrimmon & Gots, 1985). Overall the results from the experimental redd provide further evidence for a relationship between light level and nightly movements.

2.6 NIGHTLY MOVEMENTS OF ALEVINS AWAY FROM THE REDD, AT 3 LUX,1993

The field station disaster of 1992 prompted a further replicate to be done in the final year, 1993, on the influence of a 3 lux night-time incident light level on nightly movement patterns. It was carried out to provide sufficient data for an overall analysis of light level effects on alevin movement away from the redd and was set up to replicate the previous two year's work using a separate sibling stock of salmon.

2.6.1 MATERIALS AND METHODS

In the spring 1993 the same artificial redds were used as in the spring of 1992 (see Section 2.31.). The eyed ova used in these experiments were the progeny of a single pair of wild grilse (Male 73.5 cm fork length & Female 73.5cm) from the river Garry, a tributary of the River Tay, and were stripped on the 6/11/92. The ova were kept under constant low light and ambient water temperatures at the Almondbank hatchery, Perthshire. Two hundred eyed ova were split up into two groups of 100 and placed into the two artificial redds (one experimental redd and one control redd) in Glasgow University Zoology Department at night on the 25/3/93. Smaller numbers of eyed ova were used in each system than in the second year simply because fewer were available from the hatchery.

Eyed ova were kept in the hatchery at a temperature of around 4°C . The ambient temperature of the University water was 8°C so during moving the ova were brought up to this temperature over a 6 hour period. This meant that the hatch time was slightly accelerated. The water temperatures for the rest of the gravel incubation period came from an outside source of dechlorinated water which flowed through the system at a rate of 1.51 l/min. Temperature recorded with a Squirrel data logger, averaged temperatures were 8.815 +/- 0.1°C (2 SE).

For both redds combined daylight intensity at the water surface averaged 92.6 +/- 6.65 (2 SE) lux. For the experimental redd, a night time incident light intensity of 3.1 +/- 0.85 (2 SE) lux, was simulated on alternate nights using a 40W bulb on a dimmer switch. The alevins in the experimental redd therefore experienced alternate light and dark nights. Alevins caught in the control and the experimental redds were then weighed, measured and assessed for their stage of development, as described in section 2.3.1.

2.6.2 RESULTS

In the control redd 64% of the alevins survived and in the experimental redd 84% of the alevins survived. Measures of skewness and kurtosis were calculated using the data plotted in Figures 2.6A & 2.6B. The number of alevins moving nightly away from the experimental redd was not normally distributed with time (Kolmogorov-Smirnov test, d.f. 84, $z = 0.1201$, Skewness = -0.6087, Kurtosis = -0.4916, $p < 0.005$). Relatively fewer alevins moved around the mean date, thus making the overall shape of the distribution platykurtic (kurtosis = -0.4916). The nightly movements of alevins in the control redd did not differ significantly from a normal distribution (Kolmogorov-Smirnov test, d.f. 64, $z = 0.1146$, Skewness = -0.554, Kurtosis = -0.244, n.s.).

Taking neighbouring nights in the experiment as matched pairs showed that there was a significant suppression of nightly movement on lighter nights (Wilcoxon paired-sample test, N=11, $t = 56$ $p < 0.021$). No significant effect was found for the control experiment (Wilcoxon paired-sample test, N=10, $t = 23$, n.s.)(Table 2.8). No significant differences were found for the median weights, lengths and yolk sacs when the same pairs of nights were compared in the control (Table 2.9).

Interestingly, the fish from the control were significantly lighter (t-test = -2.24; D.F. = 139.69, $p < 0.05$) and had smaller yolk sacs (t-test = -2.00; D.F.132.06, $P < 0.05$). The

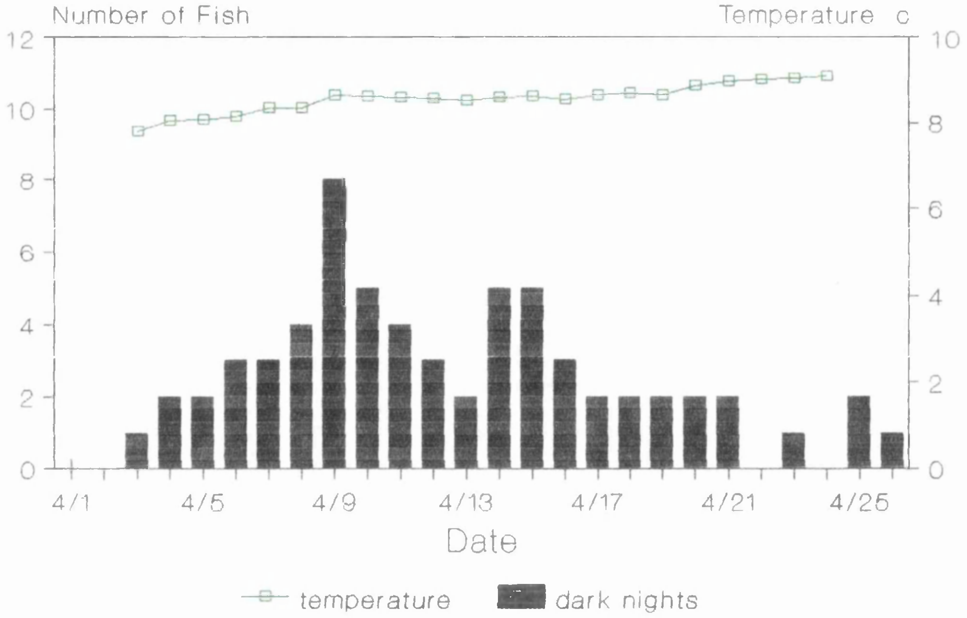
Figure 2.6.A

Number of alevins moving nightly from the control (Total n = 64). Each division on the x-axis is represented as a date, the total period of movement lasted from 3rd of April to the 26th of April 1993. Daily mean temperatures are plotted against the right hand y-axis. During the period of movement the average temperature was 8.82 ± 0.1°C (2 SE).

Figure 2.6.B

Number of alevins moving nightly from the experiment (Total n = 84). On alternate nights (marked in blue) the alevins were exposed to a 3 lux light level. Each division on the x-axis is represented as a date, the total period of movement lasted from the 1st of April to the 23rd of April 1993. Daily mean temperatures are plotted against the right hand y-axis. During the period of movement the average temperature was 8.82 ± 0.1°C (2 SE).

CONTROL REDD



EXPERIMENTAL REDD

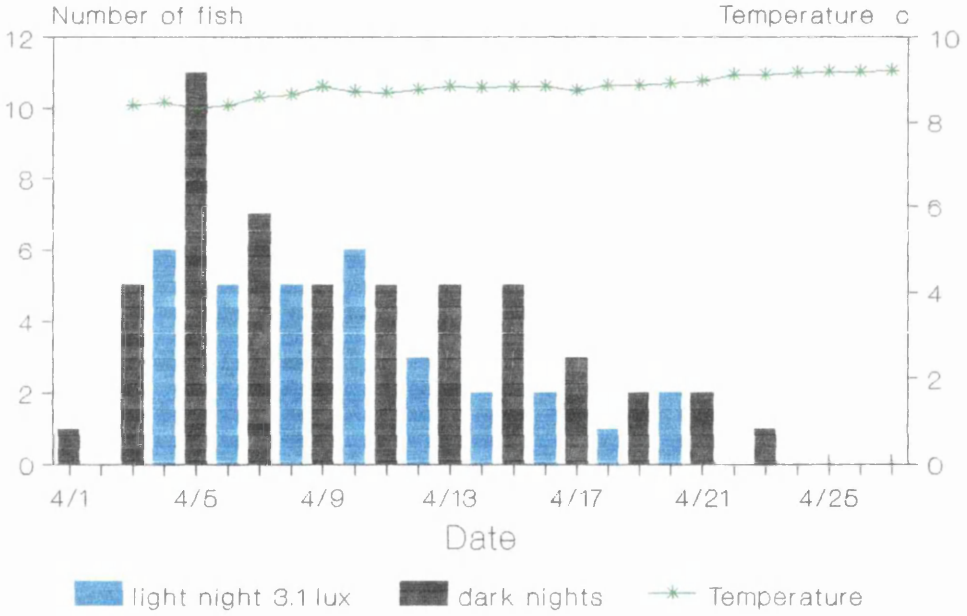


Table 2.8.
The numbers of alevins moving away from the redd on light and dark nights in each artificial redd, 1993

Artificial Redd	**Variable**	**Light Night (3 Lux)**	**Dark Night (0 Lux)**	n	t	p†
Experimental Redd	Total number	32	52	11	56	$P < 0.05$*
University 1993	Percentage	38.1%	61.9%			
Artificial Redd	**Variable**	**Light Night (0 Lux)**	**Dark Night (0 Lux)**	n	t	p†
Control Redd	Total number	30	50	10	23	n.s.
University 1993	Percentage	37.5%	62.5%			

p† Wilcoxon matched-pairs signed ranks test using the number of alevins moving on adjacent nights as matched pairs

Significantly more alevins moving on dark nights : * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Table 2.9.
Median size differences between alevins moving on light and dark nights, 1993.

Artificial Redd	**Variable (Median)**	**Light Night (3 Lux)**	**Dark Night (0 Lux)**	n	t	p†
Experimental Redd	Weight (g)	0.126	0.124	7	17	n.s.
University 1993	Fork Length (mm)	24.5	24.5	6	7	n.s.
	Yolk sac (sq mm)	17.5	16.25	5	3	n.s.
Artificial Redd	**Variable (Median)**	**Light Night (0 Lux)**	**Dark Night (0 Lux)**	n	t	p†
Control Redd	Weight (g)	0.122	0.124	9	-22	n.s.
University 1993	Fork Length (mm)	24	24	3	4	n.s.
	Yolk sac (sq mm)	14	14	5	-4	n.s.

Significantly larger midwater alevins : * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

p† Wilcoxon matched-pairs signed ranks test using median measurements of alevins on adjacent nights as matched pairs

relative proportions of fish moving away from the redd (R_n) on a given night was calculated for both the experiment and the control (See section 2.3.2). This transformed data was then used as the dependent variable in a stepwise multiple regression analysis, where water temperature and date were the independent variables. This showed that the only predictor of the nightly movements was date both in the control ($F_{1,19}$=19.35, $r^2 = 0.504$, $P < 0.001$) and in the experimental redd ($F_{1,18}$ =20.247, $r^2 = 0.529$, $P<0.001$).

2.6.3. DISCUSSION

A three lux light level in the experimental redd significantly suppressed nightly movements, which provides further evidence for a relationship between light level and alevin movement away from the redd. A light level of three lux is thought to be well above the visual threshold for juvenile Atlantic salmon alevins (Ali, 1961) and yet nightly alevin movements continued even on light nights, which suggests that this behaviour is more likely the result of a timed behavioural decision than a temporary disorientation (Ali, 1961). No size differences were found between fish moving on a light night compared to those moving on adjacent dark nights i.e. there were no visible ontogenetic differences between alevins. However, clear size differences were found between alevins moving each night in the control and the experimental redd. The developmental differences seen between the control and the experimental redd are most likely to be linked to the difference in shape between the two distributions. In the experiment the peak of alevin movement away from the redd was before that of the control redd.

2.7 NIGHTLY MOVEMENTS OF ALEVINS AWAY FROM THE REDD, AT 0.7 LUX, 1993

In the final year a very low night-time incident light level was selected for an additional redd run alongside the control from the last section. The purpose behind this was to simulate the only natural source of night time incident light in the wild : moonlight.

Moonlight has been found to be an important environmental factor influencing the behaviour of salmonids. In smolting populations of salmonids many migrations are known to peak during the darkest nights of the lunar phase (Mason, 1975; Youngson et al., 1983). Pacific salmon alevins downstream movements are also thought to be influenced by moonlight: Field-Dodgson (1988) found a weak negative relationship between number of alevins dispersing and moonlight and Mason (1975) showed peaks in movement of alevins synchronised with new moons.

The level of moonlight is dependent on lunar phase and local climatic conditions, such as cloud cover. This means it is not as strong a cue as daylight. Nevertheless the intensity of moonlight can reach 0.7 lux, or 0.28 Wcm^{-2}, at the full moon (Saunders, 1977) which is within the visual threshold of Atlantic salmon alevins (Ali, 1961). So moonlight may be an important influence on the movement of Atlantic salmon alevins away from the redd. The aim of this experiment was therefore to determine whether a light threshold level of 0.7 lux would significantly suppress movements away from the redd, as light levels of two lux have been shown to do.

2.7.1 MATERIALS AND METHODS

In the spring 1993 a third identical semi-natural redd (Section 2.4.1) was set up to examine the effects of moonlight on movement of alevins using the same stock of fish as described in Section 2.5.1. The experimental set up and conditions were almost identical as in the previous materials and methods section. The only difference was the night time incident light intensity of 0.7 +/- 0.56 lux (2 SE), which was simulated on alternate nights using a 40W bulb on a dimmer switch. So the alevins in the redd did experience alternate light and dark nights but at a much lower level. Alevins caught from the control and the experiment were then weighed, measured and assessed for their stage of development as described in Section 2.3.1.

2.7.2 RESULTS

In the experimental redd 84% of alevins survived. As this work was carried out in the spring of 1993 the same control redd as in Section 2.5.2 was used for comparison (Figure 2.7.A). A similar histogram of numbers each night was also plotted for the experimental redd (Figure 2.7.B). The number of alevins moving nightly from the experimental redd was not normally distributed with time (Kolmogorov-Smirnov test,

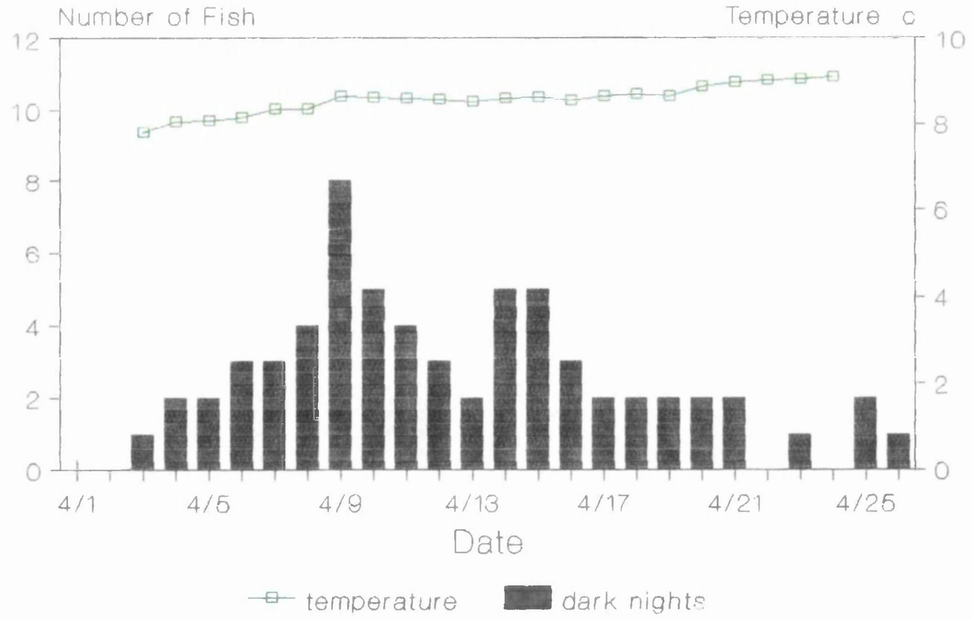
Figure 2.7.A

Number of alevins moving nightly from the control redd(Total n = 64). Each division on the x-axis is represented as a date, the total period of movement lasted from 3rd of April to the 26th of April 1993. Daily mean temperatures are plotted against the right hand y-axis. During the period of movement the average temperature was 8.82 ± 0.1°C (2 SE).

Figure 2.7.B

Number of alevins moving daily from the experiment (Total n = 80). On alternate nights (marked in blue) the alevins were exposed to a 0.7 lux light level. Each division on the x-axis is represented as a date, the total period of movement lasted from the 2nd of April to the 25th of April 1993. Daily mean temperatures are plotted against the right hand y-axis. During the period of movement the average temperature was 8.82 ± 0.1°C (2 SE).

CONTROL REDD



EXPERIMENTAL REDD

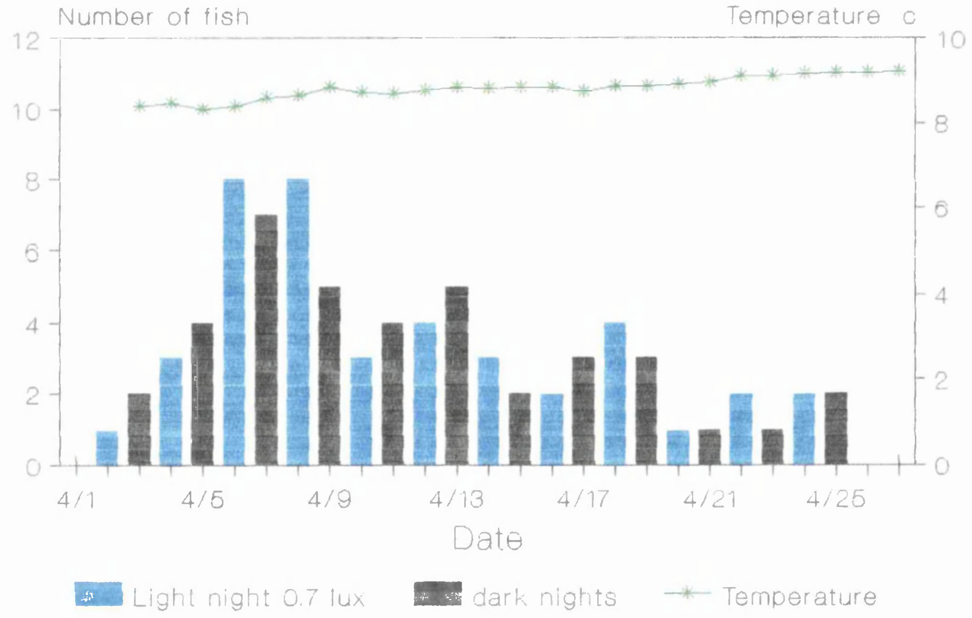


Table 2.10.
The numbers of alevins moving away from the redd on light and dark nights in each artificial redd, 1993.

Artificial Redd	Variable	Light Night (0.7 Lux)	Dark Night (0 Lux)	n	t	p†
Experimental Redd	Total number	41	39	9	15	n.s.
University 1993	Percentage	51.25%	48.75%			
Artificial Redd	**Variable**	**Light Night (0 Lux)**	**Dark Night (0 Lux)**	**n**	**t**	**p†**
Control Redd	Total number	30	50	10	-23	n.s.
University 1993	Percentage	37.5	62.5			

p† Wilcoxon matched-pairs signed ranks test using the number of alevins moving on adjacent nights as matched pairs

Significantly more alevins moving on dark nights : * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Table 2.11.
Median size differences between alevins moving on light and dark nights, 1993.

Artificial Redd	Variable (median)	Light Night (0.7 Lux)	Dark Night (0 Lux)	n	t	p†
Experimental Redd	Weight (g)	0.125	0.122	7	22	n.s.
University 1993	Fork Length (mm)	24	24	7	12	n.s.
	Yolk sac (sq mm)	17.5	12	4	-2.5	n.s.
Artificial Redd	**Variable (median)**	**Light Night (0 Lux)**	**Dark Night (0 Lux)**	**n**	**t**	**p†**
Control Redd	Weight (g)	0.122	0.124	9	-22	n.s.
University 1993	Fork Length (mm)	24	24	3	4	n.s.
	Yolk sac (sq mm)	14	14	5	-4	n.s.

Significantly larger midwater alevins : * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

p† Wilcoxon matched-pairs signed ranks test using median measurements of alevins on adjacent nights as matched pairs

d.f. 84, $z = 0.1358$, Skewness = -0.5927, Kurtosis = -0.6132, $p < 0.001$). The control trial histogram did not differ significantly from normality (Kolmogorov-Smirnov test, d.f. 60, $z = 0.111$, Skewness = -0.554, Kurtosis = -0.244, $p > 0.05$). In the experimental redd there was no significant suppression of movement on lighter nights (Table 2.10). In addition no differences were found in body sizes and weights of alevins either between nights (Table 2.11) or between trials (Paired t-test, $p > 0.1$). A stepwise multiple regression using the relative proportion of fish moving nightly (R_n), see Section 2.3.2, as the dependent variable and temperature and date as the independents showed that the best predictor for both trials was date : control ($F_{1,19} = 19.35$, $r^2 = 0.504$, $P < 0.001$), experiment ($F_{1,20} = 16.32$, $r^2 = 0.449$, $P < 0.001$).

2.7.3 DISCUSSION

Atlantic salmon alevins have a much lower visual threshold than any species or stage of Pacific salmon, and can possibly see down to 0.01 lux (Ali, 1961). They would have been able to see at the simulated moonlight level of 0.7 lux and yet this did not significantly suppress nightly movements on light nights. However, the peak of alevin movement away from the redd in the experiment was before that of the control redd which is the same result found for other trials. So although moonlight would appear to be below the threshold at which alevin movements can be significantly suppressed on any one night, it may not be below the level to which alevins will respond behaviourally. This result is similar to that found before and suggests that the peaks of movement of Atlantic salmon alevins in the wild may well be shifted by an increase in natural light levels. No size differences were found between fish moving on a light night compared with those moving on adjacent dark nights and additionally no size differences were found between alevins moving each night in the control and the experimental redd. This result again implies that a 0.7 lux light level will not significantly influence alevin behaviour in a manner similar to that described in Section 2.4.3 & 2.6.3.

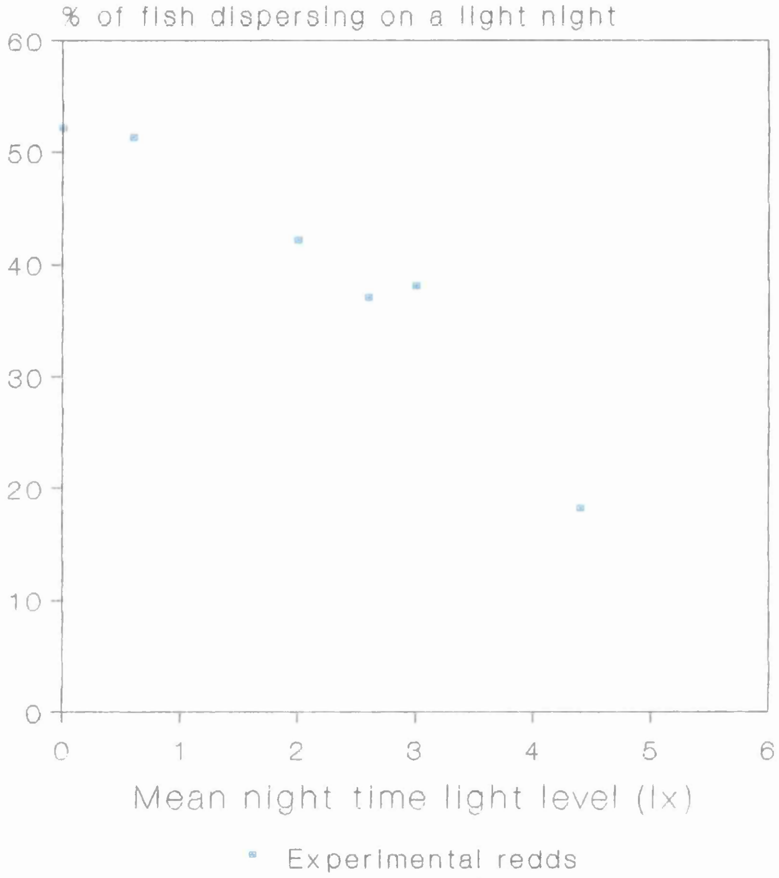
2.8 GENERAL DISCUSSION

The three year's results show that above 2 lux there is a significant suppression of nightly alevin movements away from the redd. No size differences were found between fish moving on a light night compared with those moving on adjacent dark nights in any experimental redd. In the 1991 pilot study the temperature was significantly higher than in 1992 (ANOVA; $F_{1,19} = 860.76$, $P < 0.001$) and 1993 (ANOVA; $F_{1,19} = 384.45$, $P < 0.001$), which is likely to have led to the distinct leptokurtic shape the distribution of numbers of alevins moving each night (Godin, 1980; Brännäs, 1988). In addition, the dispersal period was much later than in other years because of the lower temperature the alevins were kept at hatching. In 1992 and 1993 the peak of movement away from the experimental redds was always earlier than in the equivalent control redds. The difference in distribution between the experiment and control suggests that the peaks of movement of Atlantic salmon alevins away from the redd may well be shifted by an increase in natural light levels. This provides some circumstantial evidence for the observed alevin movements being more closely linked to a timed behavioural decision and not a temporary disorientation (Ali, 1959a,b). Further evidence for a controlled movement of animals away from the redd comes from a recent study by Bardonnet et al.,(1993) who found that visual landmarks (phosphorescent rocks) could delay but not suppress nightly movements of alevins

Combining the three years data together shows that there is a clear relationship between light level and nightly movement of alevins (Figure 2.8). This relationship can be seen when the proportion of alevins moving on light nights for each trial is ranked and correlated with the equivalent night time incident light intensity (Spearman Rank correlation $r = -0.9429$, $N = 6$, $p < 0.01$). This specific behavioural response to light may be interpreted as a negative photokinesis, because the frequency of movement is dependent on the intensity of the stimulation (Fraenkel & Gunn, 1940). This correlation alone is strong evidence for a simple photoresponse and not for the temporary disorientation hypothesis, as put forward by Ali (1959). However this conclusion still does not explain why individual fish choose to move on a light night while others do not.

Two possible explanations are either that a retinal developmental difference has led to some fish becoming visually disorientated or that some alevins are prepared to take the extra risk of movement on a light night. Evidence for the first of these explanations comes from a study by Manteifel et al.(1978) on roach fry (Rutilus rutilus) where he found that larger fry moved downstream later in the night and at lower light intensities. His explanation for this behaviour was 'during growth, the threshold values of light intensity for the optomotor reaction become lower'. Hence in the series of

Figure 2.8


% of fish dispersing on a light night
60
50
40
30
20
10
0
0
1
2
3
4
5
6
Mean night time light level (lx)
Experimental redds

studies presented in this chapter one might expect to find smaller less developed alevins which presumably have poorer retinal responses to be moving away from the redd on lighter nights. No such developmental differences were found between the alevins moving on a light night compared with those moving on a dark night. However, the development of retinomotor responses may not be related to the body size of the Atlantic salmon alevin as it is in the roach; so further work on this is required, investigating the relationship between retinal development and alevin movement away from the redd. The second explanation as to why some alevins are still choosing is that an alevin is faced with certain biotic requirements that must be fulfilled by a certain stage of their development this may push alevins into taking greater risks i.e. moving away from the redd on a lighter night. This alternative explanation also implies that alevins more advanced in their development (i.e. less yolk sac) should be moving away from the redd on light nights but in none of the above experiments were such size differences found.

Ali's (1959) original idea that disorientation may be the cause of movement may therefore still be right if we allow for possible retinal developmental differences which are not reflected by size differences in alevins. If these retinal differences did exist then we would still expect to find alevin movement away from the redd beginning soon after dark as less developed alevins become disorientated. This latter point is investigated in the next chapter where fine scale patterns of the timing and method of movement away from artificial redds were studied.

CHAPTER 3
THE TIMING AND METHOD OF MOVEMENTS AWAY FROM THE REDD

3.1 INTRODUCTION

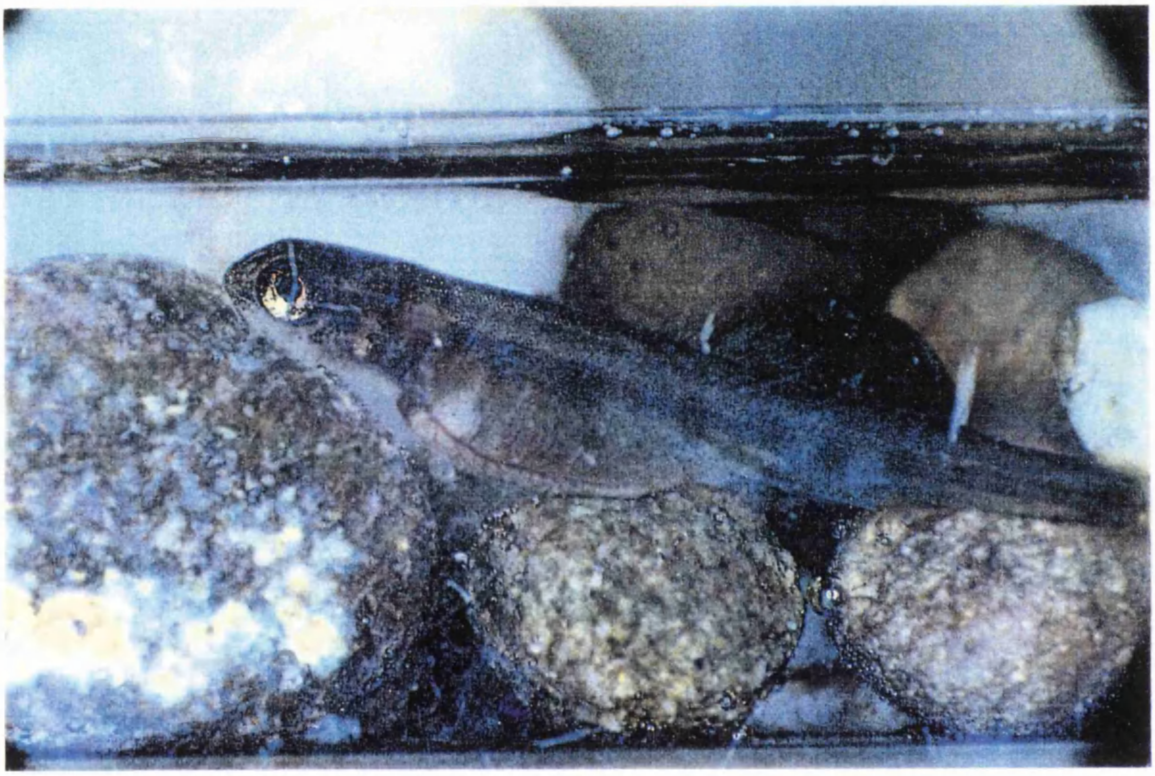
In Scotland wild Atlantic salmon normally hatch out into their gravel nest in March. Twenty to thirty days after hatching, alevins from a single family will be spread through the gravel around the redd from a depth of 0.5 metres to a depth of around 1 metre (Stuart, 1953; Garcia de Leaniz et al., 1993a,b). Towards the end of April they begin their upward ascent through the gravel towards the surface of the stream bed. Upon reaching the near surface layers of the streambed, they sense the natural light / dark cycle (Bardonnet & Gaudin, 1990a,b). At this point alevins begin to move away from the redd at night into the stream and the total period of movement for any alevin may span a number of nights with successive downstream movements (Plate 2). Moving at this point is very risky: alevins are entering a completely new environment where they may encounter a great number of potential predators (see Chapter 1). Not surprisingly alevin behaviour has evolved to increase their chances of survival; as pointed out by Hoar (1958) "When many small fish must face a fixed number of predators, the shorter and more precise the period of contact, the better will be their chance of survival". Thus first movements away from the redd are clearly important for survival and each night alevins must choose when to start and stop moving. This chapter therefore investigates the timing and method of movement away from the redd during this critical stage.

3.1.1 THE TIMING OF MOVEMENT AWAY FROM A REDD

The movement of single alevins from the redd has not been documented very accurately in the past, partly because of the design of artificial redds used to examine alevin behaviour and partly due to the difficulties involved when trying to monitor alevin movements throughout the night (Nunan & Noakes, 1987; Brännäs, 1988). However the work that has been done suggests that alevins choose to leave the redd singly, but that on any given night the interval between individual movements is temporally clumped (Garcia de Leaniz et al., 1993a). However, often these studies have sampled only a small fraction of alevins or have observed only hourly movements of alevins. Studying the timing of individual movements will therefore show when alevins leave the redd and will give an idea as to why they move at a particular time.

Plate. 2

Alevin with yolk sac soon after moving away from the redd.



3.1.2 THE METHOD OF MOVEMENT AWAY FROM A REDD

A recent field study has indicated that there maybe substantial movement of alevins within or near the stream substrate as well as in the water column (Garcia de Leaniz et al., 1993b). In this study a single isolated natural redd was studied and the downstream movement of alevins was monitored using three downstream traps placed 20 metres apart. All marked fish were trapped, yet throughout the trapping period, a significant proportion were caught in the second trap of the series as unmarked alevins suggesting that many alevins had somehow evaded capture in traps further upstream. Since the traps had been carefully buried into the streambed and covered the width of the stream it was suggested that the only possible means of evasion was through the gravel (Garcia de Leaniz et al., 1993a,b). If substantial proportions of alevins do choose to move through the gravel away from the redd then it may have a substantial influence on other related behaviours such as temporal clumping and photokinesis (Chapter 2).

This chapter therefore concentrates on the timing and method of alevin movements away from the redd and is a companion chapter to Chapter 2. Investigations were carried out both during the course of the experiments described in Chapter 2 and in a newly designed artificial redd. Three broad sections cover the behaviour observed and they are as follows :

3.2 TIMING OF INDIVIDUAL MOVEMENTS: RESULTS OF FILMING

3.3 UNDERGRAVEL MOVEMENTS AWAY FROM THE REDD : RESULTS OF TRAPPING

3.4 DEPTH AND DIRECTION OF MOVEMENTS AWAY FROM THE REDD

3.2 TIMING OF INDIVIDUAL MOVEMENTS : RESULTS OF FILMING

In chapter 2 it was shown that light level is an important environmental factor influencing the nightly movements of alevins away from the redd. This result is also evidenced by the fact that as the summer days get longer, the start of alevin movements shifts accordingly (Bardonnet & Gaudin, 1990a,b). Ali (1961) suggested that a temporary state of night blindness at dusk may cause Atlantic salmon alevins to lose reference points in the stream, resulting in disorientation and downstream movement. If such a disorientation does occur, then the commencement of the nightly movement should coincide with the first darkness. Alternatively alevins may wait until their retinae are fully dark-adapted (circa 35 minutes) before beginning any movements away from the redd (Ali, 1959a,b; Ali, 1961). To date, the only timing of this nightly movement has been studied on an hourly basis (Gustafson-Marjanen & Dowse, 1983; Bardonnet & Gaudin, 1990a,b; Garcia de Leaniz et al., 1993a), so the detailed timing of movements of alevins away from the redd is still unclear.

It is well documented that the bulk of alevins from a single family leave their redd and move downstream in the first few hours of the night (Godin, 1980; Gustafson-Marjanen & Dowse, 1983; Bardonnet et al., 1993). This high degree of temporal clumping during nightly movements has led some authors to suggest there is some interaction between individuals, leading to a bulk movement of alevins away from the redd (Peterman and Gatto 1978; Gustafson-Marjanen & Dowse, 1983). Such interactions are most likely to include tactile and visual stimuli either above or below the surface of the gravel near the redd. If such a bulk movement of alevins occurs then it could be interpreted as a further possible predator swamping effect since overall predator damage is reduced when prey concentration is high (Hoar, 1958; Brown, 1975). The experiment described below therefore investigates: (1) the time at which alevins begin moving away from the redd each night and (2) the temporal clumping of fry movements.

3.2.1 MATERIALS & METHODS

This work was carried out in the spring of 1992 and 1993. The movements of alevins were filmed in the 1992 control redd (see section 2.3.1). The artificial redd used for this work is described in Section (2.3.1) and the only modification to the setup was a white plastic grid card, 10 x 25 cm, attached to the platform at the far end of the redd. A small hole was then cut in the black plastic sheeting surrounding the tanks to allow a camera to view this section of stream from outside the aquarium (Plate 3). The flow, photoperiod, water temperature, light and stock of alevins are described thoroughly in Section 2.4.1. A CCTV camera, with a newvicon tube, allowed this section of the artificial redd to be viewed with a Dennard 880N50 infra red light at night. A 880nm filter was used on the light so that the alevins would not detect its presence (Ali, 1961). The controlled photoperiod of 8hrs dark/ 16 hrs light allowed for eight hours of filming each night. All films were subsequently analysed to detail the depth and timing of individual nightly movements. Accurate measurements of alevin size were not possible from the video film.

3.2.2 RESULTS

In total, 56 hours of tape were recorded (7 nights out of 19). All but 4 of the alevins caught on these nights were seen on the film record (72 out of a possible 76). Of the 72 observed alevins only four moved away from the redd in the second half of the night. The interval between individuals was significantly temporally clumped and the majority of movements (66% of the total) taking place within ten minutes of each other (Table 3.1). Furthermore, it was evident from the film analysis that there were two very different types of behaviour exhibited by alevins: mid-water and bottom movements.

A midwater moving alevin would swim actively (mean velocity :10.9 ± 1.76 cm/s) downstream and was not observed to settle onto the streambed at any time. On the other hand a bottom moving alevin would remain stationary on the stream bed for short periods of time before moving off either up into the water column or they would creep very slowly (mean velocity: 4.03 ± 0.95 cm/s) through the gravel (Figure 3.1A). There is a slight overlap in the speed and depth measurements of the two groups (Figure 3.1A & 3.1B). This overlap is related to the behaviour of the some of the bottom moving alevins who on occasion would swim up into the water column and swim downstream. This vertical movement up into the water column increased the average depth and speed of certain individuals. At no time were midwater alevins seen to touch the substrate.

There was no significant difference between the nightly dispersal times of the bottom-moving and midwater moving (Covariance analysis showed that there was no significant difference in elevation between the two regression lines, $F_{2,67} = 2.06$, n.s.; or in slope $F_{2,65} = 0.06$, n.s.) (Figure 3.1C). Towards the end of the experiment mid-water moving alevins took a significantly higher route through the water column than at the beginning (Covariance analysis significant difference in slope between the two regression lines; $F_{1,5} = 4.61$, $P < 0.05$; Figure 3.2.B.).

3.2.3 DISCUSSION

The movement of alevins from the artificial redd was highly synchronised to the external light/dark cycle with the peak time of nightly movements occurring between 2-3hours after dark (Figure 3.1C). This is slightly later than the peak time of nightly movements seen in Brännäs

Plate 3

The section of stream, downstream of the artificial redd viewed by a camera through the side of the aquarium. A single grid square was 2 x 2 cm and the total stream depth was 8 cm.

Table 3.1 Observed temporal clumping of alevins (measured as the frequencies of intervals between successive alevins) and the expected pattern of temporal clumping. Poisson distribution used to calculate expected values (Sokal & Rohlf, 1969), significant differences shown by partitioned X^2.

INTERVAL	OBSERVED	EXPECTED	Partitioned X^2
< 5 mins	24	5.57	
5-10 mins	20	13.61	2.95
10-15 mins	6	16.61	12.37***
20-25 mins	2	13.51	10.82**
25-30 mins	6	8.24	0.42
> 30 mins	6	6.46	0.019

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Figure 3.1A

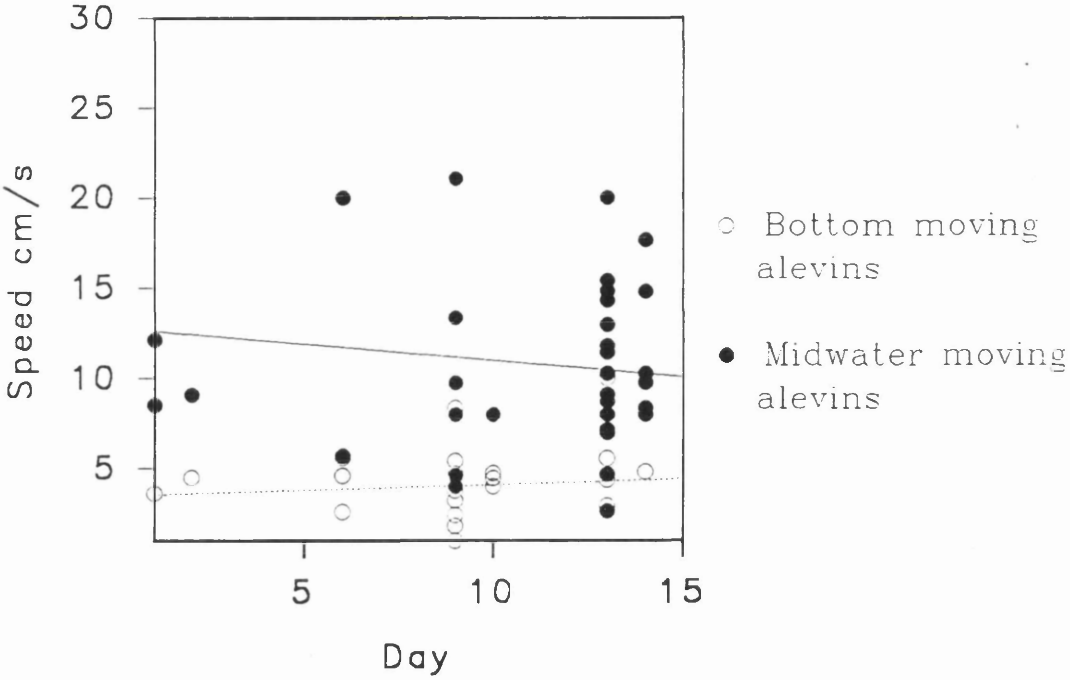
The speed of the two methods of movement (midwater and bottom) seen against date. The average speed of a bottom moving alevin (4.03 +/- 0.95 cm/sec^{-1}) was faster than the average the average speed of a midwater moving alevin (10.91 +/- 1.76 cm/sec^{-1}). This is shown by the significant difference in elevation between the two regression lines (ANCOVAR ; $F_{1,55} = 35.55$, $p < 0.001$)

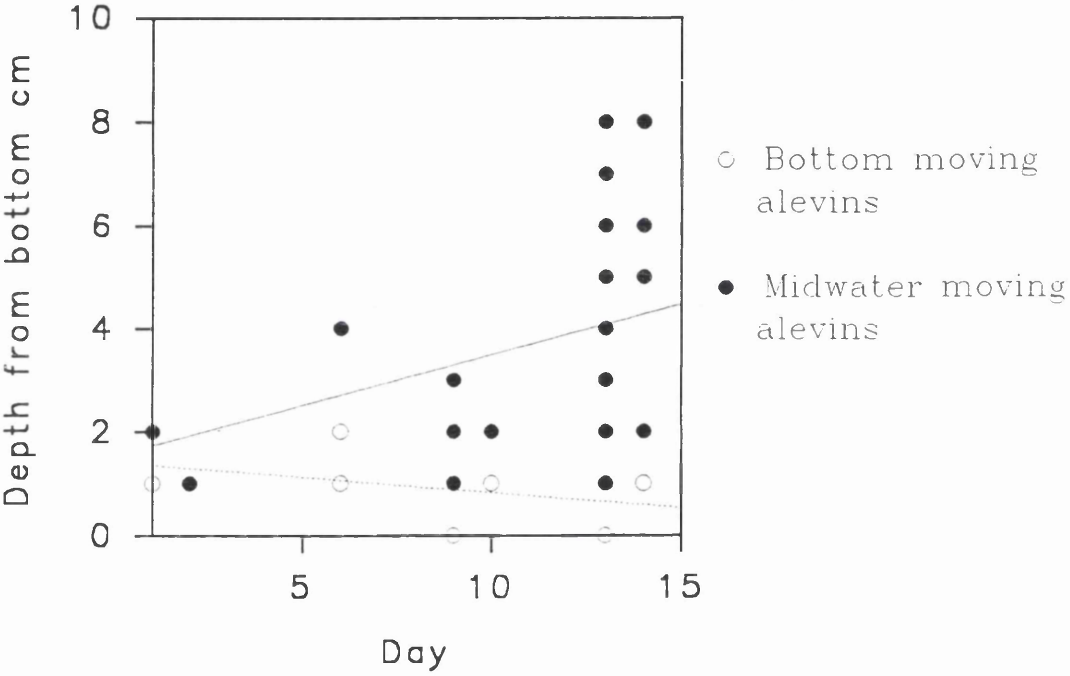
Figure 3.1B

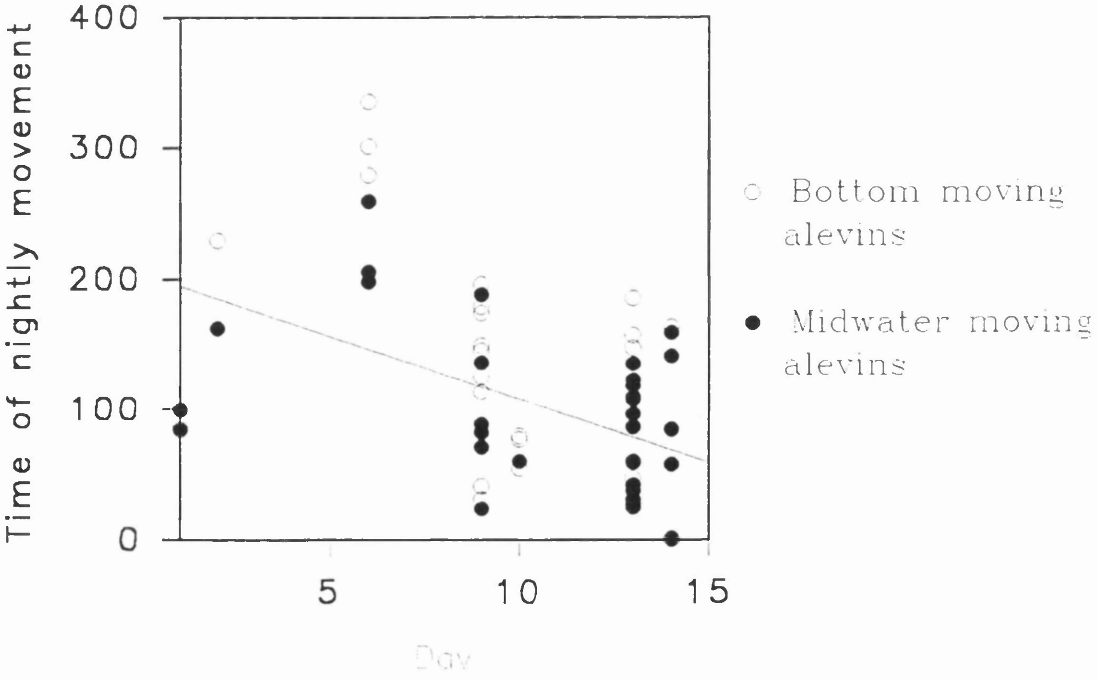
The change in depth of the two methods of movement against time. The average depth of a midwater moving alevin was 3.57 ± 0.71 (2SE) cms above the stream bed, whilst a bottom moving alevin averaged a depth of 0.8696 ± 0.198 (2SE) cms above the stream bed. There is also a significant difference in the slope of the two regression lines (ANCOVAR ; $F_{1,55} = 35.55$, $p < 0.001$) i.e. midwater moving alevins were moving closer to the surface by the end of the experiment.

Figure 3.1C

The timing of nightly movement away from the redd, expressed as minutes after dusk. Alevins from both groups were moving earlier in the night towards the end of the experiment (bottom moving group $r = -0.365$, $n = 23$, $p = 0.086$); midwater moving group $r = -0.558$, $n = 35$, $p < 0.001$).


Speed cm/s
30
25
20
15
10
5
5
10
15
Day
○ Bottom moving alevins
● Midwater moving alevins


Depth from bottom cm
10
8
6
4
2
0
5
10
15
Day
○ Bottom moving alevins
● Midwater moving alevins


Time of nightly movement
400
300
200
100
0
5
10
15
Day
○ Bottom moving alevins
● Midwater moving alevins

(1988) study, 0-1 hour after dark, and slightly later than Gustafson-Marjanen & Dowse's study in 1983, 1-2 hours after dark. However, this result is in general agreement with most work done on alevin movements away from the redd which all points towards the bulk activity occurring in the first half of the night (Northcote, 1962; Godin, 1982). The one hour change to an earlier time of movement towards the end of the experiment suggests that late moving fry have a stronger urge to move; this may well be linked to the depletion of their yolk sac and the need to start first feeding and is opposite to what Ali's hypothesis would predict (i.e. that the peak time for nightly movement should not change). The temporal clumping of alevins seen here is also similar to that found in other studies with the interval between alevin movement remaining relatively short (Garcia de Leaniz et al., 1993a). Gustafson-Marjanen & Dowse (1983) suggested that this might be a group movement similar to that seen in other salmonids, but at no time in this present study were groups of alevins seen moving together. So although the temporal clumping pattern indicates an association in movement patterns, it is not a group behaviour associated with schooling or with shoaling (Pitcher, 1986) as found in Pacific salmon fry (Hunter, 1959).

The film work carried out showed that there were two very different types of behaviour; one involved an alevin emerging from the gravel swimming rapidly head up into the water column and then swimming downstream in midwater; the other type of behaviour is close to or under the stream bed. The filmed behaviour of these bottom moving alevins showed that they remain stationary for long periods (39.07 seconds ± 33.42 (2SE)) before resuming movement. In addition, these bottom moving alevins would often stop and then burrow into the gravel before re-appearing further downstream, i.e. having moved through the gravel. This once again reaffirms the problem of applying rigid definitions, such as emergence or dispersal, to alevin movement away from the redd. Overall the behaviour of moving alevins is very diverse, with some alevins choosing to move into their first stream environment with great caution, while others effectively throw their bodies into the current and swim downstream. This difference in style is clearly reflected by the average velocity of a midwater moving alevin which was twice that of a bottom moving alevin (i.e. they are travelling a longer distance in a shorter time).

In 1961 Ali suggested that movements of Atlantic salmon alevins at night away from the redd could be the result of a reduced or impaired visual contact with the environment. In this section the average time at which the first alevin moved away from the redd was 1 hour 43 minutes and 44 seconds after dark. This is well past the theoretical time limit taken for dark adaptation of the Atlantic salmon retina (Ali, 1959a,b; 1961). This suggests that movement away from the redd is not correlated with a visual disorientation. In addition, more developed alevins, with presumably better developed retinas, were moving earlier in the night towards the end of the experimental period, which is opposite to what Ali's hypothesis would predict.

3.3 UNDERGRAVEL MOVEMENTS AWAY FROM THE REDD : RESULTS OF TRAPPING

During 1992 & 1993 all the artificial redds described in chapter 2 incorporated under-gravel siphon traps, to separate any alevins moving under the gravel from midwater moving alevins. This addition to the redd was designed to investigate the recent findings on undergravel movement away from a natural redd (Garcia de Leaniz et al., 1993b).

3.3.1 MATERIALS & METHODS

Photoperiod, flow, night-time incident light, temperature, tank design and stock of alevins used in these experiments are thoroughly described in Chapter 2. The undergravel trap was attached to the end of the 20 cm platform of surface gravel which extended downstream of each artificial redd (see Figure 3.2A). Alevins moving through the surface gravel on this platform would eventually reach a mesh trap where a siphon tube would transport them out of the flume and into a bottle trap below the height of the flume. A bottle trap consisted of a standard plastic container bottle, 12 cms high, with a hole cut in its side which was covered in mesh. The siphoned water entered through the top of the bottle and flowed out through the meshed hole in the side wall of the bottle (Figure 3.2B). The siphon trap was between 8-10cm below the water surface and a continuous flow of 1.5 l/min through the system ensured that the siphoned outflow did not exceed the inflow. The siphoned outflow was set at 0.7- 0.8 l/min by adjusting the height of the bottle traps outside the redds. Siphon trapping retention efficiency was measured by placing 10 alevins in the bottle trap for a 12 hour period. After 12 hours all the ten alevins were caught again alive, i.e. a 100% retention efficiency.

3.3.2. RESULTS

In both years between 10 and 40 % of the total alevins trapped in every artificial redd were caught in an undergravel trap. In all redds alevins moving through the gravel (undergravel) were significantly smaller by at least one condition (weight, yolk sac or fork length) than midwater moving alevins (Table 3.2). At light levels above two lux midwater moving alevins in the experiments were significantly larger either by yolk sac size (t-test ; d.f. 330, $t = -5.55$, $P < 0.001$) or by weight (t-test ; d.f. 139, $t = -2.24$, $P < 0.05$) than in the controls.

The only exception to this was the experiment carried out at the Field Station in 1992. However this may result from the low number of alevins caught moving through the gravel which in turn may be related to the high levels of silt in both artificial redds(see Table 3.3). The actual number moving through the gravel on each night are shown in Figure 3.3 -3.7. The number moving

Figure 3.2A
Artificial redd used for the study of undergravel movement of alevins. The container was modified to allow fish to move either through a platform of surface gravel where they were caught by a siphon tube leading to a bottle trap(see Section 3.3 for results) or downstream in the water column.

Figure 3.2B

Under gravel trap attached to the artificial redd. Side view

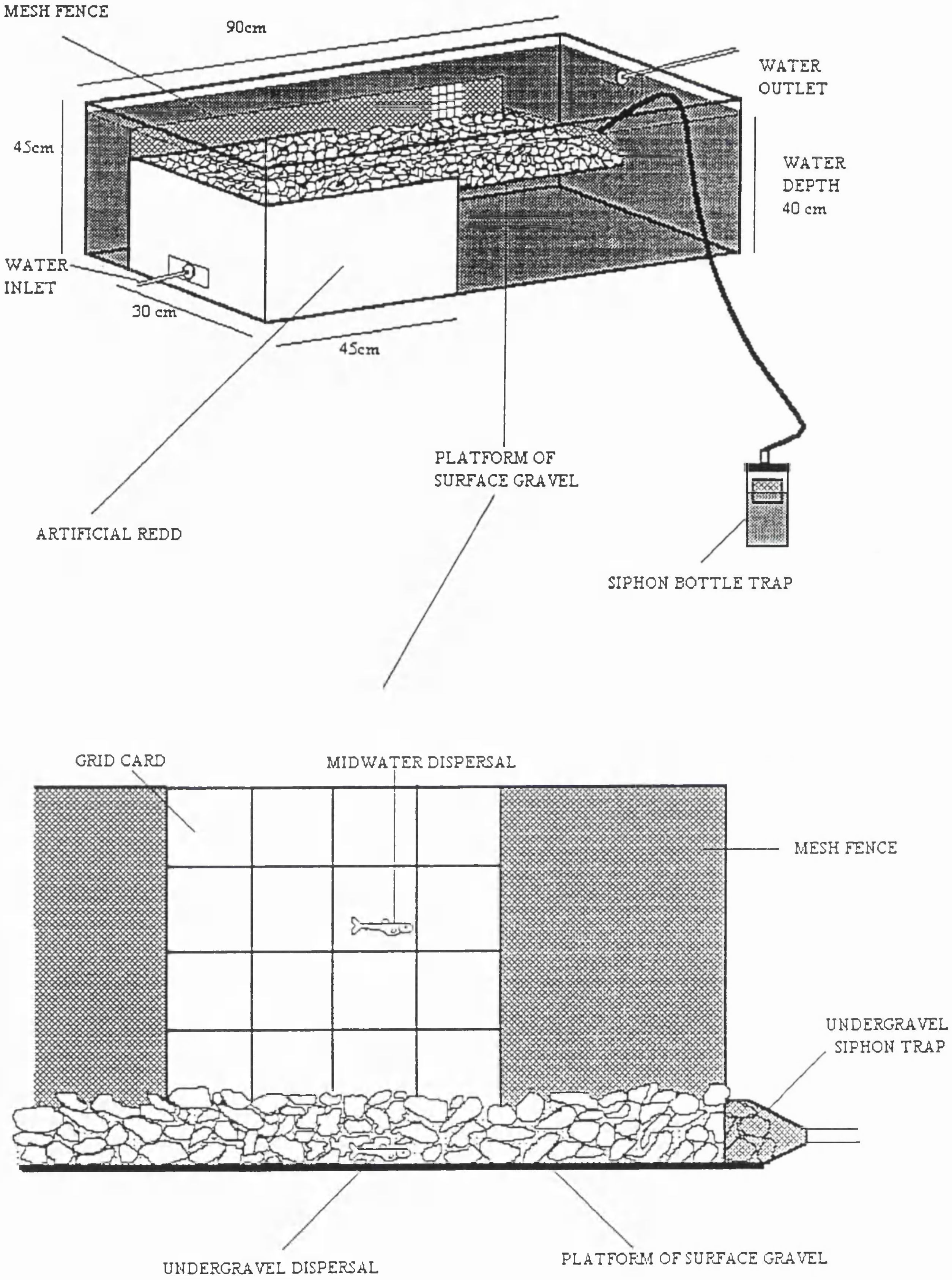

MESH FENCE
90cm
WATER OUTLET
45cm
WATER DEPTH 40 cm
WATER INLET
30 cm
45cm
PLATFORM OF SURFACE GRAVEL
ARTIFICIAL REDD
SIPHON BOTTLE TRAP
GRID CARD
MIDWATER DISPERSAL
MESH FENCE
UNDERGRAVEL SIPHON TRAP
UNDERGRAVEL DISPERSAL
PLATFORM OF SURFACE GRAVEL

Table 3.2 Paired t-tests comparing the size differences between midwater and undergravel moving alevins

		Lux (night)	**Undergravel group**	**Midwater group**	**Difference between groups**		
Artificial Redd	**Variable**		**X ± SE**	**X ± SE**	**df**	**t-test**	**p**
Experimental Redd	Weight (g)	2	0.130 ± 0.001	0.131 ± 0.001	170	0.85	0.395
University 1992	Fork Length (mm)		26.65 ± 0.074	26.52 ± 0.075	165	-1.24	0.217
	Yolk sac (sq mm)		6.21 ± 0.386	7.98 ± 0.441	170	3.04	0.01**
Control Redd	Weight (g)	0	0.129 ± 0.001	0.132 ± 0.000	3.86	3.86	0.001***
University 1992	Fork Length (mm)		26.41 ± 0.104	26.69 ± 0.052	50.5	2.41	0.05*
	Yolk sac (sq mm)		5.01 ± 0.591	5.05 ± 0.282	49.2	0.06	0.953
Experimental Redd	Weight (g)	2.6	0.130 ± 0.002	0.132 ± 0.001	18.6	0.59	0.561
Field Station 1992	Fork Length (mm)		26.76 ± 0.187	26.63 ± 0.066	20.1	-0.65	0.52
	Yolk sac (sq mm)		7.23 ± 1.15	5.01 ± 0.487	22.2	-1.78	0.08
Control Redd	Weight (g)	0	0.168 ± 0.004	0.109 ± 0.002	4.69	-1.66	0.162
Field Station 1992	Fork Length (mm)		25.75 ± 1.031	24.24 ± 0.217	3.27	-1.44	0.239
(High mortality)	Yolk sac (sq mm)		15.5 ± 1.5	16.11 ± 1.08	6.67	0.33	0.748
Experimental Redd	Weight (g)	3	0.123 ± 0.001	0.127 ± 0.001	63.2	4.03	0.001***
University 1993	Fork Length (mm)		24.17 ± 0.102	24.43 ± 0.077	48.5	2.02	0.05*
	Yolk sac (sq mm)		15.46 ± 0.897	15.73 ± 0.419	32.1	0.28	0.785
Control Redd	Weight (g)	0	0.119 ± 0.001	0.125 ± 0.001	25.4	4.01	0.001***
University 1993	Fork Length (mm)		24.11 ± 0.083	24.28 ± 0.072	32.3	1.54	0.134
	Yolk sac (sq mm)		14.57 ± 1.07	14.4 ± 0.52	18.1	-0.15	0.885
Experimental Redd	Weight (g)	0.7	0.123 ± 0.001	0.125 ± 0.001	47.1	3.13	0.01**
University 1993	Fork Length (mm)		24.19 ± 0.111	24.44 ± 0.07	28.1	1.94	0.063
	Yolk sac (sq mm)		14.47 ± 1.14	14.69 ± 0.515	21.5	0.18	0.858

Significantly larger midwater alevins :*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

Table 3.3 The numbers of alevins adopting each method of movement in each artificial redd

					Influence of light (night)	**Difference between trials**
Artificial Redd	**Variable**	**Lux (light nights)**	**Undergravel group**	**Midwater group**	**p†**	**p††**
Experimental Redd	Total number	2	68	105	P >0.05	P < 0.05*
University 1992	Percentage		39.3%	60.7%		
Control Redd	Total number	0	34	140	----	
University 1992	Percentage		19.5%	80.5%		
Experimental Redd	Total number	2.6	18	155	P >0.05	HIGH SILTATION
Field Station 1992	Percentage		10.4%	89.6%		
Control Redd	Total number	0	4	20	----	
Field Station 1992	Percentage		16.6%	83.4%	(High mortality)	
Experimental Redd	Total number	3	23	61	P >0.05	P < 0.05*
University 1993	Percentage		27.3%	72.7%		
Control Redd	Total number	0	16	64		
University 1993	(Percentage)		20%	80%		
Experimental Redd	Total number	0.7	13	38	P >0.05	P > 0.05
University 1993	(Percentage)		25.4%	74.6%		

p† Wilcoxon matched-pairs signed ranks test using the relative proportion of fish moving under the gravel on adjacent nights as matched pairs

p†† Wilcoxon matched-pairs signed ranks test using the relative proportion of fish moving under the gravel on equivalent nights as matched pairs

Significantly more undergravel alevins caught in the experimental redd : *$P < 0.05$; ** $P < 0.01$; ***$P < 0.001$.

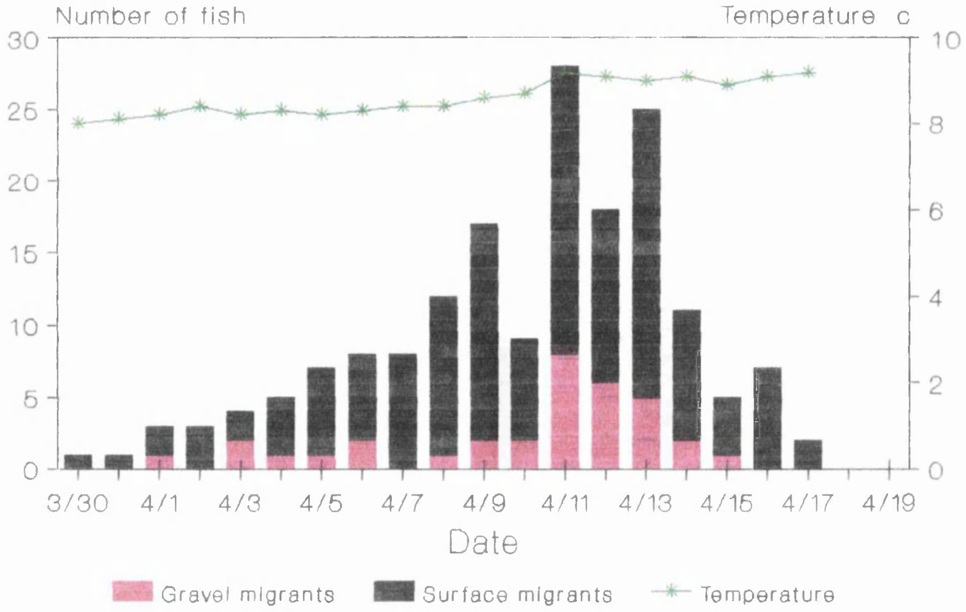
Figure 3.3A

The total number of alevins caught nightly from the control by the two different methods of movement : undergravel (n = 34) and midwater (n = 140) at Glasgow University. Each division on the x-axis is represented as a date, the total experimental period lasted from the 30th of April to the 17th of May 1992. Daily mean temperatures are plotted against the right hand y-axis; the average temperature was 8.6°C +/- 0.19 (2SE).

Figure 3.3B

The total numbers of alevins caught nightly from the experiment by the two different methods of movement : undergravel (n = 68) and midwater (n = 105) at Glasgow University. Each division on the x-axis is represented as a date, the total experimental period lasted from the 30th of April to the 14th of May 1992. Daily mean temperatures are plotted against the right hand y-axis;. average temperature was 8.55°C +/- 0.18 (2SE).

CONTROL REDD



EXPERIMENTAL REDD

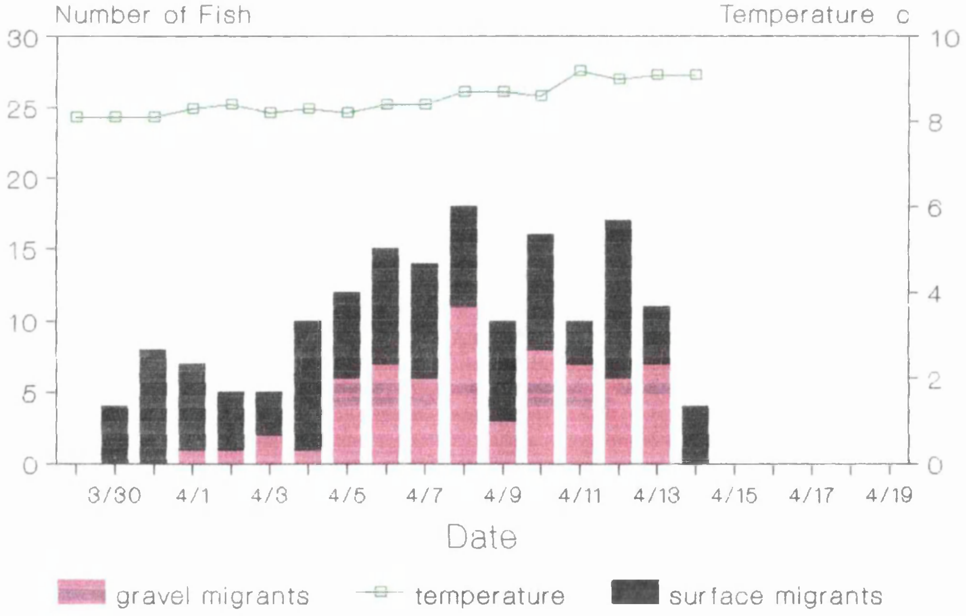


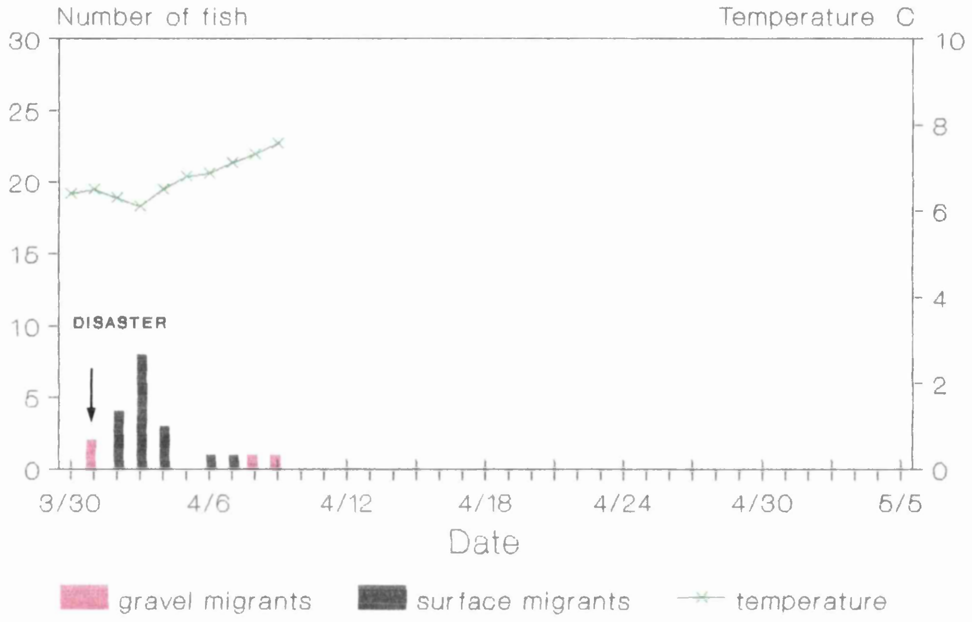
Figure 3.4A

The total numbers of alevins caught nightly from the experiment by the two different methods of movement : undergravel (n = 4) and midwater (n = 20) at the University Field Station. Each division on the x-axis is represented as a date, the total experimental period lasted from the 30th of April to the 9th of May 1992. Daily mean temperatures are plotted against the right hand y-axis;

Figure 3.4B

The total numbers of alevins caught nightly from the control by the two different methods of movement : undergravel (n = 18) and midwater (n = 155) at the University Field Station. Each division on the x-axis is represented as a date, the total experimental period lasted from the 30th of April to the 6th of June 1992. Daily mean temperatures are plotted against the right hand y-axis; the average temperature was 7.22°C +/- 0.26 (2SE).

CONTROL REDD



EXPERIMENTAL REDD

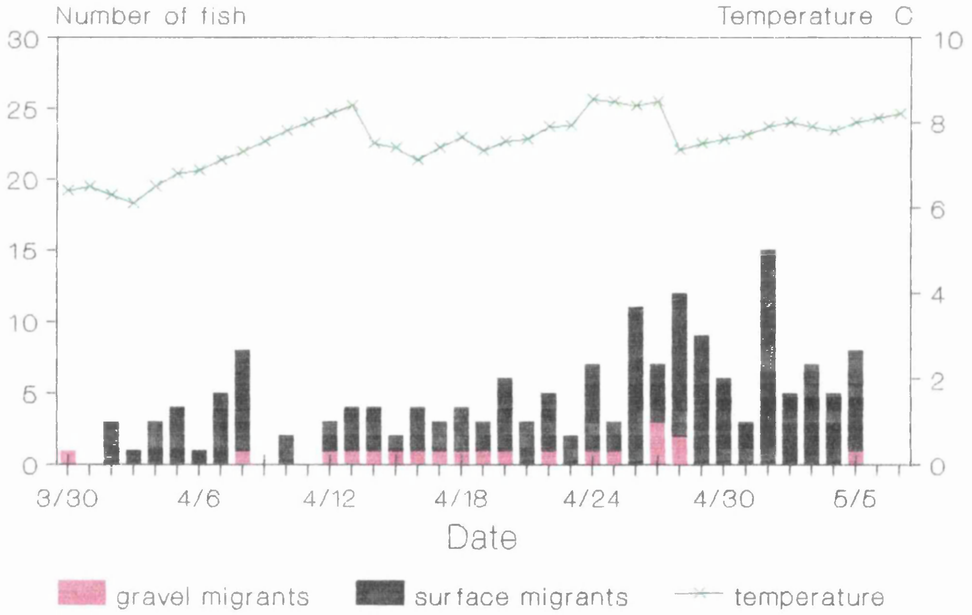


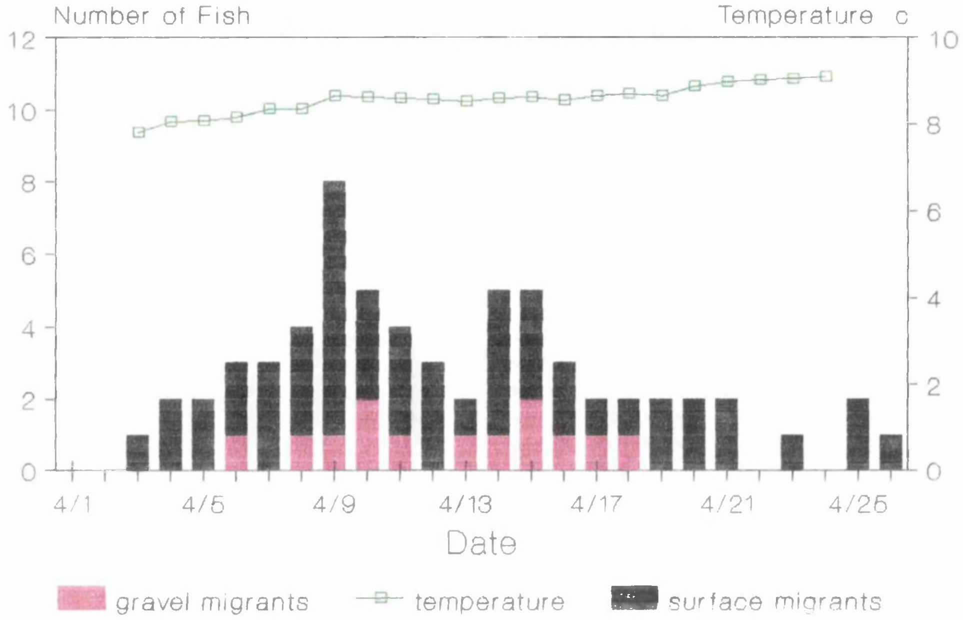
Figure 3.5A

The total numbers of alevins caught nightly from the control by the two different methods of movement: undergravel (n = 13) and midwater (n = 51). Each division on the x-axis is represented as a date, the total experimental period lasted from the 3rd of April to the 26th of April 1993. Daily mean temperatures are plotted against the right hand y-axis; the average temperature was 8.82°C +/- 0.1 (2SE).

Figure 3.5B

The total numbers of alevins caught nightly from the experiment by the two different methods of movement : undergravel (n = 23) and midwater (n = 61). Each division on the x-axis is represented as a date, the total experimental period lasted from the 1st of April to the 23 of April 1993. Daily mean temperatures are plotted against the right hand y-axis; the average temperature was 8.82°C +/- 0.1 (2SE).

CONTROL REDD



EXPERIMENTAL REDD

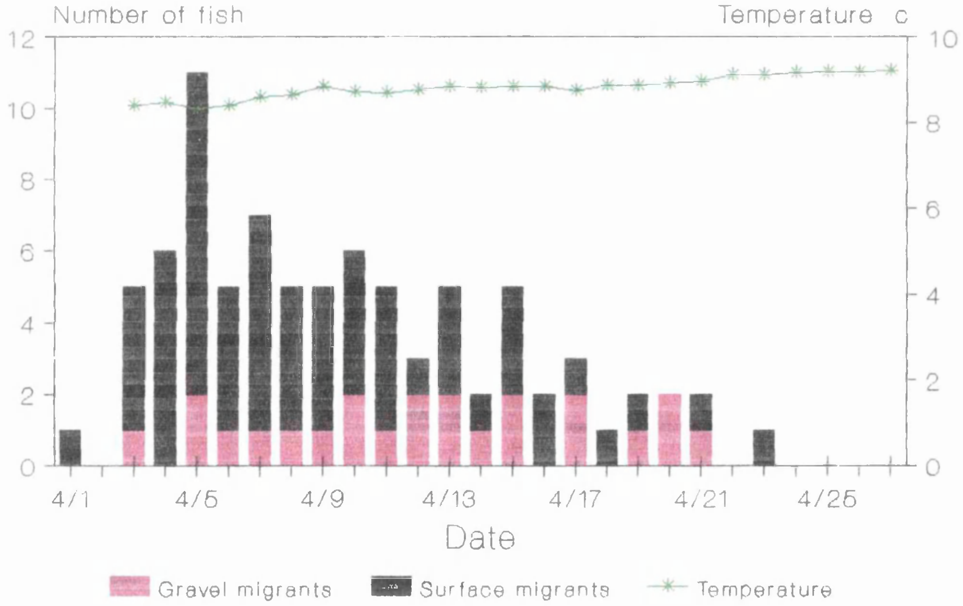


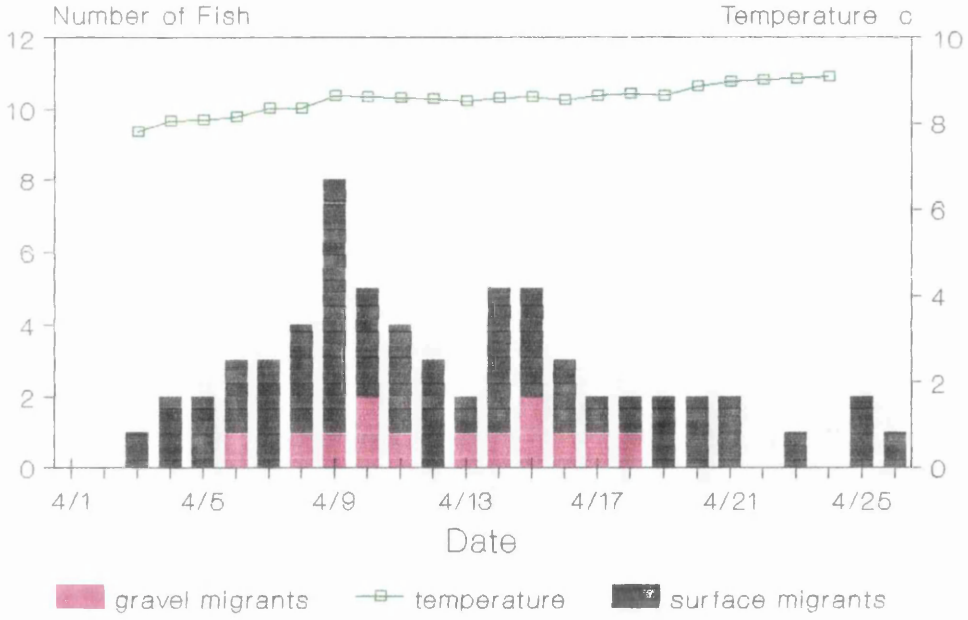
Figure 3.6A

The total numbers of alevins caught nightly from the control by the two different methods of movement : undergravel (n = 13) and midwater (n = 51). Each division on the x-axis is represented as a date, the total experimental period lasted from the 3rd of April to the 26th of April 1993. Daily mean temperatures are plotted against the right hand y-axis; the average temperature was 8.82°C +/- 0.1 (2SE).

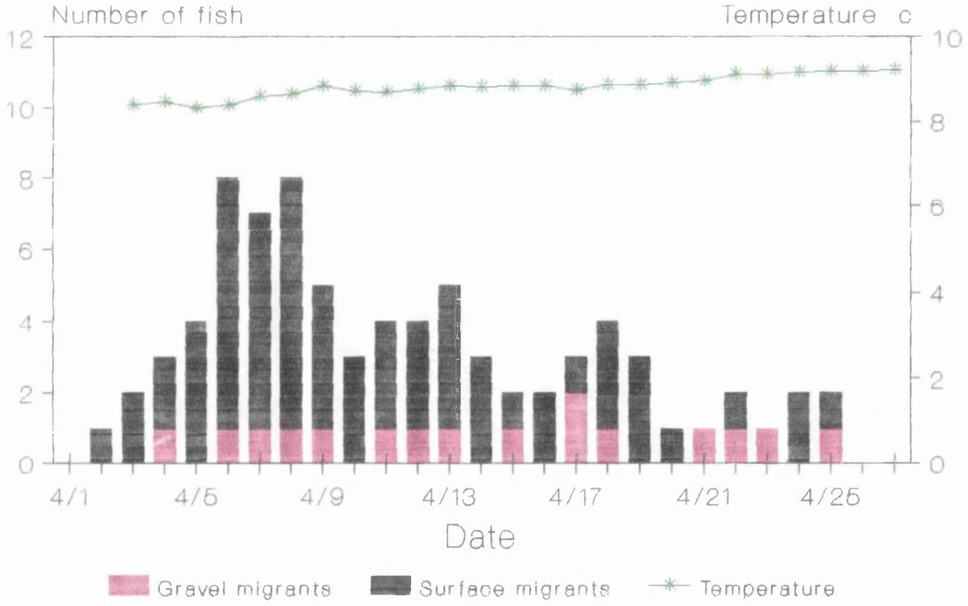
Figure 3.6B

The total numbers of alevins caught nightly from the experiment by the two different methods of movement: undergravel (n = 16) and midwater (n = 64). Each division on the x-axis is represented as a date, the total experimental period lasted from the 2nd of April to the 25th of April 1993. Daily mean temperatures are plotted against the right hand y-axis; the average temperature was 8.82°C +/- 0.1 (2SE).

CONTROL REDD



EXPERIMENTAL REDD



through the gravel on adjacent nights was unrelated to night-time incident light level (Table 3.3) in the experimental artificial redds. A final cross comparison between experiments and their accompanying controls showed that at light levels above two lux there were significantly more undergravel moving alevins caught in the experimental redds than in the control redds (see Table 3.3).

3.3.3 DISCUSSION

In all the redds undergravel movements was an important means of movement away from the artificial redds. However, the silt build up at the field station in the spring of 1992 may have made more alevins move above the surface of the gravel than normal (Table 3.3). Undergravel moving alevins were significantly smaller than the midwater moving fish in all redds, except for those at the field station, by at least one size measurement (Table 3.2). Similar size differences were found in Garcia de Leaniz et al., 1993a field study. This suggests that the gravel medium may act as a size filter. If smaller alevins are able to use the gravel as a medium for movement more effectively than large alevins then it might be possible to manipulate the numbers choosing to move through the gravel simply by changing the size of the interstitial gravel spaces.

In addition, at night time incident light levels above 2 lux, significantly more alevins were caught moving through the gravel, again with the exception of the field station (Figure 3.8). This suggests that an increase in incident light might make alevins more wary of their environment and hence they choose the safest possible method - through the gravel. Further evidence for this comes from the fact that at light levels above 2 lux fish moving in midwater were larger in the experimental redds than in the control redds. Overall, undergravel movements observed shows that alevins are able to respond to the structure of their environment and shows that they have the ability to control the method of their movement.

3.4 THE DEPTH AND DIRECTION OF ALEVIN MOVEMENTS AWAY FROM THE REDD

Garcia de Leaniz et al's (1993b) suggested that Atlantic salmon alevins might be able to move considerable distances (in excess of three metres) through the interstitial spaces within the gravel. The extent and direction of these movements cannot be investigated in the wild because of the difficulties involved in trapping and following alevins moving through the gravel. However, it is possible that artificial redds could be designed in such a way as to follow the movements of alevins within the gravel environment. In the following study a new artificial redd system was designed and set up to investigate the depth and direction of undergravel movements.

3.4.1 MATERIALS & METHODS

In the second year, spring 1992, two artificial redds were set up at the University Field Station, Rowardennan, in a large outdoor flume (see Figure 3.7A). The artificial redd system was designed to offer an alevin a limited number of alternatives on its way to the surface through a long series (4.5m) of interconnecting tubes linking an artificial redd to the surface, in effect giving alevins a limited choice of routes within the gravel. Each redd consisted of a small artificial redd buried 0.5 metre into the gravel but connected to the surface by a grid of clear plastic tubing of 1 cm diameter (Figure 3.7B). These grids were put in position when the flume was dry and then buried under gravel before the flume was filled with water. Fresh water was piped down through the gravel to each artificial redd. Two hundred eyed ova were put into each artificial redd on the 2/3/92 through a second pipe which was then sealed. The 400 eyed ova used in this experiment were the progeny of the same pair of wild grilse from the river Almond as used in Section 2.3.1. The water in the flume flowed over the surface of the redd at a rate of 10cm/s, to simulate a stream current. A standpipe and a constant supply of fresh water to the flume allowed the water depth to be maintained at a constant 15cm above the gravel. Flume water could also enter the embedded grid of tubes by means of 2, mesh-screened filter funnels attached to the upstream tubes (Figure 3.7B). This allowed a flow of water through the grid of tubes in the direction of the current flow.

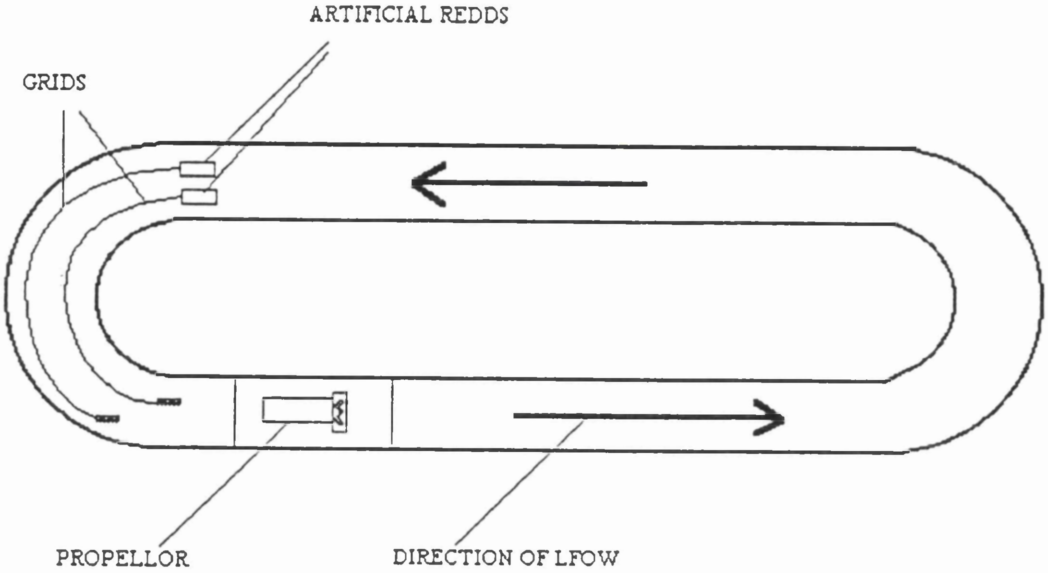
Once an alevin had left its artificial redd it was faced with a choice of moving either downstream or vertically up inside the grid (Figure 3.7B). The alevins that moved downstream had 2 more options of moving upwards through the grid before entering an undergravel siphon trap, 4 metres downstream. Alevins moving up towards the surface of the stream at any point arrived at another junction where they could move along a surface tube either downstream or upstream (Figure 5.7B). In the surface tube, downstream-moving alevins could be caught in three consecutive downstream surface siphon traps. Upstream moving alevins were caught in one surface siphon trap, so alevins were eventually separated out according to the distance and the

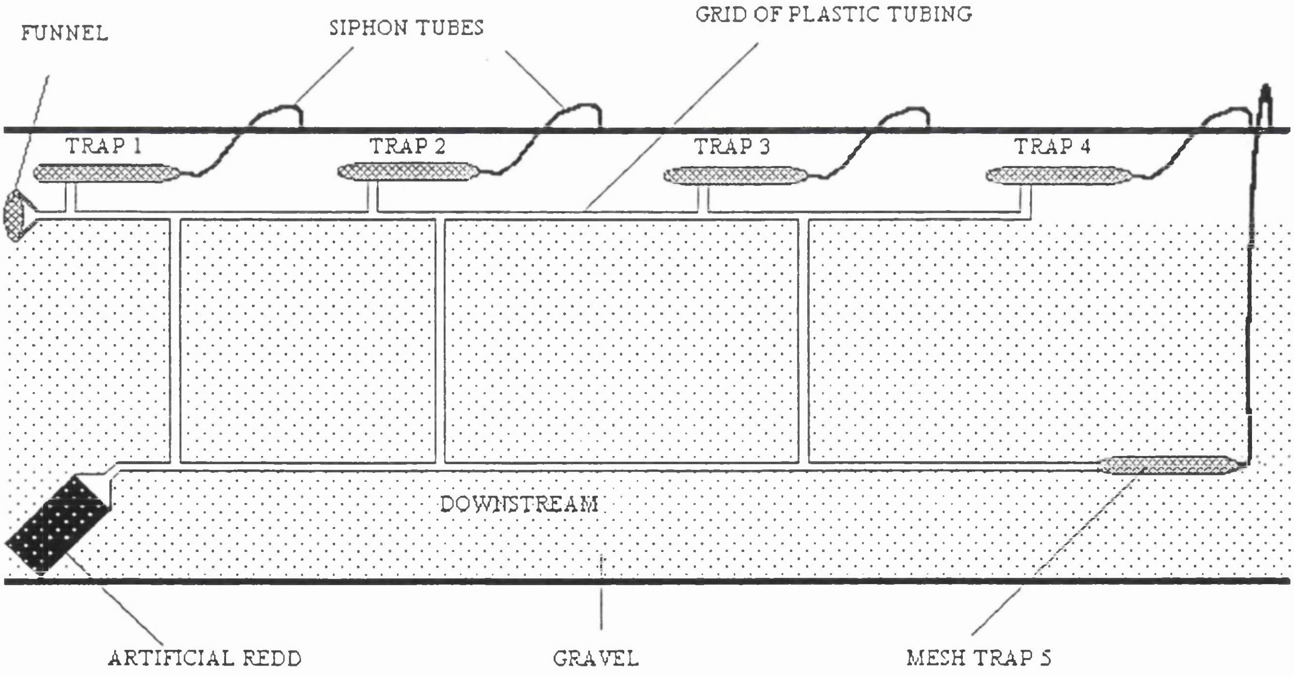
Figure 3.7A

Top view of the flume tank with the two experimental redds inside. Flume Dimensions: Total length = 60cms, depth = 60cms and length c. 15metres. Large arrows represent direction of water flow.

Figure 3.7B

Exploded side view of experimental redds inside flume. Total length of tube grid : 4 m; maximum depth = 0.5 m ; tube diameter 1cm.


ARTIFICIAL REDDS
GRIDS
PROPELLOR
DIRECTION OF LFOW


FUNNEL
SIPHON TUBES
GRID OF PLASTIC TUBING
TRAP 1
TRAP 2
TRAP 3
TRAP 4
DOWNSTREAM
ARTIFICIAL REDD
GRAVEL
MESH TRAP 5

method of movement. In total five submersed sealed netlon mesh siphon traps, in each trial, were used to catch alevins in each redd (Figure 3.7.B). This proved a very effective trapping mechanism which did not inflict any damage to the alevins. The experiment was run under ambient light and temperature conditions until no further alevins were being caught. Collection of nightly moving alevins from each bottle trap took place each morning and all alevins were weighed, measured and assessed for their stage of development (See Section 2.3.1).

3.4.2 RESULTS

At the beginning of May the first few alevins began to move out of the two artificial redds and into the grid of tubing. Figures 3.8A & 3.8B show the total number of alevins caught in each redd during the experimental period. The overall survival of alevins was 69% in experimental redd A and 51% in the experimental redd B. The overall seasonal pattern of movement can be broken down further into the total number of alevins caught at each bottle trap during the course of the experimental period (Figures 3.9A & 3.9B). In experimental redd A the first downstream surface trap (trap 2, black) and the under gravel trap (trap 5, red) accounted for the majority of the variation between the observed and expected catch rates (Table 3.4). In experimental redd B the first downstream surface trap (trap 2, black), the second downstream surface trap (trap 3, green) and the under gravel trap (trap 5, red) accounted for the greater part of the variation between the observed and expected catch rates (see Table 3.5 & 3.6 for partitioned X^2). In neither redd were size differences found between undergravel (trap 5, red) moving alevins and the other trapped alevins (Table 3.7 & 3.8).

3.4.3 DISCUSSION

In both redds there were no size differences between gravel and midwater moving alevins. The lack of a size difference seen in this study might be explained by the 1 cm tube diameter which is clearly larger than most interstitial gravel spaces found running through 4 metres of natural gravel. This clear route would have allowed larger alevins to move with ease downstream through the gravel (i.e. there was no gravel filtering effect, see Section 3.3.3) which may be why so many used it (Table 3.4). Alternatively the high catch rates in the undergravel trap could have been related to the rate of water flow through the tubes but no accurate measurements of internal tube flow rate could be obtained during the course of the experiment. The seasonal pattern of movement from the two redds was very different. This may have been the result of experimental differences or it may reflect the high degree of variability in the timing and method of individual movements whether within the gravel or above it. However, there is one clear similarity in alevin behaviour between the two redds : the majority of alevins appear to choose the safest possible method of movement, through the gravel (trap 5, red).

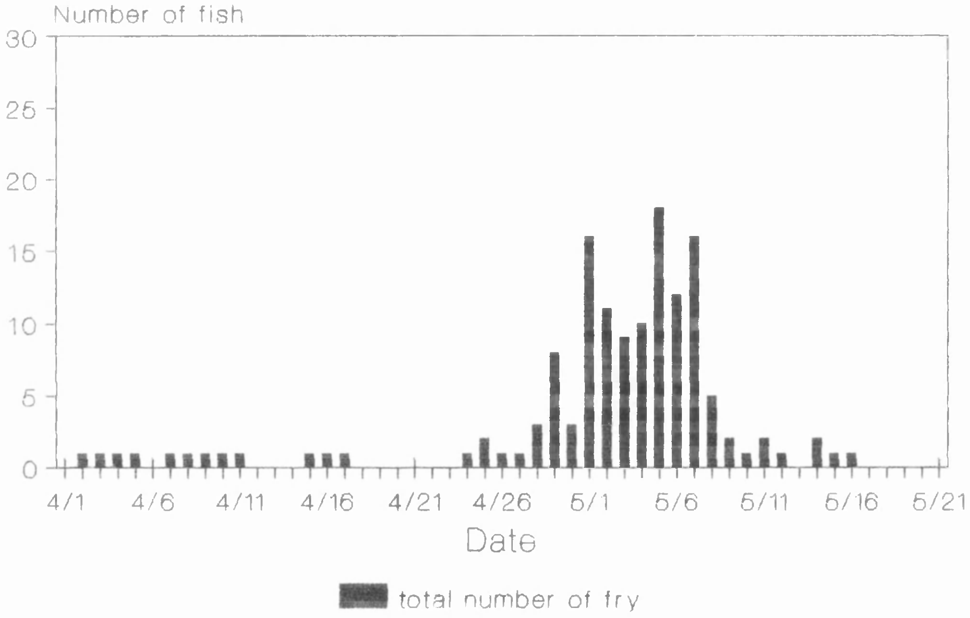
Figure 3.8A

The total numbers of alevins caught nightly from the experimental flume redd A (total n = 138). Each division on the x-axis is represented as a date, the total experimental period lasted from the 2nd of April to the 15th of May 1992.

Figure 3.8B

The total numbers of alevins caught nightly from experimental flume redd B (total n = 102) in all the siphon traps. Each division on the x-axis is represented as a date, the total experimental period lasted from the 6th of April to the 21st of May 1992.

Experimental redd A



Experimental redd B

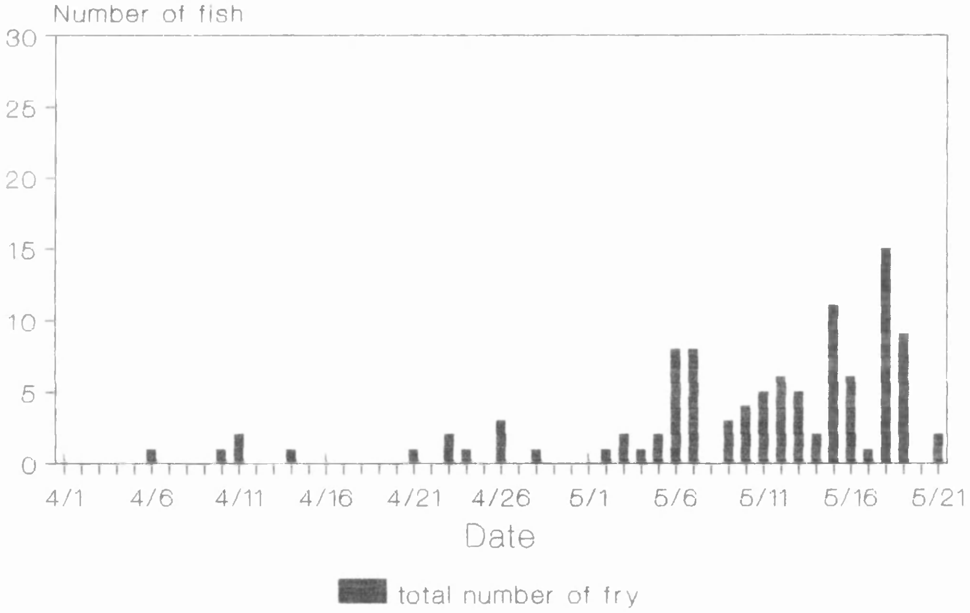


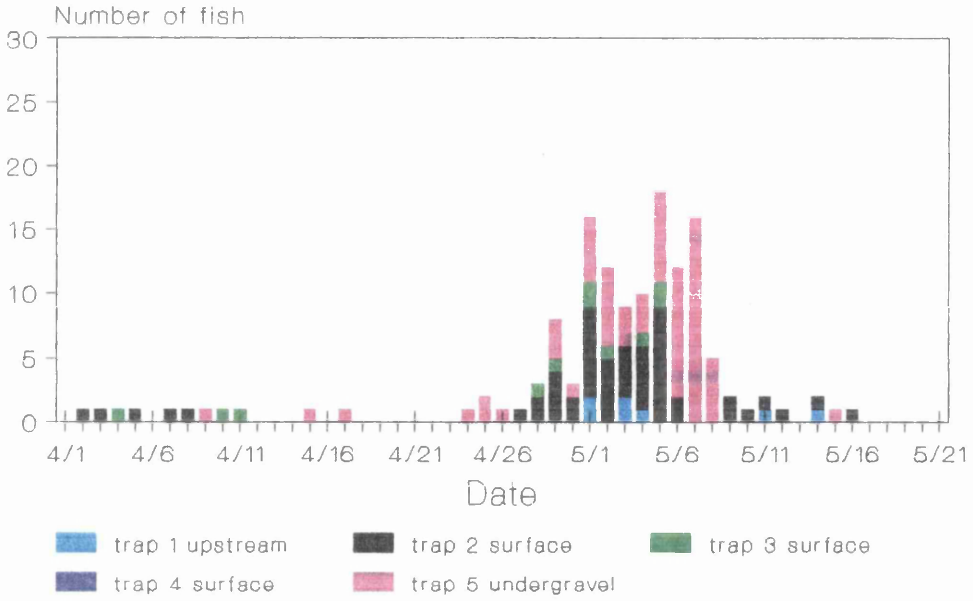
Figure 3.9A

The total numbers of alevins caught nightly from experimental flume redd A in each siphon trap. Each colour represents one siphon trap, 1992. Each trap is plotted in a different colour.

Figure 3.9B

The total numbers of alevins caught nightly from experimental flume redd B in each siphon trap. Each colour represents one siphon trap, 1992. Each trap is plotted in a different colour.

Experimental redd A



Experimental redd B

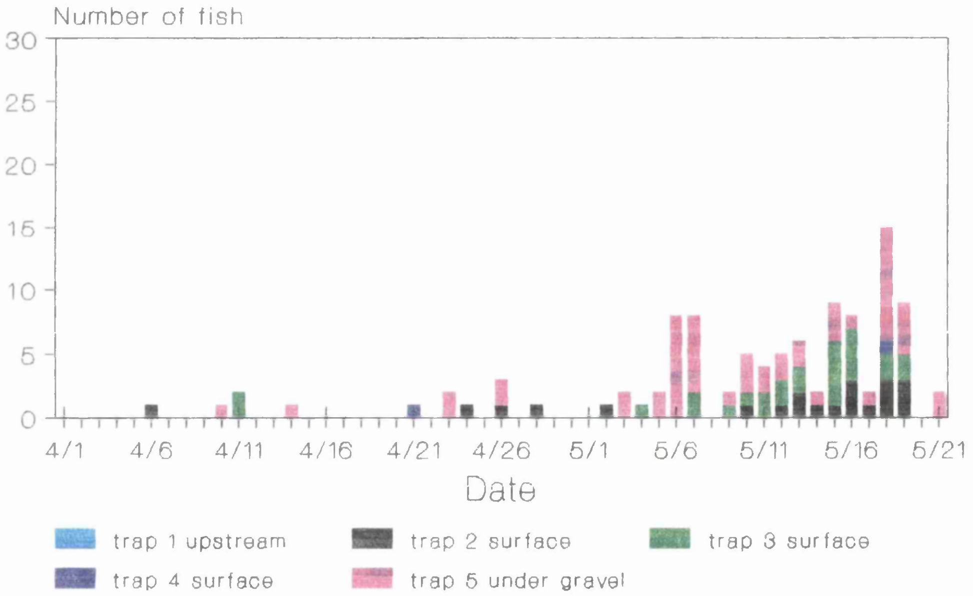


Table 3.4 The numbers of alevins adopting the different methods of movement in each artificial redd

Artificial Redd **Flume tank**	**Variable**	**Trap 1** Upstream	**Trap 2** Downstream	**Trap 3** Downstream	**Trap 4** Downstream	**Trap 5** Undergravel
Experimental Redd A	Total number	7	53	11	0	67
Field Station 1992	Percentage	5	38.4	8	0	48.6
Experimental Redd B	Total number	0	21	26	2	53
Field Station 1992	Percentage	0	20.6	25.5	2	51.9

Table 3.5 Observed and expected numbers of alevins caught at each trap in experimental redd A. Expected values calculated assuming that an alevin had an equal probability of choosing a junction within the system and that it would exit from the first trap it encountered. Single sample chi-square test showed that the observed catch did differ significantly from the expected catch in the experimental redd ($X^2 = 182.6$, d.f. = 4, $P < 0.001$).

SIPHON TRAP	OBSERVED	EXPECTED	Partitioned X^2
Upstream trap (1)	7	34.5	
Downstream trap (2)	53	51.75	13.53***
Downstream trap (3)	11	25.87	1.47
Downstream trap (4)	0	8.63	4.96 *
Undergravel trap (5)	67	17.25	42.3 ***

Significantly more caught than expected: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Table 3.6 Observed and expected numbers of alevins caught at each trap in experimental redd B. Expected values calculated assuming that an alevin had an equal probability of choosing a junction within the system and that it would exit from the first trap it encountered. Single sample chi-square test showed that the observed catch did differ significantly from the expected catch in the experimental redd ($X^2 = 165.8$, d.f. = 9, $P < 0.001$).

SIPHON TRAP	OBSERVED	EXPECTED	Partitioned X^2
Upstream trap (1)	0	25.5	
Downstream trap (2)	21	38.25	8.96**
Downstream trap (3)	26	19.125	12.7***
Downstream trap (4)	2	6.375	0.47
Undergravel trap (5)	53	12.75	36.4 ***

Significantly more caught than expected: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Table 3.7 Mean sizes of alevins caught in experimental redd A at each trap

Variable	**Trap 1** **X ± SE**	**Trap 2** **X ± SE**	**Trap 3** **X ± SE**	**Trap 4** **X ± SE**	**Trap 5** **X ± SE**	**df**	**t-test**	**p**
Weight (g)	0.134 ± 0.023	0.135 ± 0.001	0.134 ± 0.002	-	0.136 ± 0.007	125.7	0.89	0.375
Fork Length (mm)	27.14 ± 0.2827	27.26 ± 0.1137	27.1 ± 0.208	-	27.21 ± 0.06	112.3	-0.14	0.893
Yolk sac (sq mm)	-	1.85 ± 0.7015	3.5 ± 0.7015	-	0.66 ± 0.303	92.5	-1.82	0.072

Paired t-test comparing the size difference between alevins caught in the undergravel trap (trap 5) and all other alevins caught. Significantly larger alevins : * $P < 0.05$; ** $P < 0.01$

Table 3.8 Mean sizes of alevins caught in experimental redd B at each trap

Variable	**Trap 1** **X ± SE**	**Trap 2** **X ± SE**	**Trap 3** **X ± SE**	**Trap 4** **X ± SE**	**Trap 5** **X ± SE**	**df**	**t**	**p**
Weight (g)	-	0.135 ± 0.001	0.133 ± 0.001	-	0.134 ± 0.001	74.5	0.63	0.531
Fork Length (mm)	-	27 ± 0.218	26.75 ± 0.122	-	26.89 ± 0.11	74.7	0.44	0.665
Yolk sac (sq mm)	-	1.73 ± 1.39	1.34 ± 0.943	-	1.28 ± 0.59	69.9	-0.32	0.75

Paired t-test comparing the size difference between alevins caught in the undergravel trap (trap 5) and all other alevins caught. Significantly larger alevins : * $P < 0.05$; ** $P < 0.01$

3.5 GENERAL DISCUSSION

This chapter has indicated that alevins moving away from the redd have the ability to control the speed and method of their movement. This leads to complex dispersal pattern that comprises of undergravel, upstream, midwater and bottom movements. In all three studies alevins were found moving in close association with the gravel, some just above it and others below it. This supports Garcia de Leaniz et al (1993b) findings on undergravel movements. In addition, the film work showed that many of these bottom moving alevins were moving just above the gravel bed and hence only a small sample of bottom moving alevins may have been caught in the undergravel traps. Furthermore, speed of movement differed between midwater and bottom moving alevins, midwater alevins were travelling twice as fast. If we assume that the midwater and bottom moving are mutually exclusive and that the time spent moving by each group is relatively constant then it is possible that midwater moving alevins could move downstream quicker to first feeding sites than their undergravel moving siblings.

Field data however suggests the opposite. Trapping patterns of undergravel moving alevins shows that the average time, 7 days for 50 metres, taken to move between two traps did not significantly differ between marked (midwater moving alevins) and unmarked alevins (undergravel)(Garcia de Leaniz et al., 1993b). This means either that midwater moving alevins are travelling downstream for shorter periods of time each night, and hence the relative rate remains the same, or that the two distinct types of movement are not mutually exclusive with time. This latter explanation is more likely, since in the same field study (Garcia de Leaniz et al., 1993a) it was found that fish at a later stage of development, first feeding fry, were also capable of moving through the gravel.

In 1954 Hoar first suggested that the night-time downstream movement seen in many salmonids, on or around the time of movement away from the redd was a displacement initiated by the loss of all visual orientation at night. Ali(1959a,b; 1961) also used this explanation to link the visual adaptations he found in salmonids with their behaviour during downstream night-time movements. Other authors did not accept this as a complete explanation, because they had observed more intricate behaviours at night such as negative rheotaxis and downstream swimming movements which were usually faster than the current flow (Brannon, 1972; Hartman et al., 1962).

The movements of Atlantic salmon alevins away from the redd are clearly more complex than one might expect (Garcia de Leaniz et al., 1993a). The most striking feature of their behaviour is their reluctance to abandon the gravel of the streambed for considerable distances downstream.

This thigmotactic behaviour persists in freshwater for months or years after initial movements away from the redd (Thorpe, 1982). This behaviour also suggests that the streambed is an important orienting factor during nightly downstream movements of alevins and their ability to literally 'creep' along the streambed may well allow them to avoid rapid midwater displacement. The visual abilities of the Atlantic salmon alevins are considerably more acute than the equivalent stages of the Pacific salmon (Ali, 1961). Hence Atlantic salmon alevins may well be displaced downstream by midwater stream currents, but this does not appear to be linked to disorientation in the dark nor is it linked to a lack of behavioural or physiological adaptations to stream life. The overall movement downstream in the natural environment would therefore appear to be co-ordinated both by tactile and visual stimuli.

The work outlined here demonstrates that it is possible to work in the laboratory on the alevin behaviour seen in the wild. In many ways the use of artificial redds has been overlooked as a method of answering behavioural questions and, hopefully, these last two chapters have outlined a methodology and guide to future research. In addition, it is clear that the gravel medium is a natural safety zone within a stream for small fry just as it is for larger salmon parr seeking shelter (see chapter 7).

CHAPTER 4

DAILY ACTIVITY PATTERNS IN JUVENILE ATLANTIC SALMON AFTER MOVING AWAY FROM THE REDD

4.1 INTRODUCTION

The diel sequence of alternate light and dark imposes a basic 24hr rhythmicity on activity for many living organisms. Three distinct behavioural niches are recognised: *nocturnal* (animals that are active at very low light levels, 0-0.6 lux), *crepuscular* (animals that are active at twilight, 0.6 - 200 lux) and *diurnal* (animals that are active during the daylight, above 200 lux). These classifications are not fixed and some animals switch between these three distinct categories at different times of their lives and in different conditions (Pitcher, 1986).

The juvenile Atlantic salmon's first known inversion of its daily activity rhythm occurs sometime soon after the alevins disperse from the redd when they switch from nocturnalism to diurnalism (Brännäs, 1988). In chapter 2 and chapter 3 only the first night of an alevin's dispersal was investigated. However, in the natural environment alevins remain nocturnally active for a number of nights after initial dispersal from the redd and will continue dispersing at night in either an upstream or downstream direction until they finally switch over to a diurnal lifestyle (Garcia de Leaniz et al., 1993c). After alevins have switched over to a diurnal activity pattern, they can be thought of as fry since it is a clear sign that they are now feeding independently and have minimal resources left in their yolk sac. The switch over to diurnal activity after dispersal from the redd is likely to have profound consequences for survival. If a fry becomes active during the day too early in its development then it may be more vulnerable to predation. On the other hand if a fry becomes active later than the majority of its siblings then it may not be able to establish a good first feeding site. Either way, the timing of this switch is an important developmental change about which very little is known. In other salmonids, nocturnalism can persist for anything between 2 weeks and 2 months (Hoar, 1958). Hence the aim of this study was to investigate the timing of this shift in daily activity under controlled environmental conditions.

4.2 MATERIALS AND METHODS

Groups of newly dispersed alevins were restricted in two small white perspex tanks (70 x 43 cm). One tank was installed at Glasgow University Zoology Department and the other at the University Field Station, Rowardennan. The depth of water inside each tank was 4cm and the flow through of water in the tanks was kept close to 2 l/min for the majority of the experimental period, which ran from April to the end of May 1992. Each tank contained three fish hides (8 x 5 cm) and two circular drains (radius 3cm). An automatic feeder released around 20 pellets every half hour into each tank. A remote CCTV camera positioned above each tank recorded fish behaviour both during the day and the night, and also water temperature, from the screen of a digital thermometer alongside the tank (Figure 4.1.A,B). Night filming was illuminated with an infra-red light synchronised to come on just after the camera was triggered.

Each tank was kept under a constant photoperiod (10L/14D) with the light phase beginning at 07h00 and ending at 17h00. Six video recordings of 10 minutes each were made over each 24hr period, 3 at night and 3 during the day. All fish used in these experiments were from a single sibling group from the River Almond, hatched out in artificial redds kept at 16L/ 8D. A single group of 25 alevins, that had dispersed from the redd on the previous night, were put into the experimental tank at the University Field Station on the 13/4/92. A second group of 28 newly dispersed alevins were collected over a 3 day period (24-26th /4/92) and put into the experimental tank at the Zoology Department on the 28/4/92. This second group of alevins was among the very last to disperse from a single batch of eyed ova hatched out in an artificial redd, whereas the first group of alevins came from the peak of the dispersal period from a different artificial redd. This was done to ensure that two independent groups of dispersing alevins were observed.

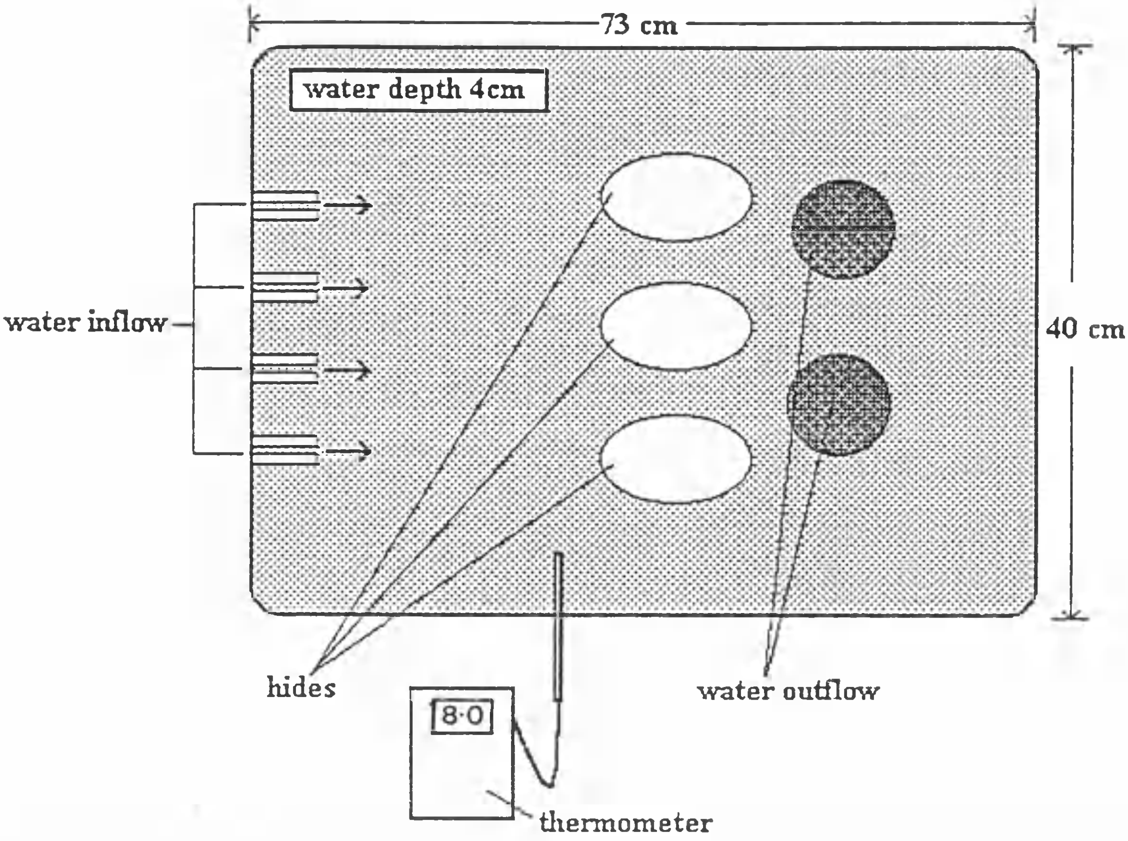
Video tapes were analysed subsequently and the following were recorded for each film session: the total number of fish visible, the number of feeding movements per fish out, the number of aggressive interactions per fish out, distances of feeding movements and water temperature. Flow rate was kept constant except for a two day period at the Field Station where there was a massive increase due to a mains supply problem. Feeding behaviour was defined as a directed movement towards a visible food item. Aggressive behaviour was defined as a fast lunging movement made by one or more fish towards; resulting in evasive action by the recipient.

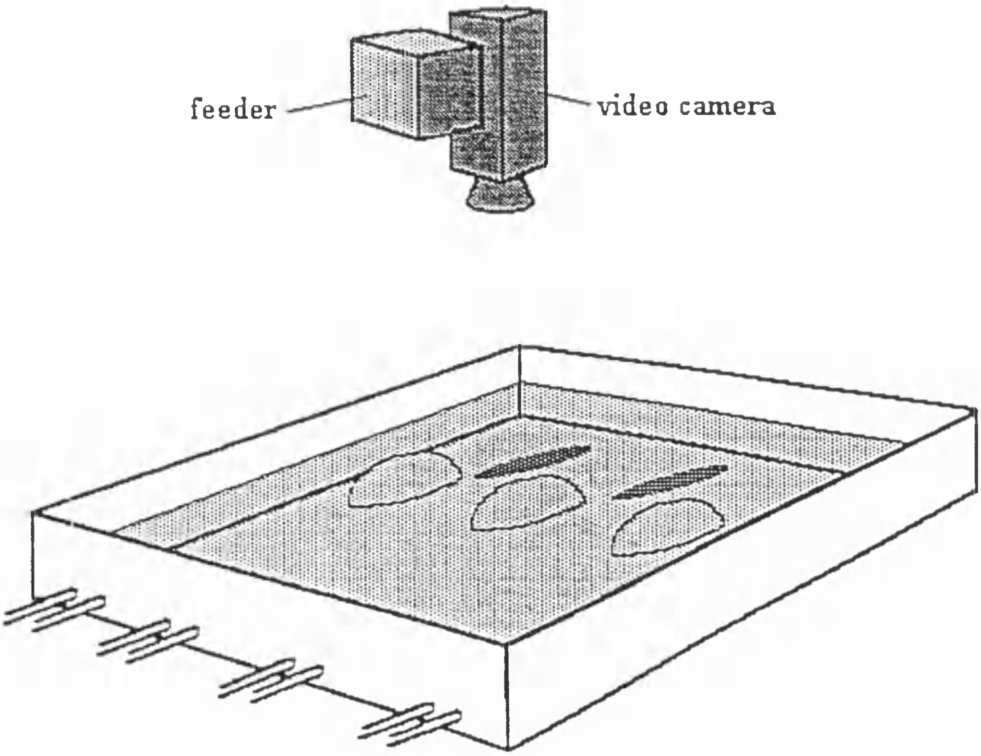
Figure 4.1A

Top view of experimental tank

Figure 4.1B

Overall view of experimental tank with feeder and camera.


73 cm
water depth 4cm
water inflow
40 cm
hides
8·0
water outflow
thermometer


feeder
video camera

The extent to which alevins were nocturnal after entry to the tank was assessed using the nocturnal activity index :

$$NAI = 100 \times E_n / (E_n + E_d)$$

where E_n is the mean number of fish out of hides each night and E_d is the equivalent value for each day. Thus a value of 50 indicates that fish were equally likely to be out of a hide by day or by night, while 100 indicates completely nocturnal activity.

4.3 RESULTS

The two trials differed in two important respects : firstly the alevins studied at the University were at a slightly more advanced stage of development (significant difference in body weights between two groups t-test, $t = 9.87$, D.F = 8, $p < 0.001$), and secondly water temperature at the University was significantly higher than at the Field Station (t-test, $t = 5.78$, D.F = 11, $p < 0.001$). Not surprisingly the mean foraging (t-test, $t = 4.11$, D.F = 4, $p < 0.05$) and aggression levels were significantly higher at the University (t-test, $t = 2.78$, D.F = 5, $p < 0.05$). Hence, the data sets from the two sites were analysed separately.

4.3.1 FIELD STATION

The degree to which fish were nocturnal over the study period is shown in Figure 4.2.A. On days nine and ten there was an accidental increase in flow rate caused by a mains supply problem, which made nearly all the alevins hide by day and by night. A Spearman rank correlation, ignoring these two days of high flow, when very few fish were seen out at all, showed that there was a significant shift away from nocturnalism by the end of the second week ($R_s = -0.7357$, $n = 15$, $p < 0.001$). Similarly there was a significant negative correlation between the nocturnal index and increasing temperature , see Figure 4.2.B (Spearman rank correlation $R_s = -0.7395$, $n = 15$, $p < 0.001$).

To evaluate the most important influence on daytime sheltering behaviour, a stepwise multiple regression was carried out with flow, water temperature and date as independent variables and mean number of fish out during the day as the dependent variable. Overall, flow was the most important predictor of number of fish out of the hides during the day ($F_{1,15} = 19.06$, $R^2 = 0.55$, $p < 0.001$). However if the days of accidental high flow are again excluded from the analysis, only water temperature is a significant predictor of exposure ($F_{1,12} = 7.001$, $R^2 = 0.37$, $p < 0.05$). The activity of

Figure 4.2A

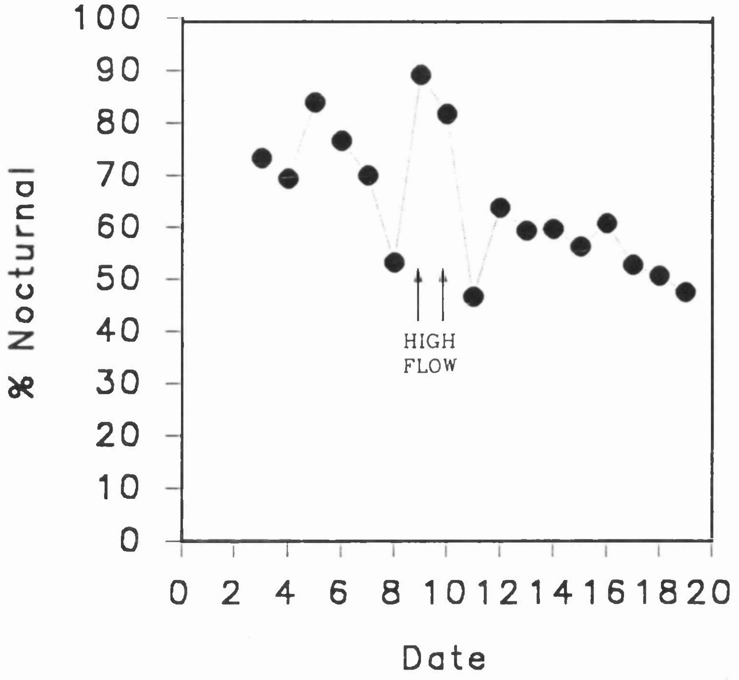
Index of nocturnal activity in newly dispersed Atlantic salmon alevins in relation to date at the Field Station.

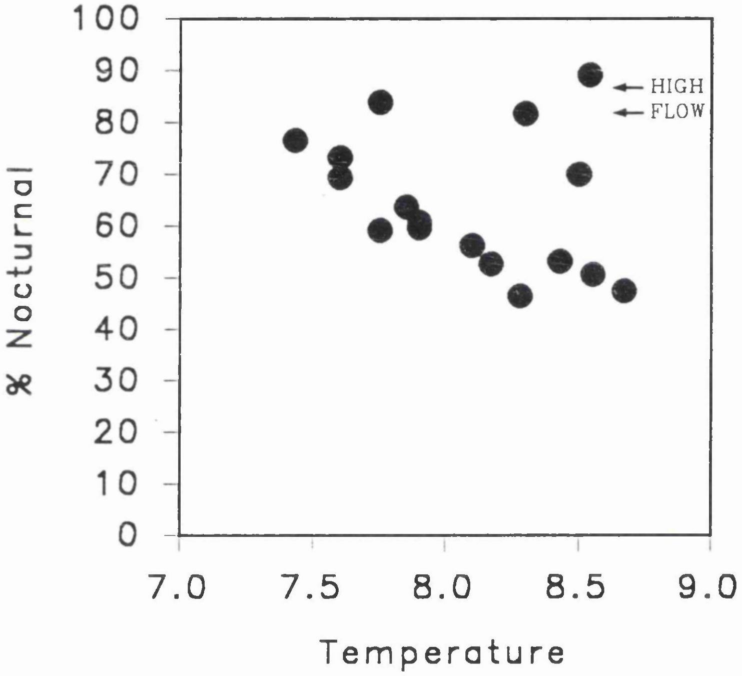
Figure 4.2B

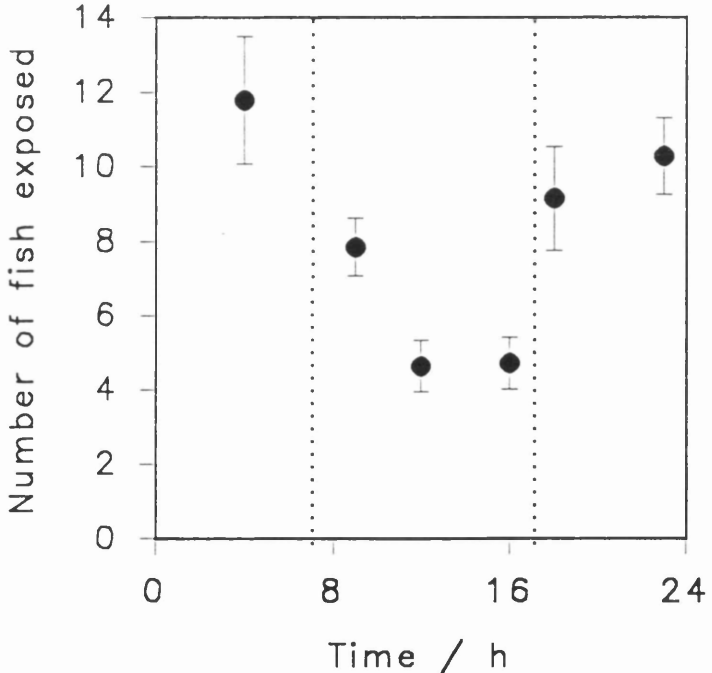
Index of nocturnal activity in newly dispersed Atlantic salmon alevins in relation to water temperature at the Field Station.

Figure 4.2C

The mean number of Atlantic salmon alevins exposed in relation to time of day at the Field Station. The vertical lines indicate the beginning and end of the daylight period. The data are presented as means +/- s.e. for each viewing time : 18h00, 24h00, 4h00, 9h00, 12h00,16h00.


100
90
80
70
60
50
40
30
20
10
0
% Nocturnal
0 2 4 6 8 10 12 14 16 18 20
Date
HIGH
FLOW


100
90
80
70
60
50
40
30
20
10
0
% Nocturnal
7.0 7.5 8.0 8.5 9.0
Temperature
HIGH
FLOW


14
12
10
8
6
4
2
0
Number of fish exposed
0 8 16 24
Time / h

fish varied slightly during the daylight hours, with fewest fish exposed towards the end of the daylight period (ANOVA $F_{2,36} = 6.55$, $p < 0.005$), see Figure 4.2.C

Foraging and aggression levels were very low throughout the filmed experimental period (Figure 4.3A & 4.3B). There was no significant difference between daytime and night-time levels of aggression (t-test, $t = -0.6$, d.f. 46.35, $p > 0.05$) or feeding (t-test, $t = -0.48$, d.f. 63.87, $p > 0.05$)(Figures 4.3.A,B). In addition, there were no significant differences in foraging with respect to time of day (ANOVA, $F_{2,17} = 0.59$, $p > 0.05$) or night (ANOVA, $F_{2,17} = 1.34$, $p > 0.05$) nor were there any differences in aggression with respect to time of day (ANOVA, $F_{2,17} = 1.21$, $p > 0.05$) or night (ANOVA, $F_{2,17} = 0.67$, $p > 0.05$). However the mean foraging distance was significantly lower at night, 2.45 +/- 0.09, than by day, 4.36 +/- 0.13cm, (Wilcoxon $z = -2.55$, $n = 16$, $p < 0.05$).

4.3.2 University

In the University experiment, flow stayed constant but there was a sampling problem. For a six day period (4/5/92 - 9/5/92) there were no nights recorded due to a timeswitch error. However the available data showed that there was no significant shift in diel activity with date (Spearman rank correlation $R_s = 0.0667$, $n = 9$, $p > 0.05$) (Figure 4.4A) or temperature (Spearman rank correlation $R_s = -0.395$, $n = 9$, $p > 0.05$) (Figure 4.4B). In addition, a stepwise multiple regression using the same independent variables as described above showed that there were no significant predictors of daytime sheltering behaviour during the study period. The activity of fish did not vary with time of day (ANOVA $F_{2,39} = 0.07$, $p > 0.05$) or time of night (ANOVA $F_{2,27} = 0.69$, $p > 0.05$) (Figure 4.4C).

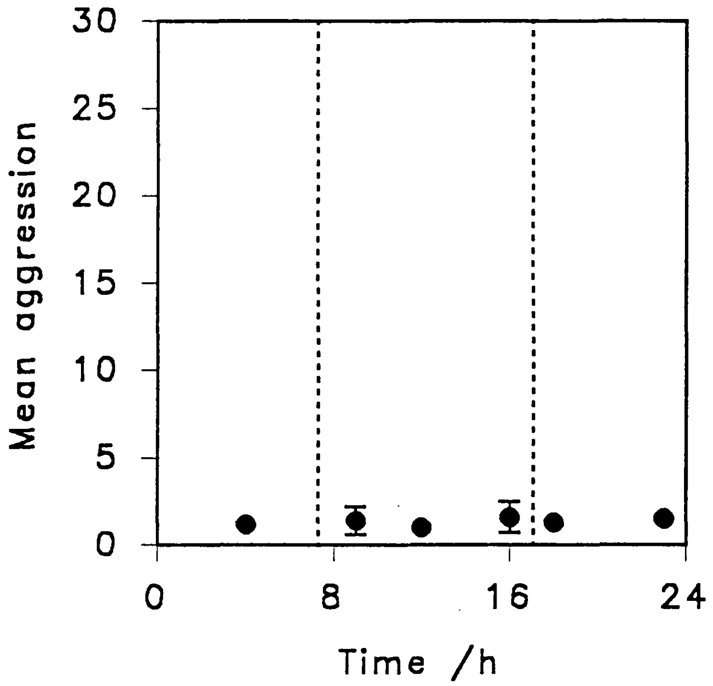
However, there was a significant difference between daytime and night-time levels of aggression and feeding (Figure 4.5.A,B). Rates of feeding were consistently higher during the day (t-test; $t = -3.62$, 19 d.f., $p < 0.005$) and so were rates of aggression (t-test; $t = -3.80$, 24 d.f., $p < 0.01$). In addition, there were no significant differences in foraging with respect to time of day (ANOVA, $F_{2,15} = 0.78$, $p > 0.05$) or night (ANOVA, $F_{2,17} = -0.375$, $p > 0.05$) nor were there any differences in aggression with respect to time of day (ANOVA, $F_{2,15} = 0.85$, $p > 0.05$) or night (ANOVA, $F_{2,17} = 1.05$, $p > 0.05$), (Figures 4.5.A,B).

Figure 4.3A

Variation in the mean number of aggressive interactions with respect to time of day at the Field Station. The thin vertical lines indicate the beginning and end of the daylight period. The data are presented as means +/- s.e. for each viewing time : 20h00, 24h00, 4h00, 10h00, 12h00, 16h00.

Figure 4.3B

Variation in the mean number of feeding attempts with respect to time of day. The thin vertical lines indicate the beginning and end of the daylight period. The data are presented as means +/- s.e. for each viewing time : 20h00, 24h00, 4h00, 10h00, 12h00, 16h00.


30
25
20
15
10
5
0
Mean aggression
0
8
16
24
Time /h

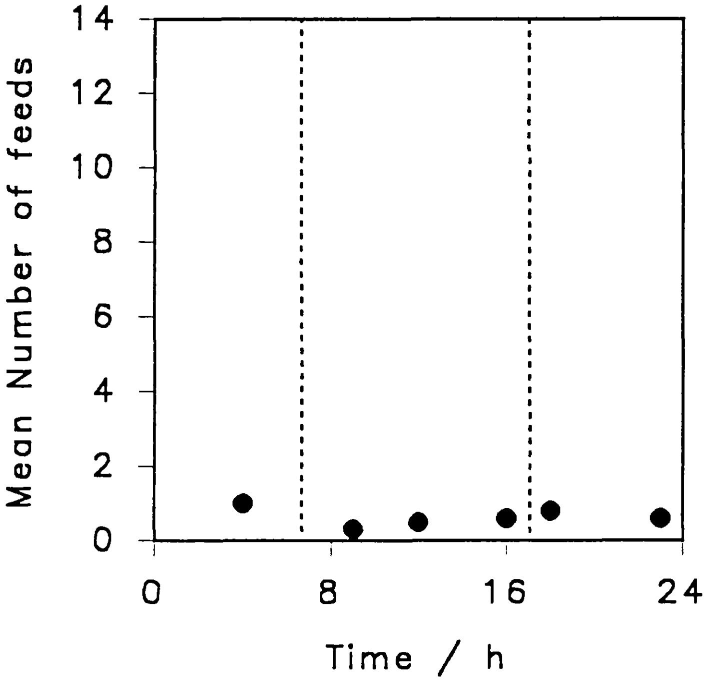

14
12
10
8
6
4
2
0
Mean Number of feeds
0
8
16
24
Time / h

Figure 4.4A

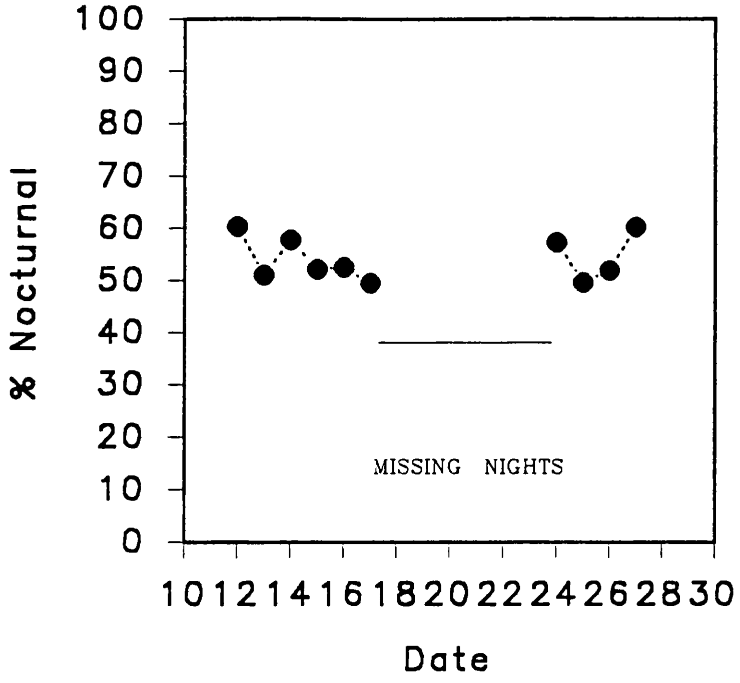
Index of nocturnal activity in newly dispersed Atlantic salmon alevins in relation to date at the University.

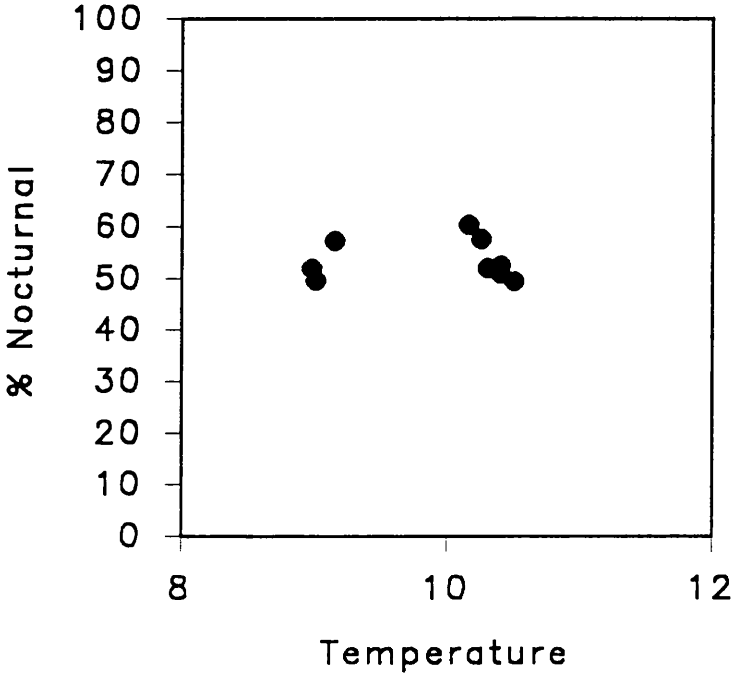
Figure 4.4B

Index of nocturnal activity in newly dispersed Atlantic salmon alevins in relation to water temperature at the University.

Figure 4.4C

The mean number of Atlantic salmon alevins exposed in relation to time of day at the University. The other vertical lines indicate the beginning and end of the daylight period. The data are presented as means +/- s.e. for each viewing time : 18h00, 24h00, 4h00, 9h00, 12h00,16h00.


% Nocturnal
100
90
80
70
60
50
40
30
20
10
0
MISSING NIGHTS
10
12
14
16
18
20
22
24
26
28
30
Date


% Nocturnal
100
90
80
70
60
50
40
30
20
10
0
8
10
12
Temperature

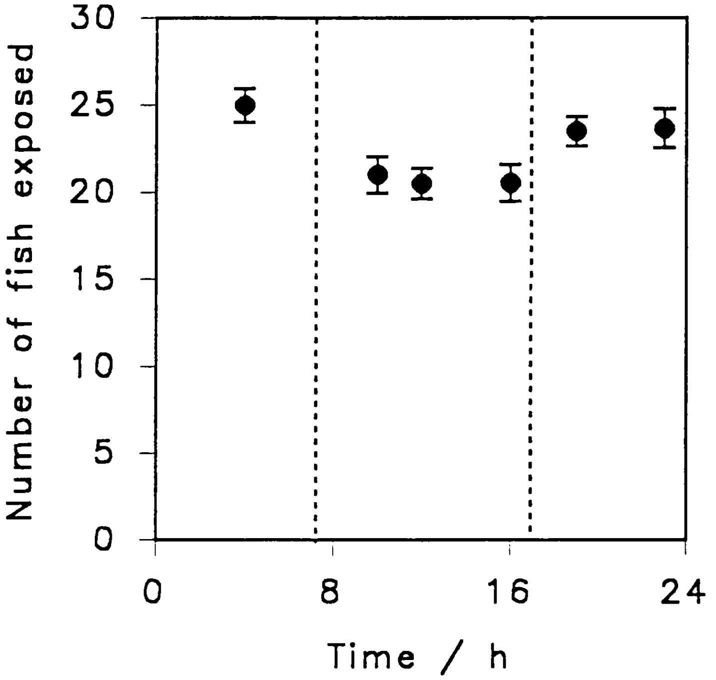
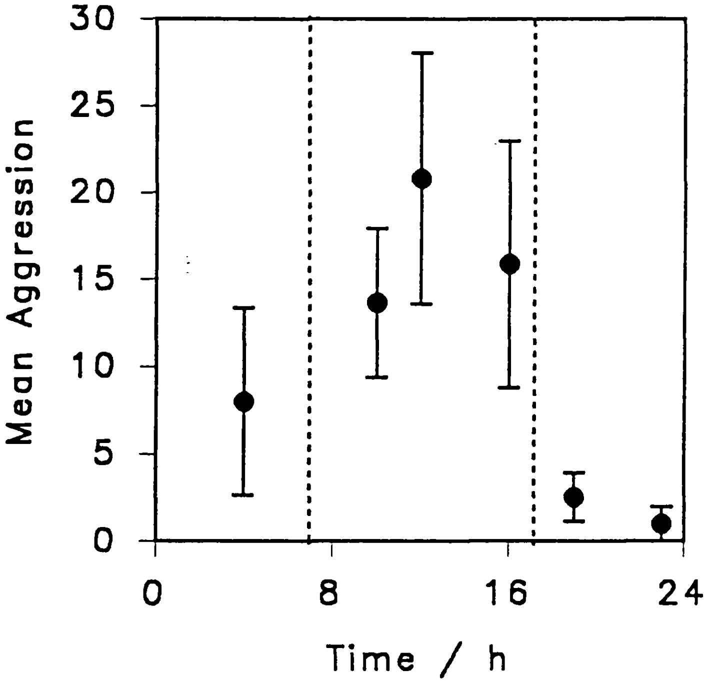

Number of fish exposed
30
25
20
15
10
5
0
0
8
16
24
Time / h

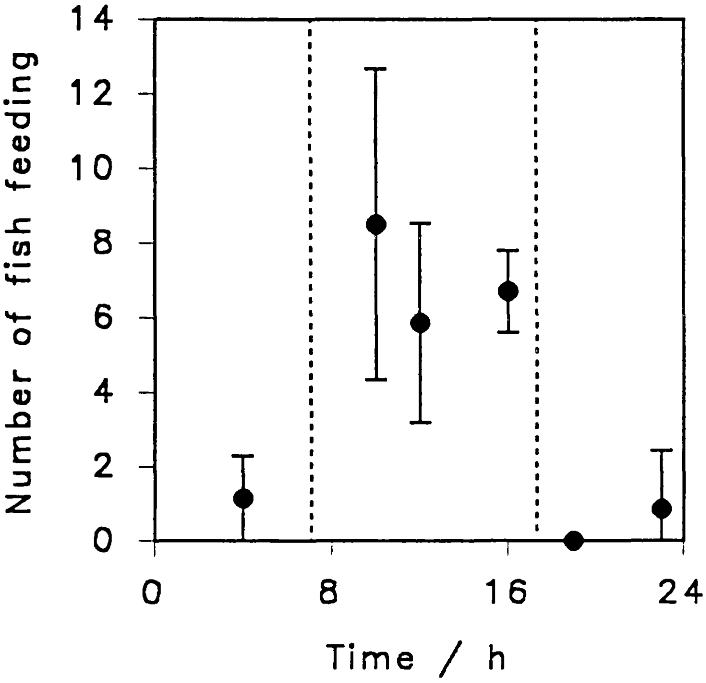
Figure 4.5A

Variation in the mean number of aggressive interactions with respect to time of day at the University. The thin vertical lines indicate the beginning and end of the daylight period. The data are presented as means +/- s.e. for each viewing time : 20h00, 24h00, 4h00, 10h00, 12h00, 16h00.

Figure 4.5B

Variation in the mean number of feeding attempts with respect to time of day. The thin vertical lines indicate the beginning and end of the daylight period. The data are presented as means +/- s.e. for each viewing time : 20h00, 24h00, 4h00, 10h00, 12h00, 16h00.


Mean Aggression
30
25
20
15
10
5
0
0
8
16
24
Time / h


Number of fish feeding
14
12
10
8
6
4
2
0
0
8
16
24
Time / h

4.4. DISCUSSION

At the Field Station there was a gradual shift away from nocturnalism over the first two weeks towards a 50% level in the nocturnal activity index (i.e. the same number of fish were seen out during the day as the night). At the University the same number of fish were seen out during the day as the night from the beginning to the end of the sample period, again a 50 % equilibrium level in the nocturnal index. This latter result, where no clear shift in activity was observed, indicates that the nocturnal/diurnal shift seen after alevin dispersal might be determined by either the experimental conditions or by the later developmental stage of these fry.

If the University results were linked to an environmental influence then the clearest difference in conditions between the work carried out at the University and that at the Field Station was the higher water temperature. Recent work on Atlantic salmon, see Chapter 5, has shown that temperature can cause shifts in nocturnal activity (Fraser et al., 1993). Alternatively the University results might have been linked to developmental stage. In a number of fish species, including Atlantic salmon, it has been shown that stage of development is a key factor in determining the phasing of activity (Hoar, 1958; Manteifel et al., 1978). Hence both these effects could have independently led to the lack of nocturnal activity in the alevins at the University. In addition these two explanations are inextricably linked with fish developing faster at higher temperatures and so in the present experiments it is impossible to say whether the fry at the University exhibited no change in nocturnal activity because they were kept at higher temperatures or because they were slightly more developed. Conversely, the fish at the Field Station may have exhibited nocturnalism to begin with because of the lower temperatures or because they were less well developed. Therefore no inference as to the controlling influence behind this behaviour can be made until it is established whether the shift away from nocturnalism is a developmental change in retinal photosensitivity or a temperature influence on phototaxis. Isolating either one of these factors would be difficult, considering how closely development time is correlated with temperature (Brännäs, 1988).

Brännäs (1988) found that at lower temperatures initial dispersal from an artificial redd (i.e. the first movement away) was predominantly nocturnal whilst at higher temperatures (14.5°C) the majority of alevins dispersed during the day. This advanced diurnal development was put down to quicker development of eye pigmentation at higher temperatures (Hayes et al., 1953) and therefore in 1988 Brännäs concluded that: " the switch from nocturnalism to diurnalism at high temperatures could be related to an induced asynchrony of development". The alternative to this explanation is that the switch to diurnalism seen at high temperatures may be a temperature-dependent one, i.e. unrelated to development, similar to that seen in later life (Fraser et al., 1993). Hence nocturnalism at this dispersal stage clearly could be caused by a number of factors, but whatever the underlying reasons implications for the behavioural ecology of juvenile Atlantic salmon still remain the same.

Nocturnal activity is a common characteristic of the downstream migrating salmonid (Hoar, 1958). Therefore it is logical to assume that a decrease in nocturnal activity is a sign that the end of the movement period is approaching. In the Field Station experiment, activity was high at night during the first two weeks. Alevins would suddenly swim towards the surface or around the tank, often colliding into other fish. During the day most alevins would hide inside the small shelters, but this behaviour slowly changed towards day activity by the end of the first week. If these fish had been in a stream, the distance they travelled away from the redd might therefore have been related to the extent of their nocturnalism. The first alevins to disperse from a redd are at an earlier developmental stage (Garcia de Leaniz et al., 1993a) and will experience lower temperature during their dispersal than later dispersing siblings. These two variables are in some way connected to the change in nocturnal activity. Hence the number of nights early dispersing alevins are active should be greater than the number of nights late dispersing alevins are active and so the early dispersing alevins might be expected to move a greater distance from the redd than late dispersing alevins, as long as the speed of night dispersal is the same.

The only behavioural field study that has managed to follow the fate of early and late dispersing alevins has shown that early dispersing alevins took longer than their late dispersing siblings to travel the first 20m downstream from the redd, but sustained lower mortalities both during initial dispersal and over subsequent months (Huntingford et al., in prep). Unfortunately Huntingford's study could not document fully the distribution in the stream of late and early dispersing alevins after dispersal due to low sample sizes, so further work is required to establish the final stream position from the redd of early and late dispersing alevins. However the difference in the speed of dispersal over the first 20 metres between early and late dispersing fry indicates that there may be no difference in the overall distance covered by the two groups.

CHAPTER 5

THE INFLUENCE OF TEMPERATURE ON THE SHELTERING BEHAVIOUR OF JUVENILE ATLANTIC SALMON

5.1 INTRODUCTION

Most animals can be classified as being either diurnal, nocturnal or crepuscular, since adaptations for activity at one light level tend to reduce efficiency at another. Juvenile Atlantic salmon (Salmo salar) have generally been considered diurnal foragers (Hoar, 1942). They feed by darting from a vantage point to intercept items passing in the current (Thorpe & Wankowski, 1979; Wankowski, 1977,1981). From spring to autumn they hold station just above or on the substrate and forage during daylight mainly on invertebrate drift (Kalleberg, 1958). However, a noticeable change in behaviour and growth occurs during the winter, in both tank reared populations (Thorpe, 1977) and in natural populations (Cunjak & Power, 1987; Garcia de Leaniz, 1990).

Daytime observations of juvenile Atlantic salmon (Salmo salar) in the wild have shown that, in common with other salmonids, they have an enhanced preference for areas of overhead cover and make increasing use of sheltered positions in the gravel in winter (Hartman, 1963; Gibson, 1978; Rimmer et al., 1983, 84; Cunjak, 1988a; Heggenes & Saltveit, 1990; Garcia de Leaniz, 1990). This has led to the assumption that the fish are largely dormant at this time of year (Gardiner & Geddes, 1980; Rimmer and Paim, 1989; Veselov & Shustov, 1991; Cunjak, 1988b). However, salmon still feed during winter (Cunjak & Power, 1987,1986), even though drift food is less abundant (Chapman & Bjornn, 1969), and there is a reduction in their ability to capture drifting prey (Rimmer et al., 1985). This slight feeding activity was thought to occur around dawn and dusk, but a recent field survey carried out at night revealed that over-wintering brown trout (Salmo trutta) use streambed refuges during the day, emerging to feed once darkness has fallen (Heggenes et al., 1993).

In a population of fish reared in a tank the winter changes in behaviour are similar to those seen in the streams. Fish show increased preference for cover and a decreased ability to hold station in fast currents as well as behavioural differences associated with life history strategy as explained in Section 5.2.1 (Metcalfe et al., 1986,89,90). Growth and appetite changes are also found and these too are interlinked with life history strategy, these are explained in Section 5.2.1 (Higgins & Talbot, 1985; Huntingford et al., 1988a,b). However, long term monitoring of swimming behaviour of juvenile salmon in tanks has also revealed a tendency towards nocturnal activity in winter (Eriksson, 1978)

Therefore in both natural and tank populations of juvenile Atlantic salmon nocturnal activity has now been recorded in the winter and yet in neither case has the foraging behaviour of the fish been recorded, nor have possible controlling influences (e.g. temperature dependency or circannually timed behaviour) been determined. The following chapter describes two experiments carried out to investigate the diel behaviour of tank reared juvenile Atlantic salmon under controlled laboratory conditions. Each experiment involves manipulation of water temperature under a constant photoperiod on different age groups of fish and at different times of year. This was done to establish whether there were any underlying annual influences behind the reported seasonal change to nocturnalism.

5.2 SHELTERING BEHAVIOUR IN JUVENILE SALMON PARR IN RELATION TO WATER TEMPERATURE AND TIME OF DAY : (1) WINTER

5.2.1 INTRODUCTION

In tank reared populations of salmon, the most apparent changes in behaviour and growth during winter are associated with life history strategy. These can first be seen in the gradual separation of an initially unimodal size frequency distribution of a single sibling population which slowly separates into a bimodal one during autumn (i.e. a group of large fish and a group of small fish) (Thorpe, 1977; Thorpe & Morgan, 1978). The group of larger fish in this distribution, the upper modal group (UMG), continue to feed and grow during winter in order to smolt and go to sea in the following spring. The group of smaller fish, the lower modal group (LMG), have a reduced appetite and stop growing for the winter period and do not smolt the following spring (Thorpe, 1977, 1989b; Metcalfe et al., 1986). Furthermore LMG fish are less able to establish and maintain dominance status within a social group, which leads to a reduced ability to compete for food (Metcalfe et al., 1989). In comparison upper modal group fish are more likely to take risks to obtain food and are better at obtaining food particles during late Autumn (Metcalfe et al., 1989).

However it is not clear from the above studies how the behaviour of tank-reared salmon adopting different life history strategies changes between day and night, nor is it known what possible controlling influences may determine diel behaviour. One possibility is that a switch to nocturnalism represents a direct response to environmental temperature, another is that it represents a circannually timed behaviour. The present study therefore investigated the influence of water temperature on the diel activity patterns of hatchery reared juvenile Atlantic salmon from both the upper and lower modal groups during their first winter.

5.2.2 MATERIALS & METHODS

All fish used in the experiment were the progeny of a single pairing of wild Atlantic salmon from the River Almond, which had been reared on commercial pellets (EWOS Baker salmon starter, size 0-3) under routine hatchery conditions before the start of the experiment. Twenty juveniles from the upper modal group (total length 88.2±0.73cm ± SE) and twenty from the lower modal group (total length 66.5±0.24cm ± SE), were obtained from the Almondbank hatchery, Perthshire. At the start of the experiment all the fish were seven months old. The 20 fish from both groups were placed together into the test tank situated at the University Field Station, Rowardennan, on the 22nd of November 1991 and taken out again 4 months later on the 16th of March.

The test tank was a 1m radial tank made from glass-fibre reinforced polyester resin with a circular central base, 0.28 m^2, coloured white (Figure 5.1)(Thorpe & Wankowski, 1979). Surrounding the central feeding base was a netlon mesh fence (0.4cm mesh). Any fish could enter or leave this central feeding arena and seek refuge in two shelters outside the perimeter fence .

Food and water entered the tank through a central pipe. The end of this inflow pipe was positioned near the centre and close to the base of the radial tank. This allowed the water flow to be deflected radially along the bottom of the tank, through the perimeter fence and out through the drain, as indicated in Figure 5.1. The water level was kept at a depth of 13-15cm by a standpipe. Bottom current velocity was 29.01 ± 2.12 (± SE) cm's s^{-1} (i.e. 0.33 bls^{-1} for the UMG and 0.436 bls^{-1} for the LMG) which is less than the critical holding velocity of the juvenile salmon (Rimmer et al., 1985) and surface velocity was 0.36 ± 0.05 cm s^{-1}. An automatic feeder dispensed 4-8 commercial food pellets of the recommended size (BP Nutrition) every 10 min into the water current, uneaten food being quickly carried into the outflow drains.

The tank contained two opaque perspex box shelters (8x8x20 cm), positioned in the peripheral drain channel. Each box shelter had a narrow entrance tunnel (3cm) that penetrated through the netlon fence, allowing fish to leave the central feeding arena and take refuge. The narrow entrance tunnel prevented food from entering the shelters, so salmon could only feed when in the central arena. The salmon thus had a choice of being exposed in the water column where they had access to food or of being concealed in a refuge without food.

The tank was in a light-proof cabinet, daylight being simulated by fluorescent lighting providing 133.2 ± 6.8 lux at the water surface with a spectrum of 560-580nm. The photoperiod was simulated as natural for a month before data collection, and then held constant at 9h light : 15h dark; lights came on at 08h00 and were switched off at 17h00. Water temperature was ambient, falling from 9.4°C to 7.5°C (mean daily values) during the first 28 days of data collection. Over the following 88 days temperature was manipulated in steps between 2 and 18.5°C (the typical annual range experienced by juvenile salmon in Scotland) in a random sequence. On all occasions except one, when the temperature was altered by almost 10°C (16.8°C to 7.3°C), the temperature was adjusted by less than 3°C between days; the results (see next section) showed that the fish adjusted their diel activity patterns immediately to the new temperature, even on the one extreme occasion .

A CCTV camera mounted above the tank recorded for 10 min at eight times: (02h30, 06h30, 08h30, 11h30, 13h30, 16h30, 18h30 and 22h30) over the 24 hr period . There were thus four samples of film in daylight and four in darkness, and each included the response of fish to one food delivery. When activated, the feeder produced a noise that was recorded on the video tapes. This allowed the responses of fish to the arrival of food to be monitored. Infrared lights illuminated the tank for night-time filming, the lights being switched on 10 min before each filming session and off 10 min afterwards. The lights also provided a slight amount of light (0.04-0.06 lux, equivalent to starlight) visible to the fish (Ali, 1961). The effect of the infrared lights on the behaviour of the fish was tested by varying the times at which the lights came on randomly; there was no evidence that the fish either anticipated the usual timing of illumination or responded to it by entering or leaving the refuges. The tank was undisturbed except during daily cleaning, which usually occurred between 09h30 and 10h30 and always at least one hour before any filming session. Daily cleaning took less than ten minutes and seemed to have a minimal effect on the fish. They had experienced this cleaning routine since the fry stage and so had habituated to it over a 6 month period. The video tapes were analysed to provide information on the number of fish that were outside the refuges in each 10 min sample, the number that attempted to feed within 1 min of food delivery, and the number of aggressive interactions (defined as a chase, lunge or bite at a neighbouring fish).

Figure 5.1 Experimental radial flow tank

Top = Side view

Bottom = Top view

1 = White tank base

2 = Tank side

3 = Netlon fence

4 = Central water inlet

5 = Circumferential drain

6 = Standpipe

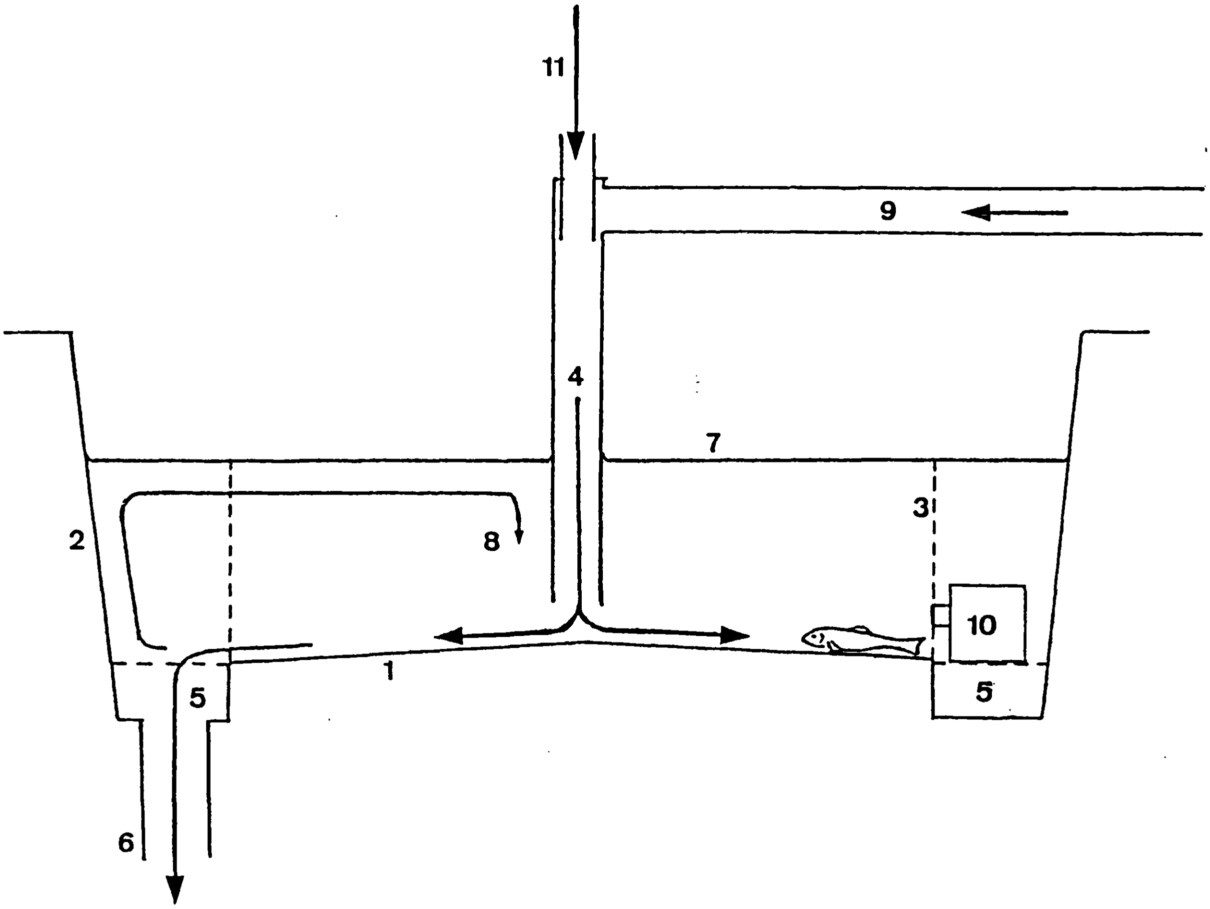
7 = Water surface

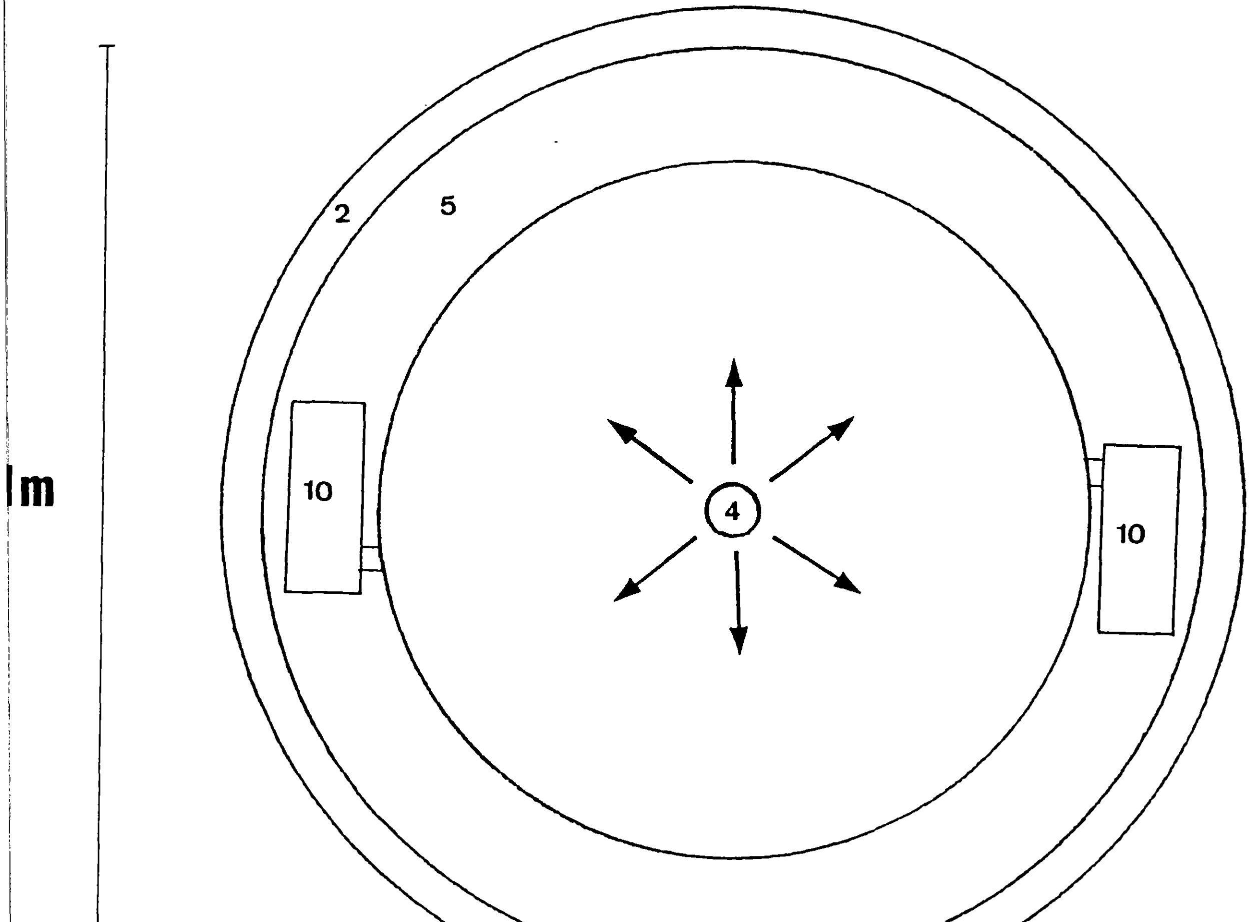
8 = Current cell

9 = Recirculating water supply

10= Box shelter

11 = Food input


11
9
4
7
2
3
8
10
1
5
5
6


1m
2
5
10
4
10

5.2.3 RESULTS

5.2.3.1 Daily patterns in sheltering behaviour

The extent to which fish were nocturnal was quantified by the ratio of nocturnal activity to total activity :

$$\text{nocturnal activity index} = 100 \times E_n / (E_n + E_d),$$

where E_n is the mean number of fish exposed (i.e. out of refuges) during each ten minute film period for each night, and E_d is the equivalent value for each day.

For UMG fish this ratio changed dramatically in response to temperature (Figure 5.2A), fish being almost exclusively nocturnal at lower temperatures. This was due both to a decrease in E_d and an increase in E_n (Figure 5.2B).

The possible effect of endogenous seasonal rhythms on activity was tested by including 'expected' values of both photoperiod (days since the winter equinox) and temperature (that of the ambient loch intake water flowing into the heating-cooling system) as well as actual water temperature experienced by the fish (after manipulation) as independent variables in a stepwise multiple regression, with the mean number of fish exposed in the daytime as the dependent variable. Only manipulated water temperature was a significant predictor of mean number of fish exposed ($F_{1,45} = 40.11, r^2 = 0.47$ $p < 0.001$). The other two variables explained none of the remaining variation, suggesting that the fish were responding directly to temperature they experienced and had no underlying seasonal pattern of activity.

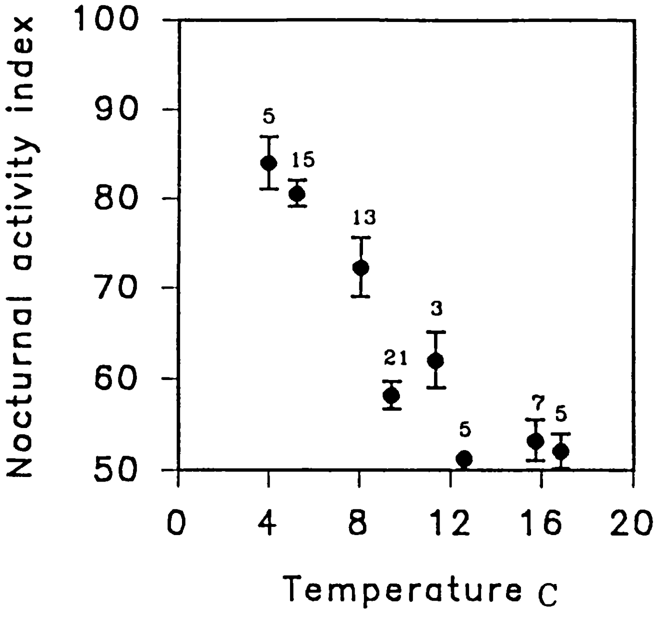
The activity of UMG fish varied slightly during the daylight hours at low temperatures, with fewest fish being exposed in the middle of the day (Figure 5.3). At high temperatures there was no distinct pattern, leading to there being a significant interaction between temperature and time of day (two-way ANOVA with temperature categorised as above or below 8°C; effect of temperature $F_{1,242} = 185.61$, $p < 0.001$; time of day $F_{3,242} = 2.60$, n.s.; interaction between temperature and time $F_{3,242} = 2.94$, $p < 0.05$). The daytime variation in activity at low temperature was trivial compared with the variation between day and night activity. There was no temporal pattern in the number of fish exposed through the hours of darkness, regardless of temperature (ANOVA : effect of temperature $F_{1,217} = 44.04$, $p < 0.001$; effect of time of night $F_{3,217} = 0.856$, n.s; interaction between temperature and time $F_{3,217} = 0.243$, n.s.).

Figure 5.2A

The extent to which UMG juvenile salmon were nocturnal in relation to water temperature. The data are expressed as a nocturnal activity index (see text). A value of 50% indicates that fish were equally likely to be exposed in the water column by day as by night; 100% indicates completely nocturnal activity. Spearman rank correlation coefficient $R_s = -.836$, $n = 74$ days, $p < 0.001$). Data are presented for clarity as means +/- s.e. (with sample size) for each 2°C range of temperatures.

Figure 5.2B

The extent to which UMG juvenile salmon were nocturnal in relation to water temperature. The number of fish exposed by day (E_d, open circles; Pearson correlation coefficient $r = 0.809$, $n = 74$ days, $p < 0.001$) and by night (E_n, filled circles; $r = -0.353$, $n = 74$, $p < 0.005$). Data are presented for clarity as means +/- s.e. (with sample size) for each 2°C range of temperatures.


Nocturnal activity index
100
90
80
70
60
50
0
4
8
12
16
20
Temperature C
5
15
13
3
21
5
7
5

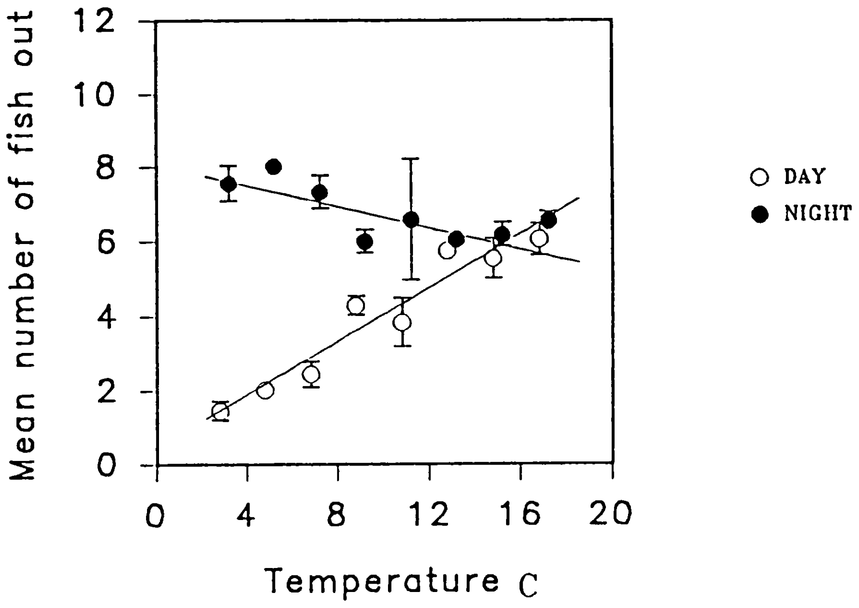

Mean number of fish out
12
10
8
6
4
2
0
0
4
8
12
16
20
Temperature C
○ DAY
● NIGHT

Figure 5.3

Variation in the number of UMG fish exposed with respect to time of day. The thin vertical lines indicate the beginning and end of daylight period. The data (presented as means +/- s.e.) have been divided into two temperature ranges : 2.0-8.0°C (•) and 8.1-18.5°C (o). Note the small temporal variation in behaviour within either the daytime or night-time periods compared with the marked switch to nocturnality at lower temperatures (see text).

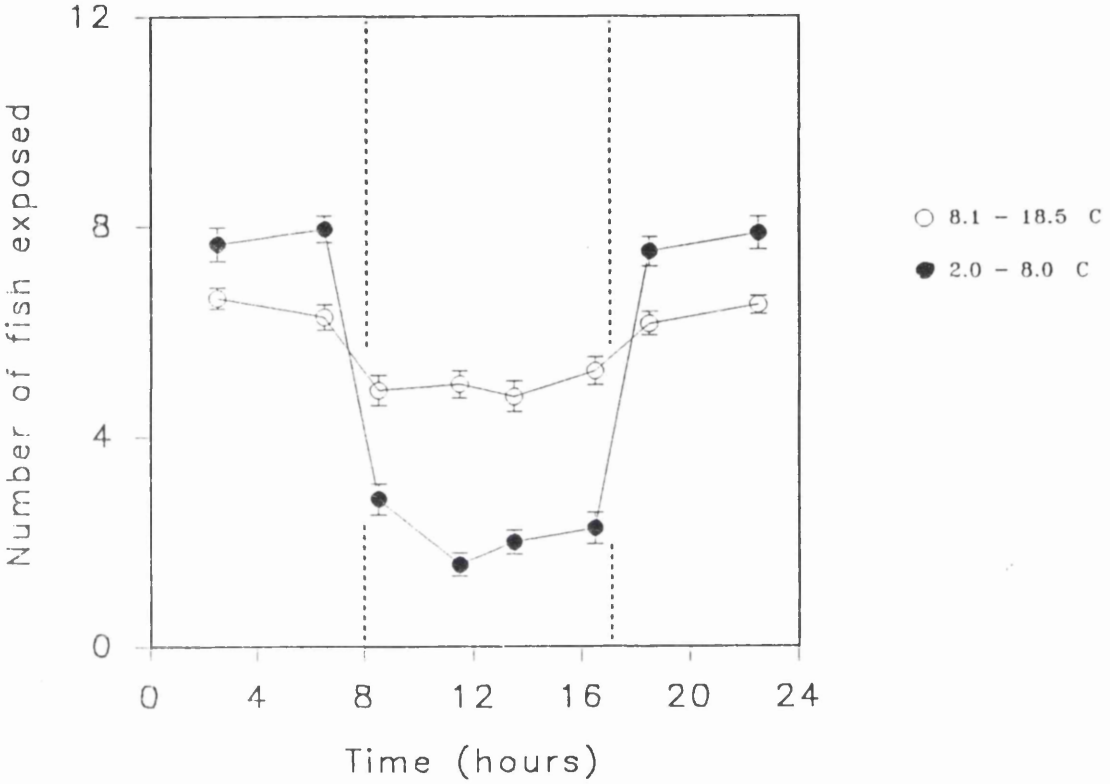
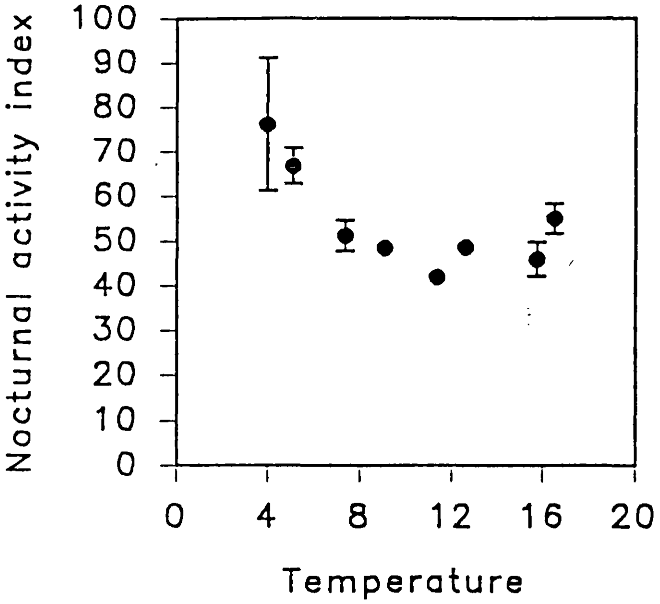

12
8
4
0
Number of fish exposed
0
4
8
12
16
20
24
Time (hours)
○ 8.1 – 18.5 C
● 2.0 – 8.0 C

Figure 5.4A

The extent to which LMG juvenile salmon were nocturnal in relation to water temperature. The data are expressed as a nocturnal activity index (see text). A value of 50% indicates that fish were equally likely to be exposed in the water column by day as by night; 100% indicates completely nocturnal activity. Spearman rank correlation coefficient $R_s = -0.3467$, $n = 74$ days, $p < 0.001$). In both graphs data are presented for clarity as means +/- s.e. (with sample size) for each 2°C range of temperatures.

Figure 5.4B

The extent to which LMG juvenile salmon were nocturnal in relation to water temperature. The number of fish exposed by day (E_d, open circles; Pearson correlation coefficient $r = 0.5127$, $n = 74$ days, $p < 0.001$) and by night (E_n, filled circles; $r = 0.209$, $n = 74$, n.s.).


Nocturnal activity index
100
90
80
70
60
50
40
30
20
10
0
0
4
8
12
16
20
Temperature

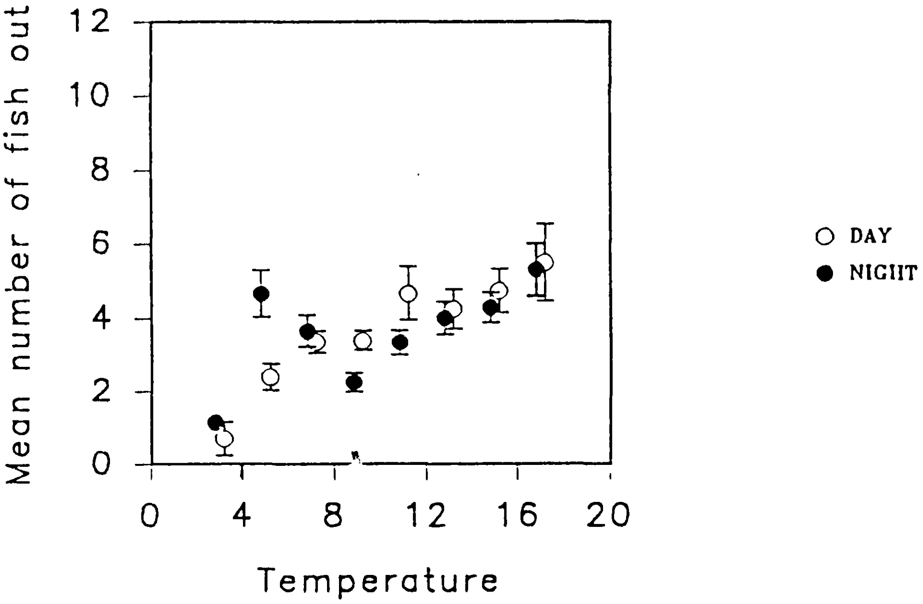
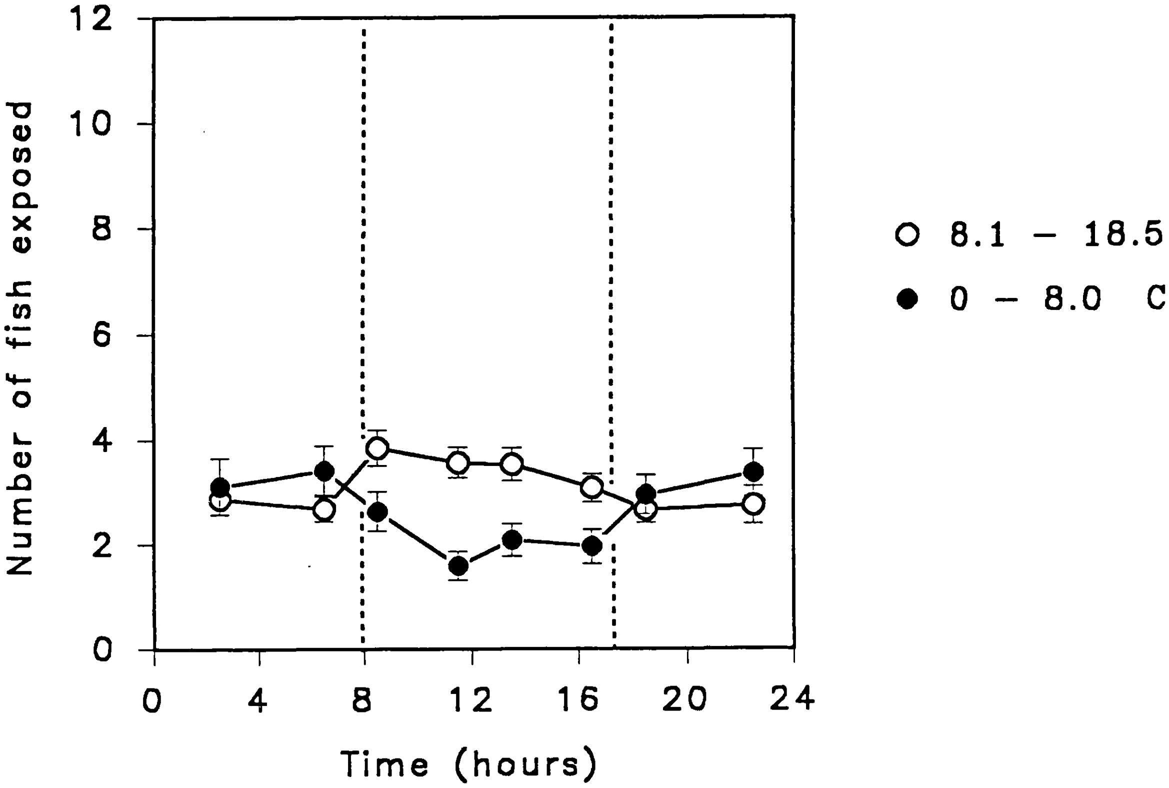

Mean number of fish out
12
10
8
6
4
2
0
0
4
8
12
16
20
Temperature
○ DAY
● NIGHT

Figure 5.5

Variation in the number of LMG fish exposed with respect to time of day. The thin vertical lines indicate the beginning and end of daylight period. The data (presented as means +/- s.e.) have been divided into two temperature ranges : 2.0-8.0°C (•) and 8.1-18.5°C (o). Note the small temporal variation in behaviour within either the daytime or night-time periods compared with the marked switch to nocturnality at lower temperatures (see text).


Number of fish exposed
0
2
4
6
8
10
12
0
4
8
12
16
20
24
Time (hours)
○ 8.1 – 18.5
● 0 – 8.0 C

For LMG fish there was a clear correlation between nocturnal activity and temperature (Spearman rank correlation, $R_s = -0.3467$, $n = 74$, $p < 0.01$) (Figure 5.4A). This was due to the mean number of exposed fish by day (E_d) decreasing at low temperatures while the mean number of fish exposed by night (E_n) remaining unchanged (Figure 5.4B). The possible effect of endogenous seasonal rhythms was tested in a stepwise multiple regression using the same independent variables as described for UMG fish but daytime mean number of LMG fish exposed as the dependent variable. Again only manipulated water temperature was significant ($F_{1,72} = 25.67, r^2 = 0.26$ $p < 0.001$). The other two variables explained none of the remaining variation ($p > 0.1$), suggesting that the LMG fish were also responding directly to temperature they experienced and had no underlying seasonal pattern of activity.

The activity of LMG fish did not vary during the daylight hours at either low temperatures (Figure 5.5) or high temperatures and hence there was no significant interaction between temperature and time of day (two-way ANOVA with temperature categorised as above or below 8°C; effect of temperature $F_{1,242} = 40.18$, $p < 0.001$; time of day $F_{3,242} = 2.017$, n.s; interaction between temperature and time $F_{3,242} = 0.716$, n.s.). There was no temporal pattern in the number of fish exposed through the hours of darkness, regardless of temperature (ANOVA : effect of temperature $F_{1,222} = 3.26$, n.s; time of day $F_{3,222} = 0.187$, n.s.; interaction between temperature and time $F_{3,222} = 0.883$, n.s).

5.2.3.2 Foraging

In general LMG fish fed infrequently compared with UMG over all the temperatures tested (see Figures 5.6B & 5.7B). In addition, very few LMG fish held station facing into the current and most remained laterally compressed against the outside fence. A feeding movement from this position involved the fish lifting itself away from the fence and sweeping its head into the current to catch the passing food item. UMG fish mostly held station facing into the current where they could intercept passing food easily.

A nocturnal foraging index, similar to the nocturnal activity index described above, was calculated as :

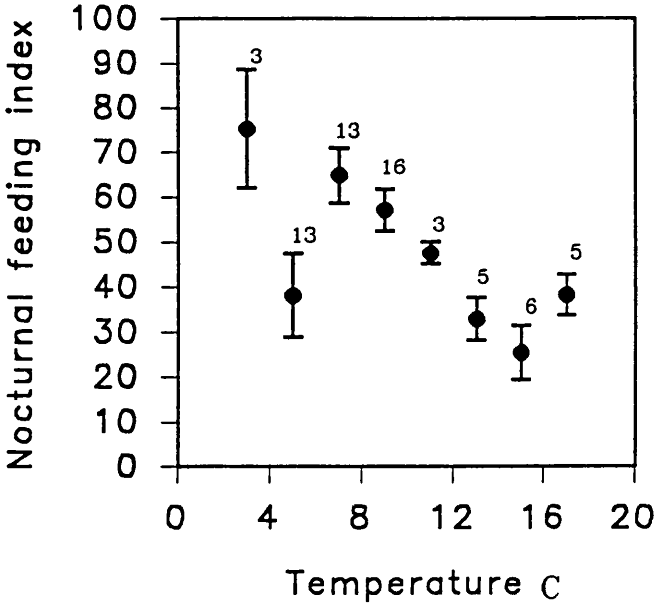
$$\text{nocturnal foraging index} = 100 \times F_n / (F_n + F_d),$$

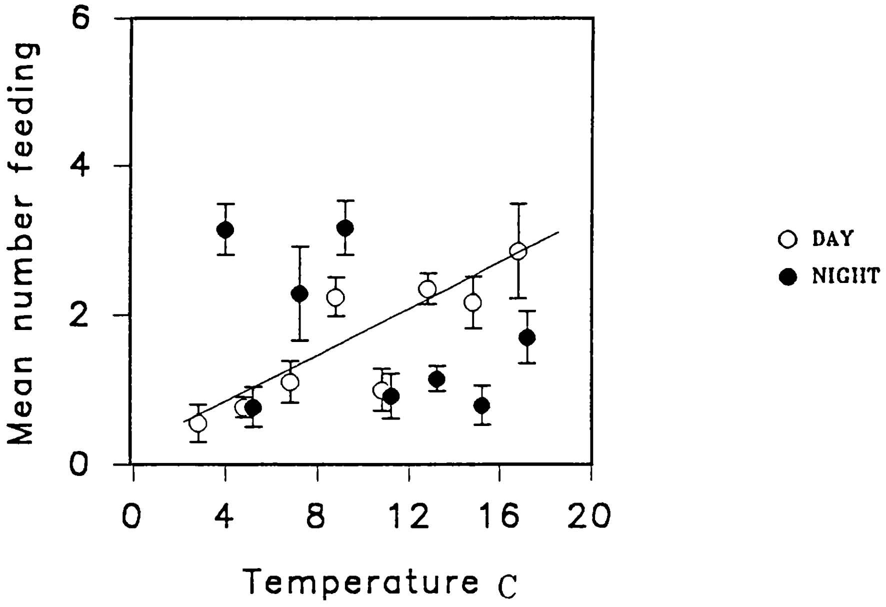
Figure 5.6A

Data expressed as nocturnal foraging index of UMG juvenile salmon ($rs = -0.289$, $n = 64$, $p < 0.001$). Data presented as in Figure 5.1B. Feeding rates were not recorded on all occasions, hence sample sizes were smaller than in Figure 5.1B.

Figure 5.6B

The mean number of foraging UMG fish per 10 min period by day (F_d; open circles and regression line) and by night (F_n; filled circles) in relation to temperature. F_d decreased with temperature (Pearson correlation coefficient, $r = 0.578$, $n = 64$, $p < 0.001$), whereas F_n showed no trend ($r = -0.027$, $n = 64$, n.s.; overall mean = 1.86 foraging fish per 10 min).


Nocturnal feeding index
100
90
80
70
60
50
40
30
20
10
0
0
4
8
12
16
20
Temperature C
3
13
13
16
3
5
6
5


Mean number feeding
6
4
2
0
0
4
8
12
16
20
Temperature C
○ DAY
● NIGHT

where F_n is the mean number of exposed fish snapping at food pellets per 10 min each night, and F_d is the equivalent value for each day. 'Snapping' was used as the criterion because the outcome of feeding attempts could not be determined from the video film.

UMG fish switched from being predominantly diurnal foragers to being predominantly nocturnal as temperature declined (Figure 5.6A & 5.6B). This was due to the mean number of fish foraging by day (F_d) decreasing at low temperatures while the mean number of fish foraging by night (F_n) remained unchanged. A stepwise multiple regression analysis similar to that described earlier in section 5.2.3.1 showed that the mean number of UMG fish foraging by day (F_d) varied significantly only with manipulated water temperature ($F_{1,40} = 15.39$, $r^2 = 0.28$, $p < 0.001$), the other two variables (anticipated seasonal changes in either photoperiod and ambient water temperature) explaining none of the variation ($P > 0.1$). In addition, there was no significant variation in foraging rates with time of day (ANOVA : effect of temperature $F_{1,235} = 62.814$, $p < 0.001$; time of day $F_{3,235} = 0.217$, n.s.; interaction between temperature and time $F_{3,235} = 1.27$, n.s.) or time of night (ANOVA : effect of temperature $F_{1,192} = 4.64$, $p < 0.05$; time of night $F_{3,192} = 2.36$, n.s.; interaction between temperature and time $F_{3,192} = 0.555$, n.s.).

There was no significant shift to nocturnal feeding in LMG fish at low temperatures (Spearman rank, $r = 0.0198$, $n = 46$, $p > 0.05$) (Figure 5.7A). LMG fish fed both during the day and night at all temperatures, but clearly fed less than UMG fish (Figure 5.7B). However the number of LMG fish attempting to feed by day (F_d) decreased significantly at low temperatures (Figure 5.7B). A stepwise multiple regression analysis similar to that described earlier in section 5.2.3.1 showed that the mean number of LMG fish foraging by day (F_d) varied significantly only with manipulated water temperature ($F_{1,66} = 19.12$, $r^2 = 0.225$, $p < 0.001$), the other two variables (anticipated seasonal changes in either photoperiod and ambient water temperature) explaining none of the remaining variation ($P > 0.1$).

5.2.3.3 Aggression

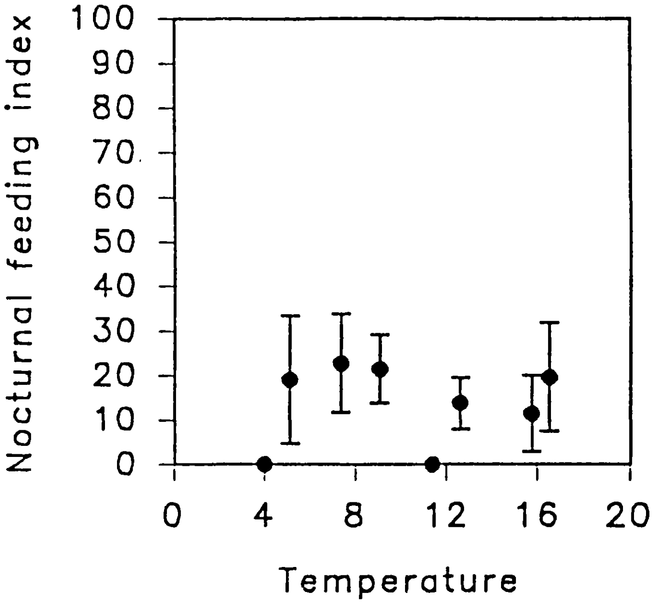
The switch from diurnal to nocturnal behaviour at lower temperatures was accompanied by a change in the social behaviour of both UMG & LMG fish. In daylight fish would initiate attacks on conspecifics up to three bodylengths away, resulting in the fish being well spaced. In darkness the salmon seemed to ignore one another, aggression only occurring when two fish apparently collided. However the levels of aggression between individuals from the same group differed : the number of aggressive interactions per exposed fish per 10 min only involving UMG decreased with temperature (Pearson correlation coefficient; $r = 0.4655$, $n = 327$, $p < 0.001$)

Figure 5.7A

Data expressed as nocturnal foraging index of LMG juvenile salmon ($r_s = 0.0198$, $n = 46$, $p > 0.05$). Data presented as in Figure 5.1B. Feeding rates were not recorded on all occasions, hence sample sizes were smaller than in Figure 5.1B.

Figure 5.7B

The mean number of foraging LMG fish per 10 min period by day (F_d; open circles and regression line) and by night (F_n; filled circles) in relation to temperature. F_d decreased with temperature (Pearson correlation coefficient, $r = 0.4740$, $n = 68$, $p < 0.001$), whereas F_n showed no trend ($r = 0.1267$, $n = 61$, n.s.


Nocturnal feeding index
100
90
80
70
60
50
40
30
20
10
0
0
4
8
12
16
20
Temperature

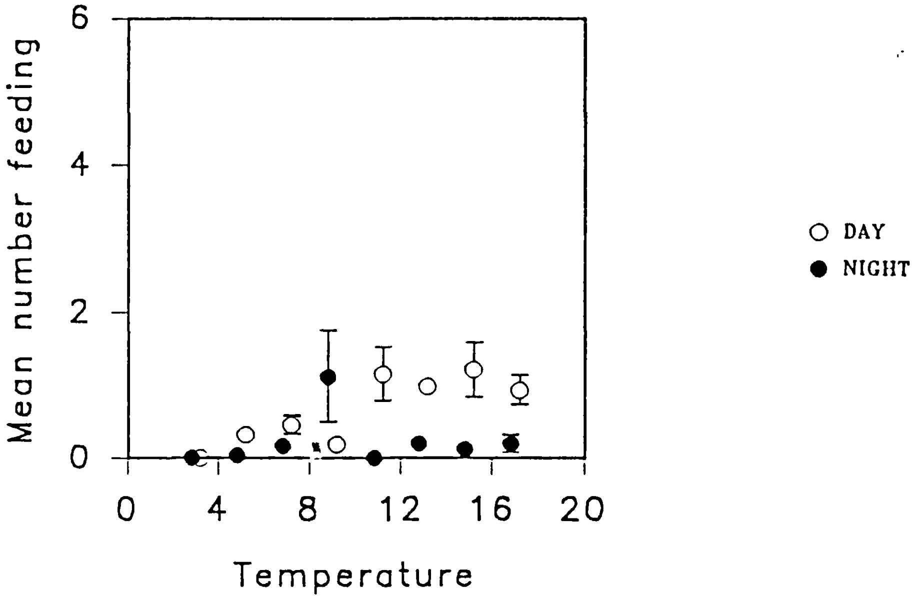
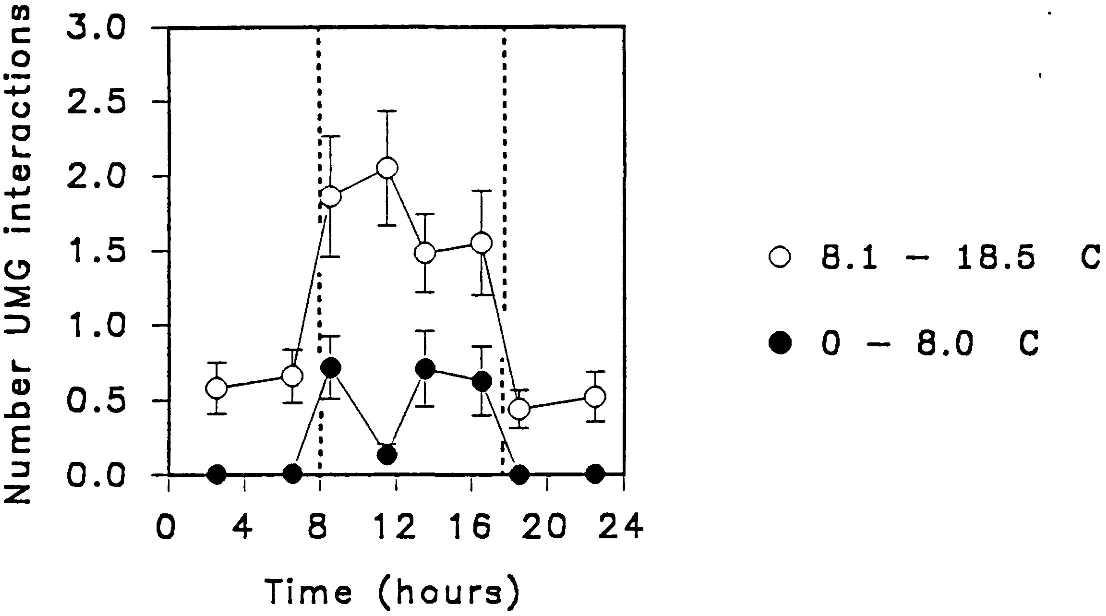

Mean number feeding
6
4
2
0
0
4
8
12
16
20
Temperature
○ DAY
● NIGHT

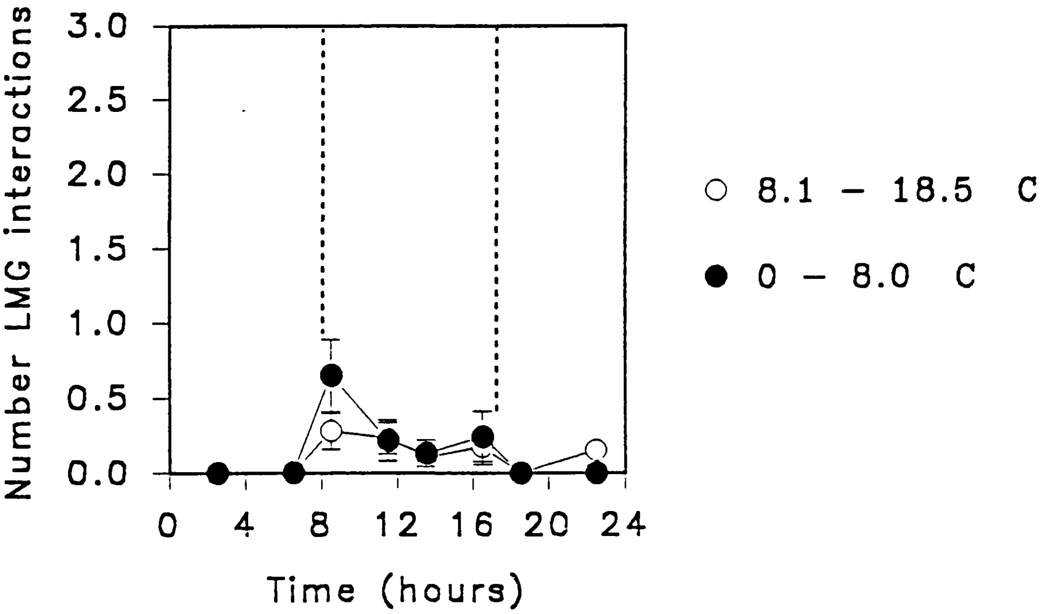
Figure 5.8A

Variation in the mean number of aggressive interactions per exposed fish per 10 min between UMG with respect to time of day. The thin vertical lines indicate the beginning and end of daylight period. The data (presented as means +/- s.e.) have been divided into two temperature ranges : 0-8.0°C (•) and 8.1-18.5°C (o). Note the variation in aggressive behaviour between daytime and night-time and note the marked influence of temperature.

Figure 5.8B

Variation in the mean number of aggressive interactions per exposed fish per 10 min between LMG with respect to time of day. The thin vertical lines indicate the beginning and end of daylight period. The data (presented as means +/- s.e.) have been divided into two temperature ranges : 0-8.0°C (•) and 8.1-18.5°C (o). Note the low levels of interactions by night and by day compared with the UMG.


Number UMG interactions
3.0
2.5
2.0
1.5
1.0
0.5
0.0
0
4
8
12
16
20
24
Time (hours)
○ 8.1 – 18.5 C
● 0 – 8.0 C


Number LMG interactions
3.0
2.5
2.0
1.5
1.0
0.5
0.0
0
4
8
12
16
20
24
Time (hours)
○ 8.1 – 18.5 C
● 0 – 8.0 C

(Figure 5.8A), whereas the number of aggressive interactions only involving LMG did not decrease significantly with temperature (Pearson correlation coefficient; $r = 0.0565$, $n = 307$, n.s.) In addition rates of aggression in UMG were consistently higher in daylight (paired t-test comparing daylight and night in each 24 h; $t = 6.24$, 35 d.f., $p < 0.001$), being on average six times higher than at night, whilst rates of aggression between LMG were low both during the day and night (Figure, 5.8B).

There was no significant variation in aggression rates between UMG fish with time of day (ANOVA : effect of temperature $F_{1,167} = 28.5$, $p < 0.001$; time of day $F_{3,167} = 0.199$, n.s.; interaction between temperature and time $F_{3,167} = 1.27$, n.s.) or time of night (ANOVA : effect of temperature $F_{1,156} = 41.67$, $p < 0.001$; time of night $F_{3,156} = 0.358$, n.s.; interaction between temperature and time $F_{3,156} = 0.299$, n.s.). Similarly there were no significant variations in LMG foraging rates with time of day (ANOVA : effect of temperature $F_{1,149} = 0.247$, n.s.; time of day $F_{3,149} = 0.81$, n.s.; interaction between temperature and time $F_{3,149} = 1.55$, n.s.) or time of night (ANOVA : effect of temperature $F_{1,177} = 1.49$, n.s.; time of night $F_{3,177} = 2.2$, n.s.; interaction between temperature and time $F_{3,177} = 0.879$, n.s.).

5.2.4 DISCUSSION

This experiment has demonstrated that juvenile salmon of both the UMG & LMG can show rapid changes in their daily activity patterns in direct response to alterations in environmental temperature. At higher water temperatures (typical of late spring, summer and autumn) both groups of fish are predominantly most active and obtain most of their food during daylight hours, as previously described by Hoar (1942). As expected, LMG were less active than UMG fish both by day and by night (Higgins & Talbot, 1985). During the day both groups were very aggressive and defended feeding territories (Kalleberg, 1958; Grant & Kramer, 1990). At night both groups remained out of refuges and exposed in the water column, but fed relatively little and were unaggressive. The lack of aggressive interactions between all fish at night, except when knocking into one another, might be due to their reduced visual capability, rather than reduced activity and lower feeding motivation. Support for this is given by the fact that the radius of the territory defended by a juvenile salmonid is closely related to the maximum distance at which prey items can be detected from the fish's vantage point (Wankowski, 1981; Grant et al., 1989; Elliott, 1990), and if salmon are only capable of detecting food items over a short range at night, then territories should likewise be very small.

Decreasing temperatures caused a drop in the numbers of fish out of shelter by day and a drop in daytime foraging rates. A drop in foraging rate is to be expected for a poikilotherm due to the slower rate of digestion at lower temperatures (Higgins & Talbot, 1985). However, nocturnal foraging rates were independent of temperature, and at low temperatures fish remained in refuges by day but emerged to forage at night. This inversion of foraging patterns need not imply that low temperatures cause a 180° phase shift in an endogenous rhythm. It is more likely that there is a temperature dependent masking effect (Aschoff, 1960): salmon become photonegative at low temperatures (Rimmer & Paim , 1989), and so remain concealed by day but emerge to feed at night. The regular daily movement of fish between daytime refuges and night-time feeding stations suggests that the nocturnal foraging was not purely a passive consequence of photophobia at low temperatures. Moreover, Heggenes et al., (1993) found that the night-time feeding stations of wintering brown trout tend to be in different stream microhabitats than their daytime refuges, with a few fish seeking areas of reduced water velocity at night. This suggests that the fish may be undertaking regular migrations between refuges and feeding areas each dusk and dawn. Heggenes et al., (1993) also suggested that the emergence of brown trout from daytime streambed refuges was in response to nightly formation of ice. However in this experiment both groups of fish switched to nocturnal activity at temperatures well above zero.

In other recent studies on the daily pattern of feeding in salmonids different results have been found. In Jorgensen & Jobling's 1992 study it was found that at temperatures of 6°C in winter juvenile Atlantic salmon consumed more food hourly by day than by night (irrespective of time of year) but the total food intake was still greater by night. However, their study differed from the experiments described here in two important respects: the fish were not provided with any refuges, and were kept in total darkness (0 lux) at night. Thus in Jorgensen & Jobling's study the fish would not have been able to adopt the preferred pattern of remaining in refuges by day, and would also not have been able to see food items by night. Both factors would contribute to the tendency of daytime feeding rates being higher than night-time rates.

5.3 SHELTERING BEHAVIOUR OF ISOLATED JUVENILE ATLANTIC SALMON PARR IN RELATION TO WATER TEMPERATURE AND TIME OF DAY: (2) SUMMER

5.3.1 INTRODUCTION

Freshwater fishes living in their natural habitat have predictable patterns of behaviour, growth and reproductive activity on both daily and annual time scales (Helfman, 1978). This rhythmic behaviour is often organised with respect to important environmental variables such as temperature and photoperiod (Thorpe, 1989a). In temperate regions these environmental variables change in an ordered way throughout the year, leading to seasonal changes in the daily pattern of activity (Müller,1978; Helfman, 1986).

The experiment described in section 5.2 suggested that the rhythmic daily routine of juvenile salmonids in winter is reorganised in relation to temperature. This study, along with all other studies on diel behaviour of juvenile Atlantic salmon (Eriksson, 1978; Heggenes et al., 1993), was carried out in the winter on groups of fish that had experienced normal environmental conditions up until the time of the observations. This means that the behaviour of some fish may have been constrained by the actions of their companions thus imbalancing the daily activity patterns of the fish. Alternatively there is a chance that the behavioural switch described in Section 5.2 is linked to an underlying annual cycle in daily activity patterns because the experiment was carried out in the winter when the expression of such annual behaviour would be expected (Cloudsley-Thompson, 1961;Saunders, 1977; Schwassmann, 1980). In order to evaluate the influence of season and social interactions on low temperature nocturnalism a further experiment was carried out in a controlled environment in the summer of 1992 on isolated underyearling salmon parr.

5.3.2 MATERIALS & METHODS

The study fish were the progeny of a single pairing of wild fish from the River Almond (Male 73cm & Female 62.5cm), Perthshire, Scotland. All fish were reared on commercial pellets (EWOS Baker salmon starter, size 0-3) under routine hatchery conditions until the start of the experiment. Ten fish were selected at random on the 7th July 1992, when they were three months old and therefore had not separated into modal groups. They were placed in a 1m radial flow tank, see Section 5.2.2, inside a temperature controlled cabinet at the University Field Station, Rowardennan. Special modifications to the radial flow tank were as follows : 10 opaque white plastic partitions divided the tank into individual compartments, each with a single refuge

Figure 5.9 Experimental radial flow tank

Top = Side view

Bottom = Top view

1 = White tank base

2 = Tank side

3 = Netlon fence

4 = Central water inlet

5 = Circumferential drain

6 = Standpipe

7 = Water surface

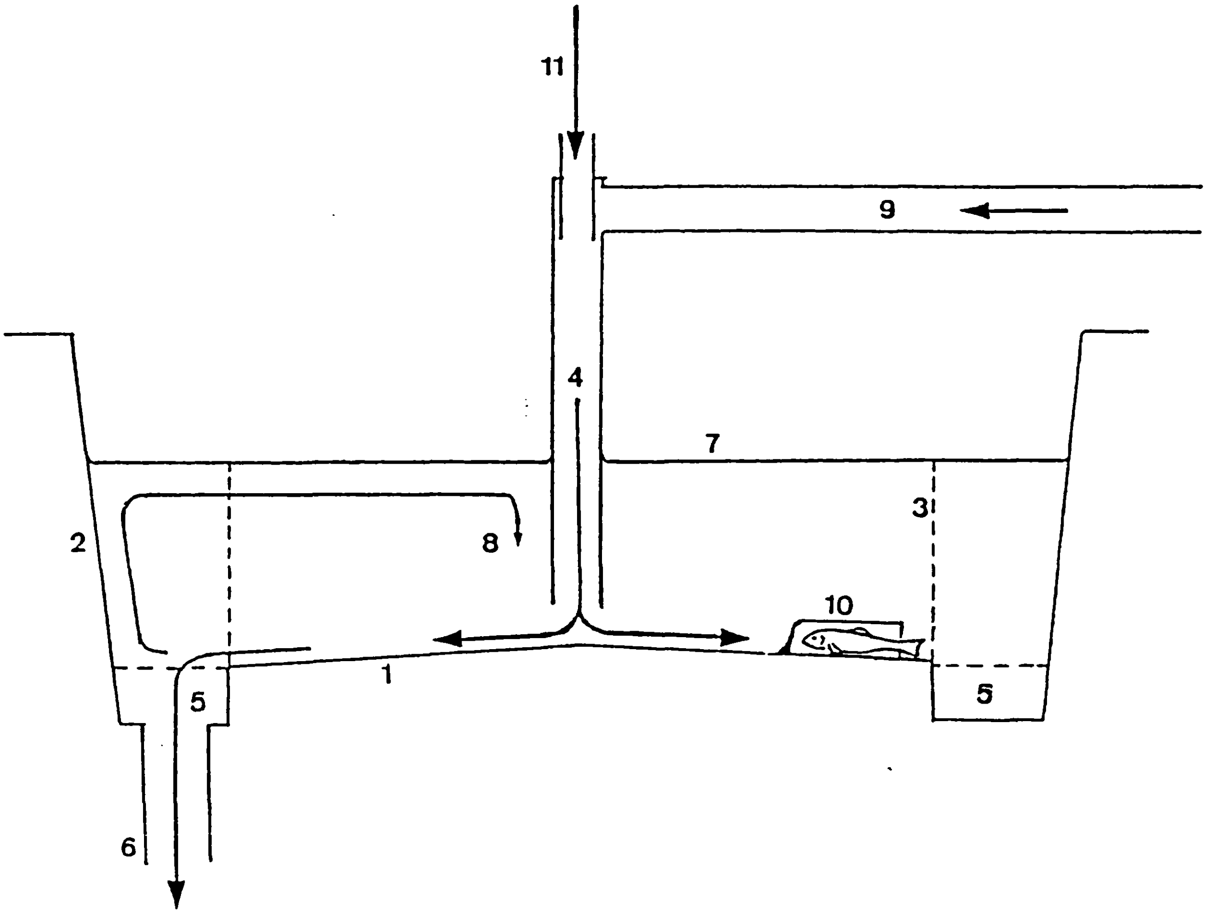
8 = Current cell

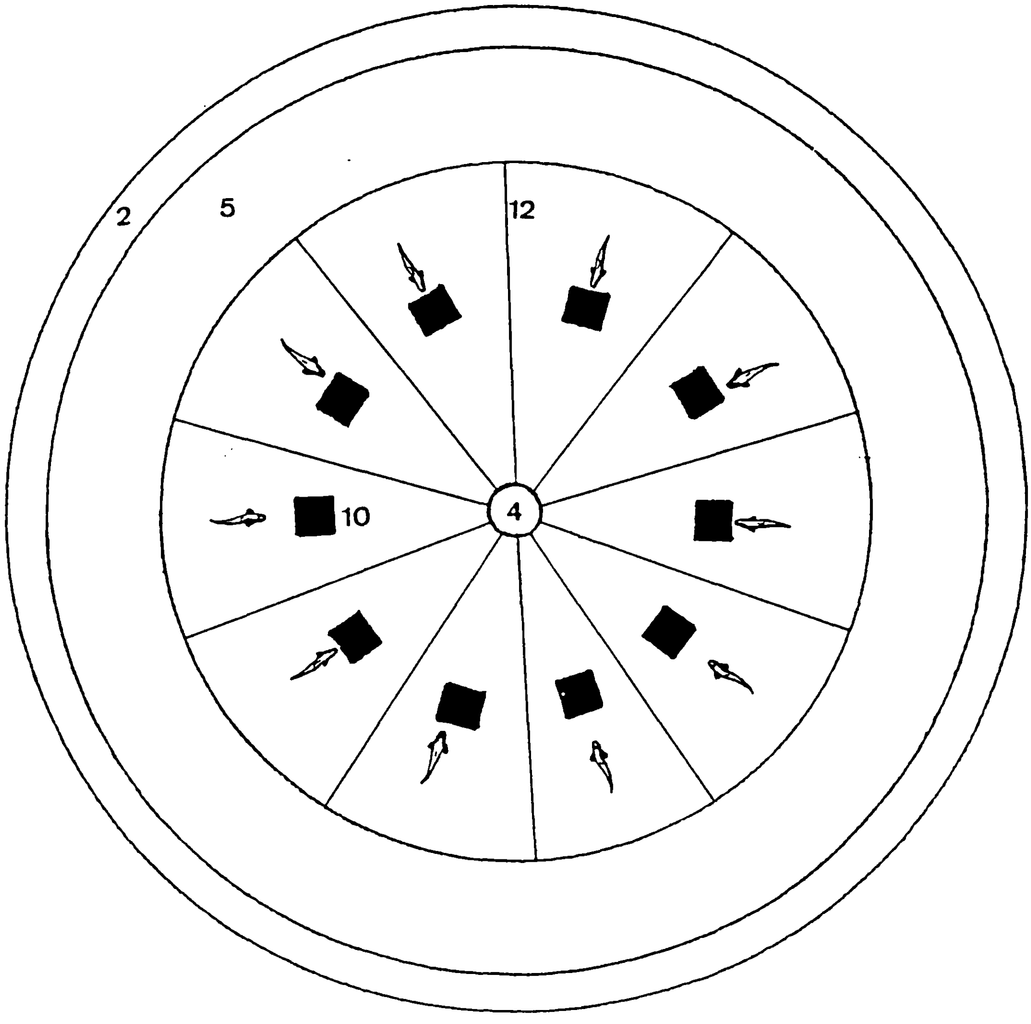
9 = Recirculating water supply

10 = Shelter

11 = Food input

12 = Partitions


11
9
4
7
3
2
8
10
1
5
5
6


2
5
12
10
4

(8 x 8 x 5 cm), see Figure 5.9. The base of the tank was coloured white to enhance the contrast between the fish and the background. When in the refuge a fish could not obtain any food; the fish thus had two options : being exposed in the water column and having access to food, or being concealed in a refuge without food. The water level was maintained at a depth of 9-11cm and the average bottom current velocity was 15.01 ± 4.18 (± SE) cm s^{-1}. An automatic feeder dispersed a delivery of between 4-8 food pellets at 10 min intervals, 24 hours a day, to each compartment. All uneaten food was quickly carried away into the outflow drains.

A CCTV camera, mounted above the tank, recorded 10 minutes of film at 6 intervals over the 24 hour period (10.00, 12.00, 14.00, 20.00, 24.00, 04.00); this allowed for one delivery of food during each 10 min sample period. The video film provided information on the number of fish out of refuges and the number feeding. The temperature controlled cabinet allowed water temperatures to be manipulated between 2-18°C. A constant photoperiod of 12L 12D was maintained throughout the experiment. Daylight was simulated as described in Section 5.2.2. Night-time light for filming was provided by two infra-red lights with 840nm filters; these lights produced a small amount of light visible to salmon, equivalent to starlight (Ali, 1961). The infra-red lights were timed to come on 30 seconds after the cameras in each 10 minute filming session. This delayed lighting up time showed that the fish did not respond to the infra-red lights coming on by entering or leaving the refuges. In addition, the timing of filming was varied to ensure that fish could not anticipate the usual timing of illumination.

Water temperature was ambient initially, rising from 16.1 °C to 17.6 °C (mean daily values) during the first 7 days of data collection. Over the following 100 days it was then manipulated in steps between 2 °C and 18.5 °C in a random sequence, so as to disassociate temperature from the time of year. On all occasions the temperature was adjusted by less than 2°C per day. Filming started on the 9th July 1992 and continued until the 15th September 1992.

The tank was undisturbed except during daily cleaning, which occurred at least 1 hour before any filming session.

5.3.3 RESULTS

5.3.3.1 Daily patterns of sheltering behaviour

There was a clear relationship between the nocturnal index (see Section 5.2.3.1) and temperature for all the salmon (Spearman rank; rs = -0.9062, n = 75, $p < 0.001$) : fewer fish came out of their hides by day at low temperatures (Figure. 5.10A). A stepwise multiple regression was carried out to determine the most important predictor of daytime sheltering behaviour, with mean number of fish exposed by day as the dependent variable and manipulated water temperature and date as the independent variables. Manipulated water temperature was the most important predictor of numbers out ($F_{1,77} = 231.47$, $r^2 = 0.75$, $p < 0.001$), followed by date ($F_{2,76} = 192.31$, $r^2 = 0.83$, $p < 0.001$).

To investigate the change in nocturnal activity in relation to temperature at the individual level, a logistic regression was carried out to determine the probability of a salmon sheltering by day and by night. During the day, manipulated water temperature had a very significant effect on the probability of the salmon being out of the shelter (prob (out) = x/(1+x), where $x = e^{0.2892(\text{temp})-2.9476}$, $p < 0.001$)(Figure 5.10B). At night temperature did not predict anything significantly ($x = e^{4.6871}$, n.s); i.e. the fish were out at night almost all the time, irrespective of temperature. Thus the shift to nocturnalism at low temperatures was attributable to an increase in daytime sheltering behaviour rather than in the number of fish out at night (Figure 5.10B).

In order to see if some individuals were consistently more often out of shelters than others and if this influenced performance, activity scores were expressed as residuals from the appropriate logistic regression line (day or night). An individual's mean residual score for activity, by day and by night was then plotted against its specific growth rate (Figure 5.11A). No significant correlation was found (Spearman rank correlation;$R_s = 0.3283$, n = 10 , n.s.).

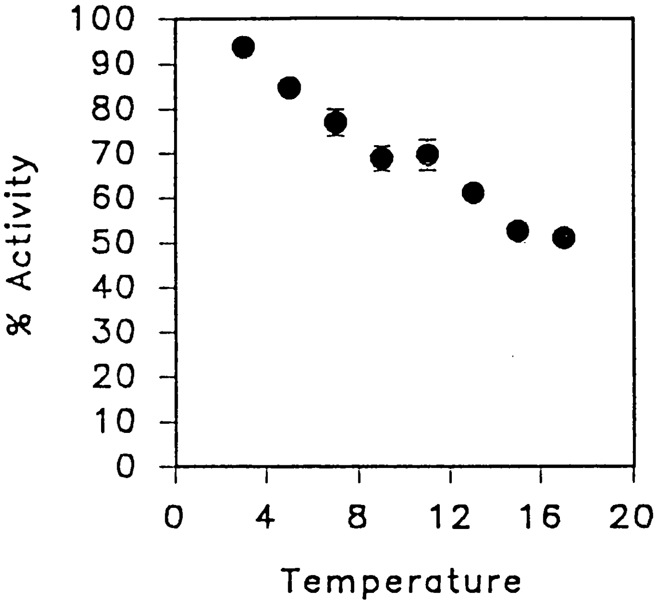
In addition, there was no significant variation in activity with time of day (ANOVA : effect of temperature $F_{1,23} = 22.373$, $p < 0.001$; time of day $F_{2,23} = 0.157$, n.s.; interaction between temperature and time $F_{2,23} = 0.57$, n.s.) or time of night (ANOVA : effect of temperature $F_{1,22} = 24.79$, $p < 0.001$; time of night $F_{2,22} = 1.65$, n.s.; interaction between temperature and time $F_{2,22} = 0.78$, n.s.), see Figure 5.11B.

Figure 5.10A.

The percentage of juvenile Atlantic salmon out of hides at night in relation to water temperature. Percentages calculated as $100 \times E_n / (E_n + E_d)$, where E_n = mean number of fish out at night, and E_d = equivalent value for each day. Data presented as means +/- s.e. for each 2°C range of temperature ($r_s = -0.9062$, $n = 75$, $p < 0.001$)

Figure 5.10B.

Probability of a fish being out of its shelter by day and by night in relation to temperature ($n = 1030$). Probabilities were calculated from the logistic regression equation prob (out) = $x/(1+x)$, where during the day $x = e^{0.2892(temp)-2.9476}$ and at night $x = e^{(temp)+4.6871}$.


% Activity
100
90
80
70
60
50
40
30
20
10
0
0
4
8
12
16
20
Temperature

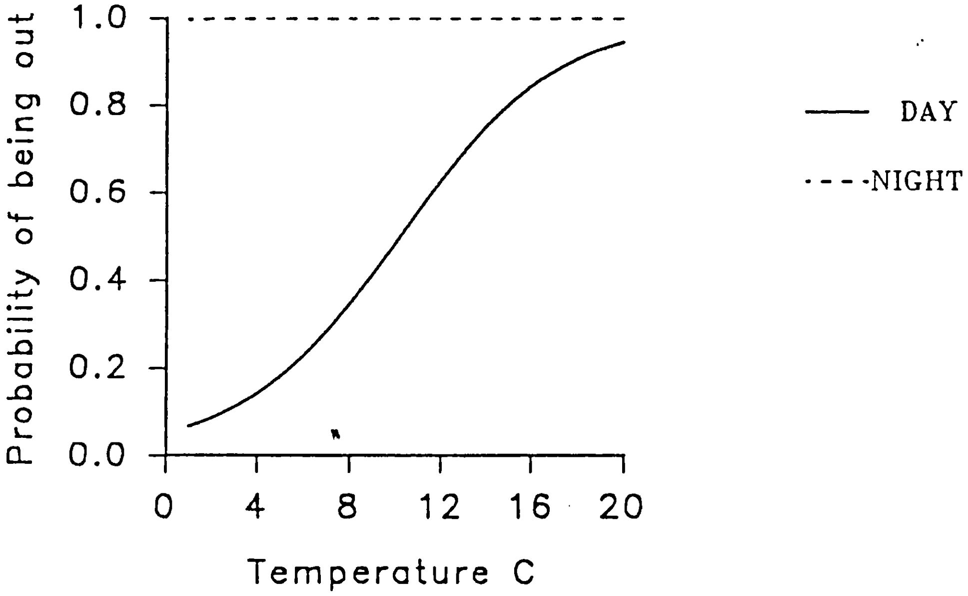
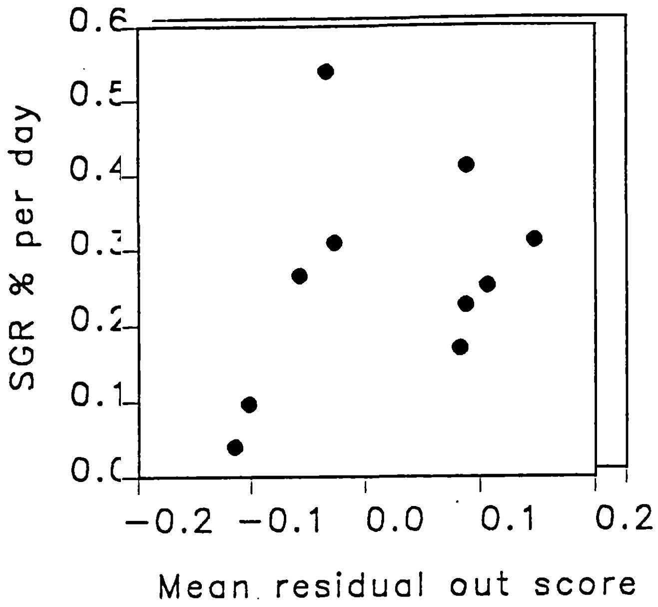

Probability of being out
1.0
0.8
0.6
0.4
0.2
0.0
0
4
8
12
16
20
Temperature C
DAY
NIGHT

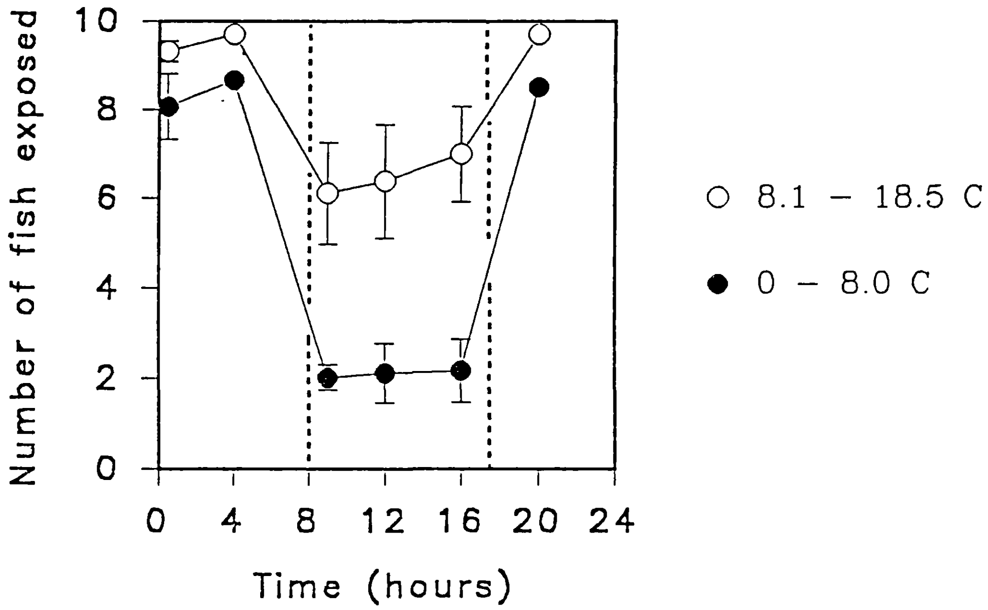
Figure 5.11A

Individual activity scores against specific growth rate. Individual scores were calculated from the logistic regression equation for activity, see text, and expressed as the mean residual for each fish.

Figure 5.11B

Variation in the mean number of fish out of shelters per 10 mins with respect to time of day. The thin vertical lines indicate the beginning and end of daylight period. The data (presented as means +/- s.e.) have been divided into two temperature ranges : 2.0-8.0°C (•) and 8.1-18.5°C (o). Note the drop in daytime activity at low temperatures.


0.6
0.5
0.4
0.3
0.2
0.1
0.0
SGR % per day
−0.2
−0.1
0.0
0.1
0.2
Mean residual out score


10
8
6
4
2
0
Number of fish exposed
0
4
8
12
16
20
24
Time (hours)
○ 8.1 – 18.5 C
● 0 – 8.0 C

5.3.3.2 Foraging

There was a clear relationship between the nocturnal foraging index (see Section 5.2.3.2) and temperature for all the salmon (Spearman rank; $rs = -0.8033$, $n = 49$, $p < 0.001$); fewer fish fed by day at low temperatures (Figure. 5.12A). A stepwise multiple regression was carried out to determine the most important predictor of daytime foraging behaviour, with mean number of fish foraging by day as the dependent variable and manipulated water temperature and date as the independent variables. Manipulated water temperature was the only significant predictor of fish foraging behaviour ($F_{1,54} = 127.84$, $r^2 = 0.715$, $p < 0.001$).

The probability of an individual salmon feeding, by day or night, at any given temperature was also examined using a logistic regression. During the day manipulated water temperature had a very significant effect on the probability on the salmon feeding (prob (feed) = $x/(1+x)$, where $x = e^{0.2622(temp)-3.9884}$, $p < 0.001$) (Figure 5.12B). At night temperature also had a very significant effect on the probability on the salmon feeding (prob (feed) = $x/(1+x)$, where $x = e^{0.1027(temp)-1.9254}$, $p < 0.001$) (Figure 5.12B). At lower temperatures there was more chance that a fish would feed by night than by day (Figure 5.12B). However at higher temperatures the probability of feeding by day was greater than by night (Figure 5.12B).

In order to compare individuals to see if some were consistently feeding more often than others, feeding scores were expressed as residuals from the appropriate logistic regression line (day or night). An individual's mean residual score for feeding, by day and by night, was then plotted against its specific growth rate (Figure 5.13A). No significant correlation was found (Spearman rank correlation; $R_s = 0.4082$, $n = 10$, n.s.).

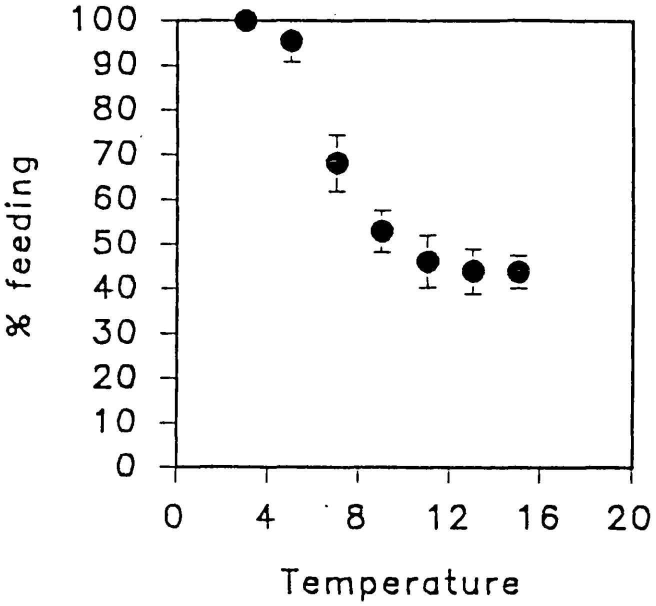
No significant variations in feeding behaviour were found with time of day (ANOVA: effect of temperature $F_{1,23} = 27.19$, $p < 0.001$; time of day $F_{2,23} = 0.519$, n.s.; interaction between temperature and time $F_{2,23} = 0.431$, n.s.) or time of night (ANOVA : effect of temperature $F_{1,22} = 4.877$, $p < 0.05$; time of night $F_{2,22} = 0.151$, n.s.; interaction between temperature and time $F_{2,22} = 0.039$, n.s., see Figure 5.13.B).

Figure 5.12A.

The percentage of juvenile Atlantic salmon feeding at night in relation to water temperature. Percentages calculated as 100 x $F_n / (F_n + F_d)$, where Fn = mean number of fish feeding by night, and Fd = equivalent value for each day. Data presented as means +/- s.e. for each 2°C range of temperature ($rs = -0.8033$, $n = 49$, $p < 0.001$)

Figure 5.12B.

Probability of a fish feeding by day and by night in relation to temperature. Probabilities were calculated from the logistic regression equations prob (feed) = $x/(1+x)$, during the day $x = e^{0.2622(\text{temp})-3.9884}$ and at night $x = e^{0.1027(\text{temp})-1.9254}$.


% feeding
100
90
80
70
60
50
40
30
20
10
0
0
4
8
12
16
20
Temperature

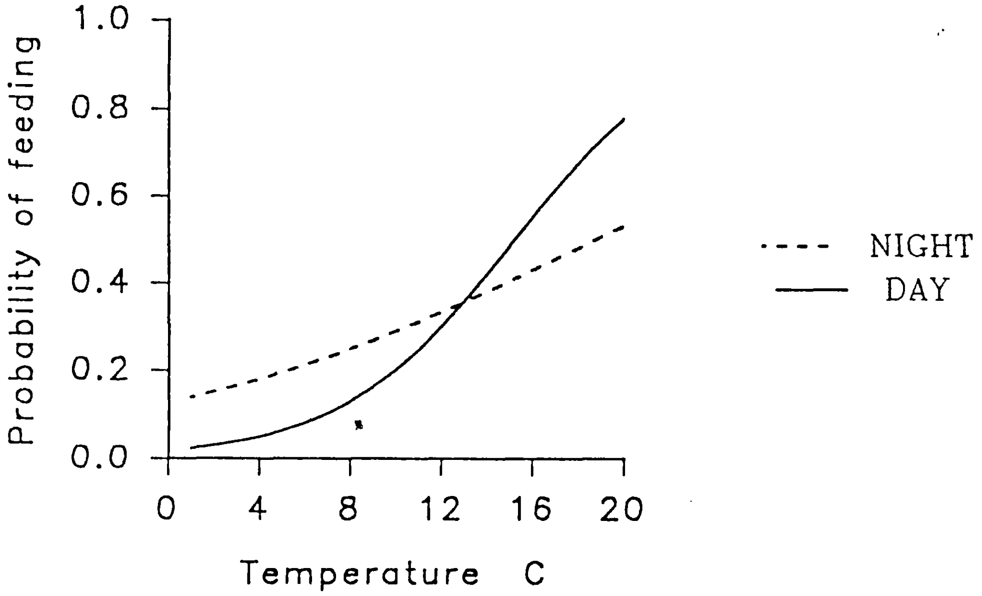
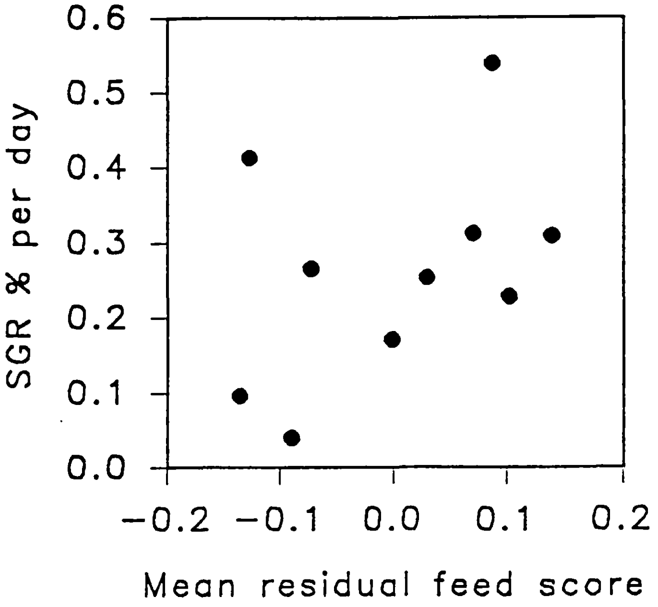

Probability of feeding
1.0
0.8
0.6
0.4
0.2
0.0
0
4
8
12
16
20
Temperature C
NIGHT
DAY

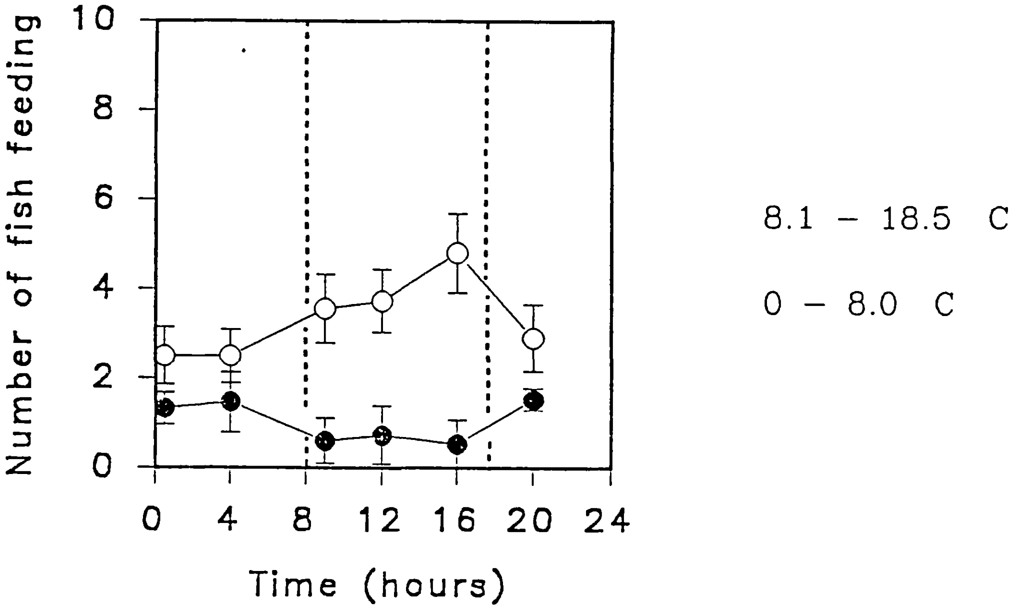
Figure 5.13A

Individual feeding scores against specific growth rate. Individual scores were calculated from the logistic regression equation for feeding, see text, and expressed as the mean residual for each fish.

Figure 5.13B

Variation in the mean number of fish foraging per 10 min with respect to time of day. The thin vertical lines indicate the beginning and end of daylight period. The data (presented as means +/- s.e.) have been divided into two temperature ranges : 2.0-8.0°C (•) and 8.1-18.5°C (o). Note the drop in daytime feeding at low temperatures.


SGR % per day
0.0
0.1
0.2
0.3
0.4
0.5
0.6
-0.2
-0.1
0.0
0.1
0.2
Mean residual feed score


Number of fish feeding
0
2
4
6
8
10
0
4
8
12
16
20
24
Time (hours)
8.1 - 18.5 C
0 - 8.0 C

5.3.4 DISCUSSION

A shift to nocturnalism at low temperatures as seen in juvenile Atlantic salmon during winter (see Section 5.2) clearly also occurs in underyearling salmon parr in July, even though such temperature extremes are never met at this time of year, except in glacial streams. Comparative field work done in three glacial rivers that remain cold throughout the year shows that juvenile Atlantic salmon in these streams also exhibit nocturnalism in the summer (Fraser et al., in prep).

By housing fish individually, the influence of social interactions on shelter seeking behaviour was removed. This gave rise to some different results from those observed in the previous section on group behaviour. For single fish, the number out at night remained unchanged at low temperatures, whilst for a group of fish the numbers out increased at low temperatures. This implies that interactions between fish may have a considerable impact on the pattern of shelter use, particularly in LMG fish, seen in Section 5.2.

The parallel result of Heggenes's glacial stream field study clearly shows that juvenile Atlantic salmon switch to nocturnal activity at low temperatures irrespective of whether they are in a controlled environment or they are in a natural stream. In addition, this behavioural switch would also appear to be part of a more widespread behavioural phenomenon exhibited by other salmonids (Heggenes et al., 1993).

5.4 GENERAL DISCUSSION

The daily activity patterns of animals are usually driven by endogenous rhythms entrained by environmental Zeitgebers, such as photoperiod. Most species are therefore consistently diurnal, nocturnal or crespuscular. However some species of fish have the ability to alter the phasing of their diel activity patterns (Eriksson, 1978). This is usually attributed to responses to the prevailing light conditions. The main result of this chapter shows that juvenile Atlantic salmon switch between diurnal and nocturnal foraging solely in response to environmental temperature and independently of photoperiod and season; the fish become increasingly nocturnal with decreasing environmental temperatures (Fraser et al., 1993). This appears to be the first demonstration of a temperature-controlled dual phasing capacity (Cloudsley - Thompson, 1961).

5.4.1 COMPARATIVE PHYSIOLOGICAL STUDIES

Few fish are both diurnal and nocturnal predators (Helfman, 1986), and the sensory capabilities of salmon are clearly more adapted for diurnal feeding (Ali, 1961). However, juvenile salmonids have previously been shown to exhibit physiological adaptations that parallel the behavioural switches in activity occurring with seasonal changes in temperature. It has been shown that environmental temperature influences the composition of the visual pigments in the retina of salmonids; the ratio of porphyropsin to its analogue rhodopsin increases at low temperatures (Tsin & Beatty, 1977; McFarland & Allen, 1977; Allen & Munz, 1983). Changes in the ratio of these two light sensitive pigments are due to one replacing the other in the pigment cells (Beatty, 1966). An increase in the proportion of porphyropsin in the retina has the effect of enhancing its sensitivity at the red end of the visible spectrum (up to 650 nm; infrared light is thus still invisible Allen & Munz, 1983). This should increase the ability of the fish to see at night, as both moonlight and starlight are relatively rich in red light; in contrast, daylight and twilight are relatively 'blue' in colour when viewed from underwater (Munz & McFarland, 1973). Moreover, the sensitivity of several salmonid species to low light in general increases in winter due to a seasonal increase in the total amount of visual pigments in the retina (Allen, 1982). Thus the retinae of all species of salmonid studied so far switch to being more nocturnally adapted at low temperatures. At the time of their discovery these physiological changes had no known function, since the fish were assumed to be both diurnal and inactive in winter (Tsin & Beatty, 1977; Allen,1982). The results presented here reveal that both the behaviour and physiology of juvenile salmonids have evolved in tandem; the eyes of the fish become adapted for nocturnal activity at the time of the year when the fish switch from being diurnal to nocturnal.

5.4.2 COMPARATIVE BEHAVIOURAL STUDIES

In the last 20 years many studies on the rhythmic activity of fishes have reported differences in the diel phasing of activity in a single species (Eriksson, 1978). In most animals it is fairly clear whether an animal is active at a particular time of day just by looking at its morphological adaptations. However in freshwater fish there is much confusion over this issue and in Eriksson's words "to look in the literature of laboratory assays to find out whether a particular fish species is nocturnal or diurnal might be hazardous indeed". This has led to the general conclusion that some fish have a dual phasing capacity. The results presented in this chapter indicate that salmon have such a dual phasing capacity i.e. they switch from a diurnal lifestyle to a nocturnal one at low temperature. This behaviour is closely related to shelter use; at low temperatures fish use shelters more during the day. Other authors have reported dual phasing for salmonids during winter but most have related this change in behaviour to photoperiod (Eriksson, 1978; Richardson & McCleave, 1974). In the light of the results presented in this chapter there may well be a further link between temperature and diel activity, which might explain some of the apparent confusion in the literature. Table 5.1 lists studies of the phasing of salmonid activity in relation to latitude, season and where all fish had access to shelter. It is clear from this table that there is a general agreement amongst most authors that juvenile Atlantic salmon and trout are diurnal at high temperatures and nocturnal at low temperatures. This suggests that many of these studies were observing a temperature dependent shift in sheltering behaviour. However one study stands out in this table in that it shows trout have a distinct diurnal phasing of activity at low temperatures (Müller, 1978). This study was carried out on rhythmic behaviour of salmonids under natural conditions close to the Arctic circle, where the mean water temperature is around 0.4°C throughout the winter and the water surface is covered by thick ice and a layer of snow during the winter. Two possible explanations for the clear diurnal phasing in the Arctic has been put forward: a reduced predation risk from the complete ice cover and a reduced daylight level under the ice (Andreasson, 1973). Predation from warm blooded predators such as birds and mammals is clearly likely to be reduced underneath the constant 20cm thick ice layer and this could explain the distinct diurnal phasing of activity. Alternatively, there is now substantial evidence to suggest that a change in light level is best possible explanation for the observed behaviour.

Table 5.1 Reported sheltering behaviour of salmon observed at different temperatures and latitudes

Salmo salar	Reported activity	Approx. temperature	Latitude	Reference
	diurnal	14-20°C	45°N	Hoar, 1942
	diurnal	> 10°C		Kalleberg, 1958
	diurnal	> 8°C	57°N	Fraser et al., 1993
	nocturnal (glacial stream)	7.7-8.4°C	60.5°N	Heggenes et al., 1993
	nocturnal	< 8°C	57°N	Fraser et al., 1993
	nocturnal (glacial stream)	3.5°C	59.5°N	Heggenes et al., 1993
	nocturnal (glacial stream)	< 2°C	60.5°N	Heggenes et al., 1993

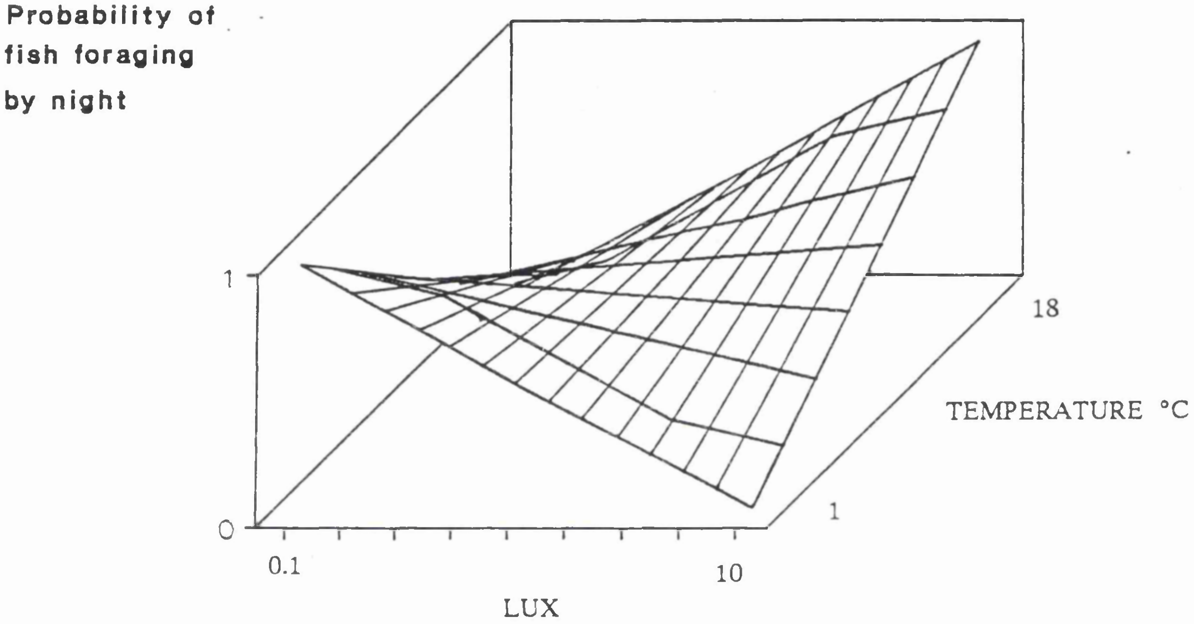
Salmo trutta	Reported activity	Approx. temperature	Latitude	Reference
	diurnal	> 10°C		Kalleberg, 1958
	diurnal	> 10°C	60.5°N	Heggenes et al., 1993
	nocturnal (glacial stream)	< 2°C	60.5°N	Heggenes et al., 1993
	diurnal	0.4°C	66°N	Müller, 1978

Strong evidence for a reduced daylight level influencing behaviour of fish living under ice comes from Andreasson's 1973 study on the behaviour of the normally nocturnal freshwater sculpin (Cottus poecilopus) in relation to light level in southern Sweden. Under natural light conditions southern populations of sculpins remain nocturnal throughout the year. However in more northern populations, close to the Arctic circle, sculpins undergo regular phase shifts during the year (Andreasson, 1973), being dark-active in summer and light-active in winter. Andreasson relates this to " a long-lasting ice cover with a thick layer of snow" since a daytime light level of 5 lux triggers a diurnal-nocturnal switch in southern populations of sculpins, which do not naturally undergo seasonal phase inversion. Andreasson therefore suggested that the daylight levels below the ice in Müller's 1978 study on trout maybe equivalent to night-time light levels. Subsequent measurements of daylight level under 20cm of ice by Müller and Andreasson at the edge of the Arctic circle showed that fish living under ice at this latitude experienced a light level somewhere between 0-4 lux during the day, depending on cloud cover. This clearly implies that a switch to nocturnalism by the trout in Müller's 1978 study is the result of very low light levels during the day.

A further implication of Andreasson's (1973) work is that light level may be a more important factor than availability of cover in determining the phasing of activity in fish since only a light level of 5 lux was needed to shift the activity patterns of Southern Swedish populations of sculpin in the same way as Northern populations living under ice cover. If we assume that Andreasson's behavioural findings are analogous to the behaviour of salmonids, then his work suggests that light level may be the key factor influencing the temperature dependent switch in activity patterns found in Chapter 5 and not shelter as suggested. In Chapter 5 the switch in activity pattern was described as an increase in daytime sheltering behaviour at low temperatures. The alternative interpretation of this result, assuming Andreasson's findings apply to juvenile Atlantic salmon, is that the juvenile Atlantic salmon in this chapter were not seeking physical shelter but the lower light level inside the shelter. If this were the case then at low temperatures an increase in activity would be expected when there is a reduction in light level (-ve photokinesis) and at high temperatures an increase in activity would be expected when there is an increase in light level (+ ve photokinesis). This alternative explanation to the results in this chapter has yet to be established but a theoretical graph of this relationship is shown in Figure 5.14. In Figure 5.14 a temperature dependent switch in photokinesis for nightly foraging activity is mapped. Circumstantial evidence for a temperature dependent switch in photokinesis comes from the work in chapter 2 on dispersal

Figure 5.14

Putative relationship between temperature, light level and nightly foraging activity. Daytime light levels in this example are kept at a constantly high level (> 1000 lux) and so the supposed temperature dependent switch in photokinesis is for nightly foraging activity only.


Probability of fish foraging by night
1
0
0.1
10
LUX
18
TEMPERATURE °C
1

behaviour and light levels and from Chapter 4 on the switch in alevin activity from nocturnalism to diurnalism. In Chapter 2 it was shown that there is a significant negative correlation between increasing light level and the amount of dispersal activity from artificial redds. Dispersal activity can however be completely switched to diurnalism at higher temperatures (Brännäs, 1988; see Chapter 4), suggesting that a temperature-dependent switch in photokinesis occurs. This suggested relationship does not detract from the functional explanations of temperature dependent nocturnalism discussed in later in this chapter but merely proposes a further relationship which may be important to take into account in any future research.

Obviously in most natural situations, shelter and light level are confounded, with increased shelter from vegetation or rocks reducing the ambient light level, and so future research would have to be done in a controlled laboratory environment, where light level and cover can be manipulated independently. One further consideration for any future studies would be to take into account the influence of light transition on activity patterns because Richardson and McCleave (1974) found that the change from light to dark was followed by a more pronounced peak of activity than that from dark to light.

5.4.3 FUNCTIONAL SIGNIFICANCE OF OVERWINTERING NOCTURNALISM

In a stream the winter is a time of severe hardship for cold blooded animals such as juvenile Atlantic salmon. Midwinter temperatures may remain just above freezing for weeks on end, which causes the formation not only of permanent and drifting ice but also of anchor ice in the streambed gravel. Suitable overwintering habitat and food are limited (Garcia de Leaniz, 1990). In addition, salmonids are more vulnerable to endothermic predators because their escape responses are much slower at lower temperatures (Webb, 1978b; Veselov & Shustov, 1991, and see Chapter 6).

These observations suggest at least three possible explanations for the shift in behaviour at low temperatures: restricted food availability, avoidance of competition and/or avoidance of predation. None of these explanations may be mutually exclusive.

5.4.3.1 Direct behavioural response to patterns of food availability

In winter, the niche dynamics of a stream change radically; invertebrate drift decreases significantly in winter months (Chapman & Bjornn, 1969). Salmonid mortalities can occur from nutritional insufficiencies (Gardiner & Geddes, 1980; Cunjak & Power, 1987; Cunjak, 1988b), which are likely to occur in winter because the available habitat is limited (Garcia de Leaniz, 1990) and the hours for foraging are short. In response to these adverse conditions stream dwelling fish may be forced to shift their behaviour in one or all of the three possible niche dimensions (the food niche, the place niche and/or the time niche) in order to survive.

In winter the most important source of food is invertebrate drift which occurs predominantly at night (Müller, 1978). At other times of the year invertebrate drift also occurs predominantly at night, but in addition there is also a large component of day drift food available. This clear limitation on the time of food availability could explain the shift towards nocturnalism in winter since there are no alternative time niches for regular food acquisition.

5.4.3.2 Avoidance of competition

In a highly competitive environment individuals may select a habitat that minimises competition and even after the competitor is removed the habit can still remain (Begon et al., 1986). In the winter stream environment food supply is low and fish require resources that are inherently scarce, deeper waters (pools) & coarser substrates (Chapman & Bjornn, 1969; Garcia de Leaniz, 1990;) all of which leads to higher competition for food and space. Furthermore salmon may forage by night at low temperatures because aggression is lower and the maximum food intake rates needed are low due to slower metabolic and digestion rates (Higgins & Talbot, 1985). Therefore a reduction in feeding efficiency is not too costly. In addition, the increases found in retinal sensitivity at low temperatures may be sufficient to compensate fully for the lower visibility of food items at night. The behavioural shift to nocturnalism shown by individuals may therefore only partially reflect the influence of competition for food and space in the daytime environment (Begon et al., 1986).

5.4.4.3 Avoidance of Predators

Salmonids are potentially extremely vulnerable to predation by warm blooded predators in winter, since the reactions of cold blooded organisms are impaired at low temperatures. As temperatures fall below 8°C there is a rapid reduction in the ability of young salmon to hold station (Rimmer et al., 1985), as well as to perform fast starts (Webb, 1978a,b; Veselov & Shustov, 1991 and see Chapter 6). Not surprisingly, in winter trout and salmon are known to select slower bottom velocities (Garcia de Leaniz, 1990) and more sheltered sections of streams with a greater degree of cover. In this situation the switch to nocturnalism may well reduce the risk of predation, since during the day juvenile salmon are probably more vulnerable to predation from visually hunting endothermic predators (Heggenes & Borgstrøm, 1988). Thus by hiding in the substrate by day they decrease the probability of predatory attacks and can then emerge to feed at night, when predation risk is reduced, since several of the main avian predators (sawbill ducks, Mergus spp., and herons Ardea cinerea) do not hunt in darkness (Cramp & Simmons, 1977; Elson, 1962).

5.4.4 CONCLUSION

The results presented in this chapter provide definite evidence for an active nocturnal lifestyle at low temperatures and refute the traditional view that juvenile Atlantic salmon enter a state of torpor throughout winter. In more scientific terminology this means that the juvenile Atlantic salmon is a 'bi-phasic' animal (Richardson & McCleave, 1974; Eriksson, 1978; Fraser et al., 1993; Fraser et al., in prep;) i.e. it can switch its daily rhythmicity in response to environmental change. This dual phasing capacity has been demonstrated in a number of other species, such as the burbot (Lota lota) and the sculpins (Cottus poecilopus; Cottus gobio), but has always been attributed to changes in other environmental conditions, such as light (Andreasson, 1969; Eriksson, 1978; Müller, 1978). The main reason for this is the equating of diel phasing with an endogenously timed rhythm of behaviour, which would then make work done on fish comparable with the numerous studies on birds and mammals. The influence of natural photoperiodic changes is however clearly confounded by seasonal temperature change and by changes in light level associated with various environmental conditions. These latter two variables have often been ignored or not properly reported in many studies resulting in the overall confusion in the literature on diel activity patterns.

Juvenile Atlantic salmon clearly exhibit a high degree of flexibility in foraging which must have originated from surviving in a hostile environment where the costs involved in maintaining an active diurnal lifestyle at low temperatures are high. Future research may reveal the extent to which other poikilothermns exhibit similar behavioural adaptations to low temperatures and may reveal the functional significance of this behaviour.

CHAPTER 6

THE EFFECT OF TEMPERATURE ON THE BURST SWIMMING PERFORMANCE OF JUVENILE ATLANTIC SALMON PARR

6.1 INTRODUCTION

Fish are ectothermic, which means that the rates of most physiological processes depend on the environmental temperature (Hochachka & Somero, 1971; Prosser, 1973; Cossins & Bowler, 1987). In extreme thermal habitats ectotherms are unable to maintain a consistent level of activity, which naturally influences their behaviour. In chapter 5, a temperature dependent switch in activity was demonstrated for both modal groups (UMG, LMG) of juvenile Atlantic salmon. It was suggested that one of the underlying reason for this low temperature activity shift may be to avoid daytime predation. The avoidance of daytime predation is clearly linked to another temperature-dependent activity, namely swimming. This chapter therefore explores the relationship between temperature and the swimming movements used to avoid a predator's attack.

As 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). Such an impaired performance of red and white muscle is likely to influence survival, since both sustained swimming and rapid acceleration will be adversely affected by a change in muscle performance. This study concentrates on burst swimming performance at low temperatures, a key component of survival for many freshwater fish during the hostile winter of many northern latitude streams and rivers.

Prey fish rely heavily on a short bout of burst swimming from standing to escape from a predator's lunging attack. Burst swimming is therefore essentially a test of the ability of an animal to avoid predators. In rainbow trout (Oncorhynchus mykiss) there is little variation in burst swimming in relation to fish size (Webb 1978a, 1978b), in agreement with studies on other species (Brett, 1964; Webb, 1976; Fuiman, 1986). The explanation for this size independency is that while muscle power increases with size, so also does the resistance to movement through water. Although there is no evidence for a direct effect of size on burst swimming, it is possible that size may interact with temperature to determine burst swimming performance (Webb, 1978b). This is difficult to study because for most animals size and age are confounded. Comparative intraspecific studies are difficult if no clear size classes can be distinguished within any one yearclass (Felsenstien, 1985). Fortunately in juvenile Atlantic salmon natural size differences exist in 1 year old fish kept in hatchery tanks (see Chapter 5).

A single sibling group splits into two different size classes of the same age, an upper modal group (UMG) and a lower modal group(LMG)(Thorpe, 1977). The study described here makes use of this natural size segregation to investigate the relationship between size, temperature and burst swimming in fish of the same age.

6.2. MATERIALS & METHODS

Experiments were performed on four groups of 10 UMG fish, mean standard length 86.9 +/- 1.004 mm (2SE), and four groups of 10 LMG fish, mean standard length 60.3 +/- 0.83 mm (2SE). All fish were selected randomly from a single family of salmon previously kept at the Almondbank hatchery, Perthshire. Prior to the experiment all fish had been reared under routine hatchery conditions: ambient temperature, natural light and excess food. Each group of fish was kept at one of four acclimation temperatures (3.1 ± 0.07, 6.14 ± 0.08, 9.87 ± 0.06, 12.5 ± 0.03°C) for a two week period during the winter of 1991 and fed an equal maintenance ration. At the end of each two week acclimation period individual fish were selected at random and conditioned for a 6 hour period in white fibreglass testing tanks, 50 x 50 x 10 cm, maintained at the same test temperature. There was no turnover or re-circulation of the water in the test tank and dissolved oxygen was maintained close to saturation by means of an air stone. Test tank water temperatures were maintained at the previous acclimation level for individuals.

After the settling period, burst swimming was initiated by means of vibrational cues generated by a swinging weight (0.5 kg) falling from a fixed distance (90°) against the side of the tank nearest to the fish. Fish were always motionless and close to the side of the tank when stimulated. The fish responded to this stimulus by burst swimming, comprising a rapid increase in velocity to a maximum before returning to a stationary position at the other side of the tank. A CCTV camera with an 18 mm lens was used to record fast starts on VHS format video tapes (25 frames/second). The film record included a time clock and the camera was mounted above the tank to record when the weight struck the tank. At the end of every trial all fish were weighed and measured (fork length). The film record of the fast start was then analysed, at 50 records per second (i.e. one every 0.02 seconds). The motion of the straight stretched body was determined by plotting a point taken directly between the eyes at each 0.02 second interval. This was then used to determine the distance covered as a function of time. Webb (1975) suggests that the best measure of performance during a fast start is the distance travelled over a specified time period, since computational errors are less likely to be made. This measure also integrates all the subtle influences of recoil movements from various parts of the body which are generated during burst swimming. So a standardised time period of 0.08

seconds from the start was chosen for the statistical analysis. This is also the time period which most prey species have to respond successfully to a predatory attack (Webb, 1976). Performance indices (acceleration and velocity) were calculated subsequently from these derived measurements and used in a group comparison of absolute distances in terms of body lengths. Temperature-induced differences between the UMG & LMG groups were tested using analysis of covariance of performance versus temperature.

6.3 RESULTS

In the first 0.08 seconds the total distance covered increased significantly with temperature for both the UMG group (regression analysis, $r = 0.502$, $n = 40$, $p < 0.005$) and the LMG (regression analysis, $r = 0.717$, $n = 40$, $p < 0.001$), see Figure 6.1A. A clear difference in group performance was apparent at low temperatures Covariance analysis showed a significant difference in the slopes of the two regression lines for the total distance covered by UMG and LMG fish ($F_{1,55} = 5.6$, $p < 0.05$) (Figure 6.1A). The total distance covered by LMG was significantly lower than that of UMG fish at 3°C (t-test = 2.3, D.F = 7.13, $p < 0.05$) and at 6°C (t-test = 2.38, D.F = 9.13, $p < 0.05$), but not at the two higher acclimation temperatures.

Average velocity, calculated as a function of distance and time, also increased significantly with temperature for both the UMG group (regression analysis, $r = 0.455$, $n = 40$, $p < 0.005$) and the LMG (regression analysis, $r = 0.697$, $n = 40$, $p < 0.001$)(Figure 6.1B). A clear difference in group performance was also apparent at low temperatures. Covariance analysis showed a significant difference in the slopes of the two regression lines for the average velocity achieved by UMG and LMG fish ($F_{1,55} = 4.74$, $p < 0.05$)(Figure 6.1B). The average velocity of LMG fish was significantly lower than that of UMG fish at 3°C (t-test = 2.16, D.F = 10.85, $p < 0.05$) and at 6°C (t-test = 2.24, D.F = 9.42, $p < 0.05$) but not at the two higher acclimation temperatures. In terms of relative performance (bodylengths per second) there was a significant increase with temperature for both the UMG group (regression analysis, $r = 0.511$, $n = 40$, $p < 0.005$) and the LMG (regression analysis, $r = 0.713$, $n = 40$, $p < 0.001$)(Figure 6.1C). A clear difference between groups was also apparent (Figure 6.1.C). Covariance analysis showed a significant difference in the slopes of the two regression lines of bodylengths per second for UMG and LMG fish ($F_{1,54} = 7.66$, $p < 0.01$)(Figure 6.1C). The number of bodylengths per second of LMG fish was significantly higher than UMG at 13°C (t-test = -3.63, D.F = 13.41, $p < 0.01$) but not at the other three acclimation temperatures.

Figure 6.1A.

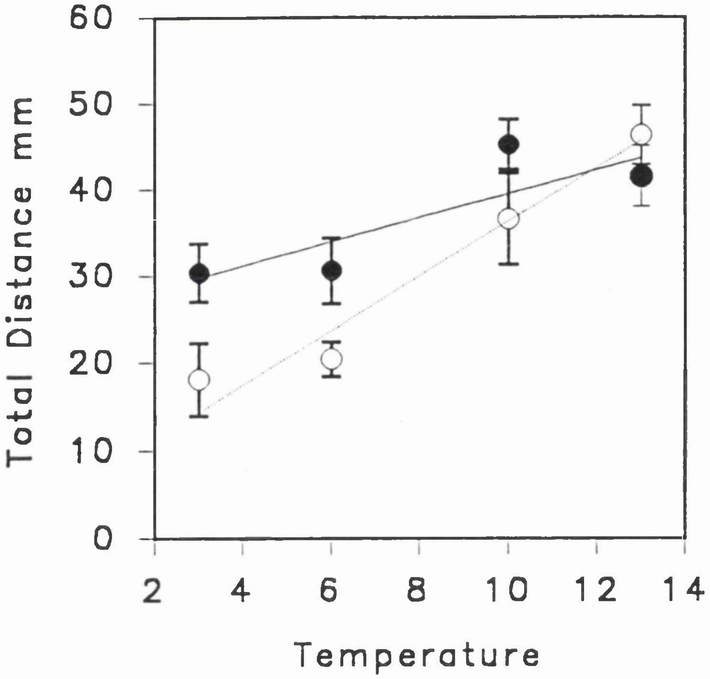
Distance travelled over the first 0.08 seconds of burst swimming in relation to temperature. Data are presented as means ± s.e. for the four temperatures : 3°C, 6°C, 10°C, 13°C. LMG: open circles with regression line; UMG: closed circles with regression line.

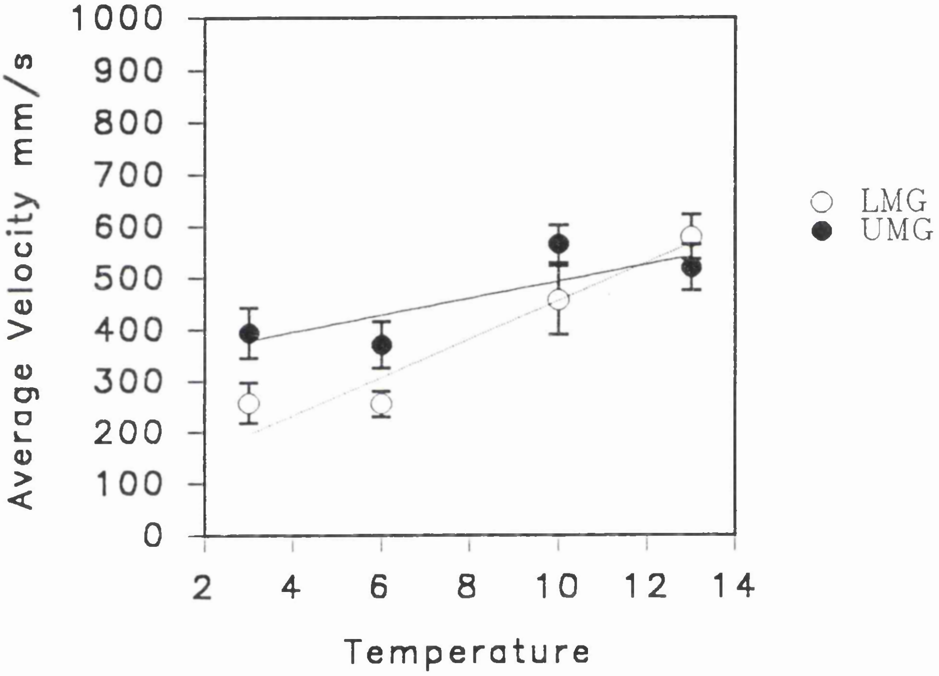
Figure 6.1B.

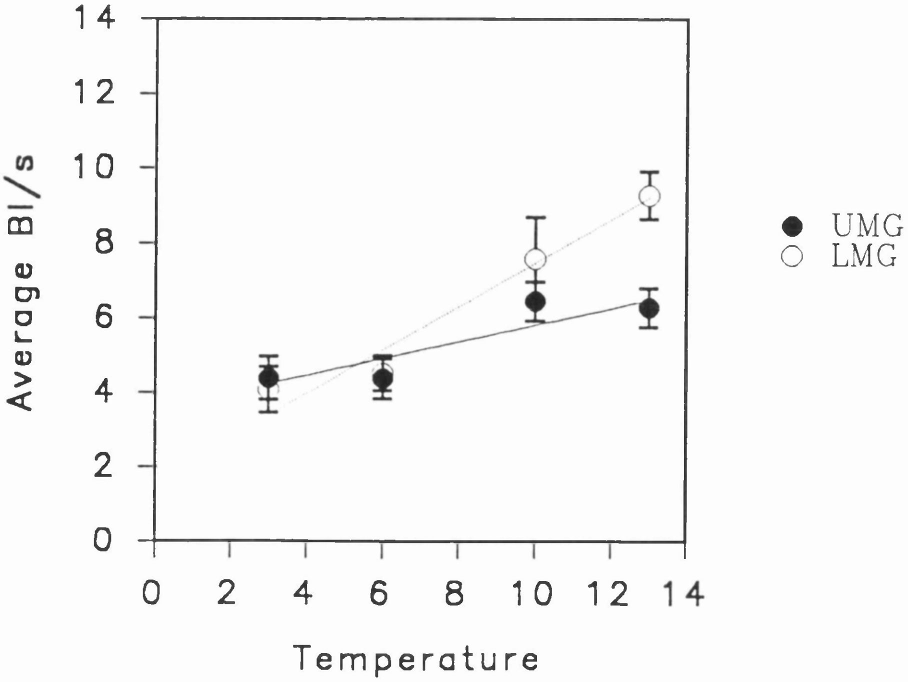
Velocity over the first 0.08 seconds of burst swimming in relation to temperature. Data are presented as means ± s.e. for the four temperatures : 3°C, 6°C, 10°C, 13°C. LMG: open circles with regression line; UMG: closed circles with regression line.

Figure 6.1C.

Speed in bodylengths/second over the first 0.08 seconds of burst swimming in relation to temperature. Data are presented as means ± s.e. for the four temperatures : 3°C, 6°C, 10°C, 13°C. LMG: open circles with regression line; UMG: closed circles with regression line.


Total Distance mm
60
50
40
30
20
10
0
2
4
6
8
10
12
14
Temperature


Average Velocity mm/s
1000
900
800
700
600
500
400
300
200
100
0
2
4
6
8
10
12
14
Temperature
○ LMG
● UMG


Average Bl/s
14
12
10
8
6
4
2
0
0
2
4
6
8
10
12
14
Temperature
● UMG
○ LMG

6.4 DISCUSSION

Maximum velocity and distance travelled over the first 0.08 seconds of a fast start are both significantly reduced at low temperatures in juvenile Atlantic salmon. This temperature dependency of burst swimming would be expected for an ectothermic animal (Prosser, 1973). Similar work on other fish has shown that both rainbow trout (Webb, 1975) and larval Zebra danios (Fuiman, 1986) have a temperature dependent burst swimming behaviour. However, differences in performances between the UMG and the LMG were apparent for total distance covered and average velocity at lower temperatures : LMG fish became more impaired as temperature decreased. A similar result was reflected by the body lengths per second since a smaller fish (e.g. a LMG fish) would need a higher relative performance, to achieve the same velocity as a large fish. Hence, in this experiment at lower temperatures the smaller (LMG) fish were not exceeding the number of bodylengths per second of the larger, UMG, fish. In summary, these results show that for both modal groups performance is impaired at low temperatures and this would increase the risk of predation; but for the smaller LMG group fish that risk of capture by a predator is significantly higher than for the UMG. To explain the cause of these temperature dependent differences in performance both physiological and environmental factors need to be taken into account.

One extraneous environmental factor that has been put forward as an explanation for this change in swimming performance is water viscosity (Webb, 1978b). At lower temperatures the viscosity of water increases, consequently the total drag over the body of a moving animal increases. However, these temperature induced changes in the physical properties of water are unlikely to explain much of the observed variation in swimming performance because a change in water viscosity is less important to an animal moving at relatively high speeds, such as a fast start, according to Reynolds's law. During burst swimming only the first 0.002-0.006s should be influenced by viscous drag, so a viscosity effect would not be noticeable (Webb, 1978b).

The most often cited, and most likely, causal explanation for the reduction in burst swimming performance at low temperatures is increased contraction time and decreased power of the white swimming muscle at lower temperatures (Bennett, 1984, 1990; Marsh & Bennett, 1985, 1986; John-Adler et al., 1989; Marsh, 1990; Swoap et al., 1993). As temperature drops there is a reduction in tailbeat frequency and hence in maximum attainable speed (Archer & Johnston, 1989). Such an effect would explain the overall effects of temperature on performance in the present experiment, but would not necessarily explain the differences found in burst swimming performance between the UMG and LMG groups.

The differences in performance between the UMG and LMG was apparent only below 10°C : LMG fish performing less well as temperature dropped. One tentative suggestion that might explain this result is that the upper modal group may modify their functional capacities in response to the thermal environment by means of temperature acclimation. A long term drop in temperature of at least 10 days may stimulate compensatory acclimation in a fish (Prosser, 1973). The problem for a fish at low temperatures is that enzyme - substrate affinity drops leaving some enzymes highly inefficient and possibly inactive. To bypass this problem some species, such as the goldfish (Carassius auratus), the common carp (Cyprinus carpio) and the roach (Rutilus rutilus), are known to mobilise new isozymes below a certain temperature threshold with higher absolute and/or maximal affinities for their substrate (Hochacka & Somero, 1971). Classic temperature acclimation is through the substitution of one isozyme with another at low temperatures which gives an individual a higher metabolic rate (Prosser, 1973). More recently temperature acclimation has been associated with an increase in red muscle and heart ventricle mass (Johnston & Goldspink, 1975; Johnston & Lucking, 1978; Sidell, 1980; Jones & Sidell, 1982; Goolish, 1987) and an increase in aerobic enzyme activity within these tissues (Shaklee et al., 1977; Kleckner & Sidell, 1985). It may be therefore that UMG, being naturally more active in winter, have undergone some sort of temperature acclimation that allows them to protect their burst swimming performance at low temperatures.

Circumstantial evidence for this idea comes from Higgins & Talbot's (1985) study on the metabolic rate and muscle histology of UMG and LMG juvenile Atlantic salmon. UMG fish had greater white fibre areas (used in fast starts (Sidell, 1980)), higher oxygen consumption (metabolic rate) and heavier heart weights when compared to LMG fish as a function of body size. They concluded that 'LMG fish have a "suppressed" metabolic response relative to the UMG which may be initiated and regulated by environmental influences acting through the endocrine system' (Higgins & Talbot, 1985). This study shows that the physiological differences seen between the two modal groups are comparable to other fish undergoing the process of temperature compensation. Given that these bimodal size differences begin in autumn, when the ambient temperature is falling towards its winter low, it is possible that the degree of temperature compensation in each group may be different

No studies have yet been done on burst swimming performance and acclimatory temperature adaptation for fish. Circumstantial biochemical evidence from the activity of myofibrillar

ATPase in white fish muscle does however suggest that partial temperature compensation may occur (Larimore & Duever, 1968; Heap et al., 1985; Rome et al., 1985; Altringham & Johnston, 1990) . This should allow for enhanced fast start performance in cold environments. To establish such a presumptive link would require extensive work on the muscle contractile properties of both modal groups in relation to the effects of temperature acclimation. In particular the contractile properties of isometric and isotonic white muscle should be measured (Else & Bennett, 1987). The possibility that thermal compensation can explain the behavioural and physiological adjustments made early in the first winter by fish that are going to smolt the following spring still remains unclear.

Regardless of their physiological origin, the differences in performance at low temperatures between UMG & LMG can have implications for their behavioural capacity. Young salmon normally feed by holding station on or near the bottom in the fastest flowing section of the stream where there is maximum drift of food (Hynes, 1970; Everest and Chapman, 1972). They intercept prey by darting (burst swimming) from their holding stations into the faster current. In winter a young salmon's critical holding velocity (Rimmer et al., 1985) and burst swimming performance (present study) are drastically reduced. So their overall ability to intercept prey and to hold station decreases with temperature. The implications of these results are that fish adopting a LMG life history in the wild will be unable to avoid predators as efficiently as their larger siblings in the UMG. LMG fish might compensate behaviourally for this adversity by taking fewer risks, as seen in Huntingford et al's (1988a) study.

For many years it has been noted that very few young salmonids are seen or caught in rivers once the temperature falls below roughly 10°C (Gibson, 1973). It is now known that the sudden disappearance of fish in the water column during the day is related to their increasing use of daytime refuges : the lower the temperature falls the more inclined the fish are to seek shelter in the streambed during the day (Lindroth, 1955; Gibson, 1978; Rimmer and Paim, 1984). More recently behavioural studies have shown that salmon become active at night during winter i.e. they leave their daytime refuges (Heggenes et al., 1993) and this shift to nocturnalism is now thought to be an almost exclusively temperature dependent effect (chapter 5). It is clear from the study described in this chapter that at lower temperatures, fish become more constrained physiologically with a consequent reduced capacity for behaviour depending on burst swimming (Webb, 1975; Wardle, 1975; Goldspink, 1977; Taylor & McPhail, 1985). This may have led to an overwintering behavioural strategy oriented around predator avoidance (Gibson & Fry, 1954; Peterman & Gatto, 1978) and might also help to explain the shift to nocturnalism at low temperatures.

CHAPTER 7

OVERWINTER HABITAT SELECTION OF JUVENILE ATLANTIC SALMON KEPT IN AN ARTIFICIAL STREAM

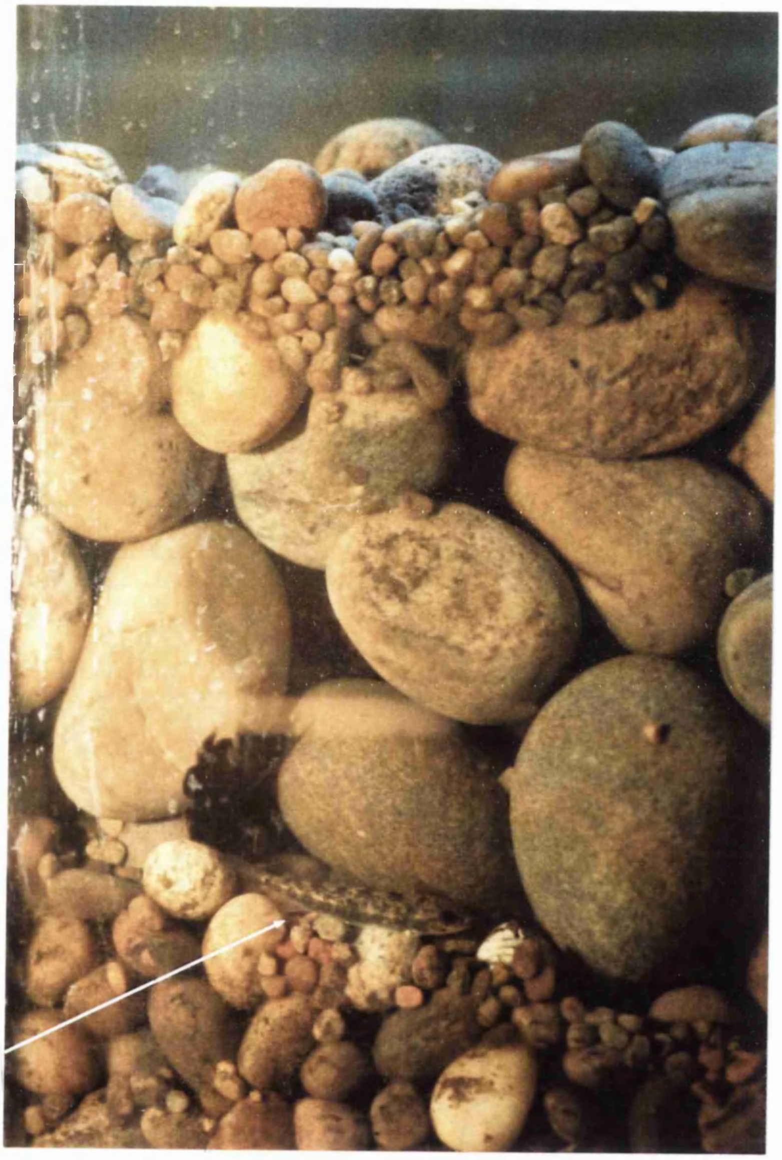
7.1 INTRODUCTION

The developmental changes in fish behaviour associated with adoption of a particular life history strategy can be most clearly seen under extreme environmental conditions, and for juvenile Atlantic salmon the first clear visible differences in life history can be seen at the beginning of winter. Thorpe (1977) showed that for a single sibling group of juvenile Atlantic salmon, kept in controlled hatchery conditions, the size frequency distribution splits into a bi-modal one (i.e. a group of large fish and a group of small fish). In the winter the larger fish (the Upper Modal Group, UMG) remain active, keep feeding and smolt in the following spring, whilst the smaller fish (the Lower Modal Group, LMG) are less active and anorexic over the winter. In addition, these smaller fish will remain in freshwater for at least a further year (Thorpe, 1977).

Much of the work done on the behaviour of the UMG and LMG has come from studies carried out in large scale hatchery tanks and these studies have shown clear differences in the overwintering behaviour of the two groups (Metcalfe et al.,1986,1987, 1989, 1990 ; Huntingford et al.,1988a,b). One problem with studies under controlled conditions is that they are hard to relate to the overwintering behaviour of salmonids in the natural environment. Field studies have shown that most young salmon and trout overwinter in the streambed in refuges similar to the one shown in Plate 4 (Hartman, 1963; Gibson, 1978; Gardiner & Geddes, 1980; Rimmer et al., 1983, 84; Cunjak, 1988a,b; Rimmer and Paim, 1989; Heggenes & Saltveit, 1990; Garcia de Leaniz, 1990; Veselov & Shustov, 1991). This behaviour appears to be unique to the stream environment and hardly anything is known about the use of such shelters by individuals. In addition none of the above laboratory or field studies take into consideration the recent findings of the shift to nocturnal activity during winter which has shown that young salmon and trout emerge from these streambed refuges by night and return to hide in them by day (Heggenes et al., 1993; Chapter 5). This behaviour has not been studied in detail in a stream environment nor has it been studied it relation to life history strategies (UMG, LMG). Consequently the present study investigates the behaviour of a combined group (66 fish) of UMG and LMG fish within a stream type environment over the first winter and into the spring. This more natural setting would give fish greater flexibility in expressing the behaviour associated with their particular life history (Kalleberg, 1958; Hartman, 1963; Gibson, 1978).

Plate 4

Daytime overwintering behaviour of juvenile Atlantic salmon. The salmon in the photograph is around 6cm long and is hiding in a refuge 50 cm below the surface of the streambed.


streambed
ile Atlantic salmon

7.2. METHODS

On the 28/10/92 thirty three UMG (fork length 92.9 +/- 1.13 mm) and thirty three LMG (fork length 57.3 +/- 1.6 mm) juvenile salmon were selected from a single sibling population kept at the S.O.A.F.D Almondbank hatchery, Perthshire. All sixty six fish had been reared together in hatchery tanks under the same conditions and were six months old at the start of this experiment. The selected fish were taken to the University Field Station, Rowardennan, where they were kept under routine hatchery conditions until the start of the experiment on the 3/11/93. In the intervening period, to aid identification of fish in the experimental stream channel, UMG fish were marked on the caudal peduncle with alcian blue; LMG fish were left unmarked

The design of the stream channel was based on that used in previous studies of salmonid behaviour (Kalleberg, 1958; Gibson, 1978). It was a 16m long oval shaped channel (depth 60cm; width 60 cm) with an inside wall made from glass panels (thickness 1.5cm) and an outside wall made from meshed fibre glass (Figure 7.1A). The glass panels ran along the straight section of the interior wall; thus providing a clear view across the width of the tank from inside the oval. In the end sections, small windows aided observation. The central section was roofed over, giving sufficient darkness to allow observations without disturbing the fish. The channel was landscaped with gravel as a single long section with alternate deep (depth approx. 55 cm) and shallow habitats (depth approx. 25cm). Gravel of mixed size was evenly spread across the width of the channel, elevated at points to form 8 shallow sections (length 20-35cm), with graded slopes in the straight sections of the stream channel. Embedded into the slopes of the 8 shallow sections were fish shelters made from PVC piping (diameter 10cm) cut in half. The bends of the tank were left empty of gravel to deter fish from occupying them. Each shelter was buried into the gravel slope alongside a glass side wall, at an angle of around 45° from vertical. This gave a fish access from the stream (Plate 5) and also allowed an observer to monitor the number of fish hiding. The presence of an observer did not displace fish from these hides during the experiment nor did the sudden illumination of artificial lights close to the hide. In total, 16 shelters were buried, one on the upstream and one on the downstream slope of each shallow section (Plate 5).

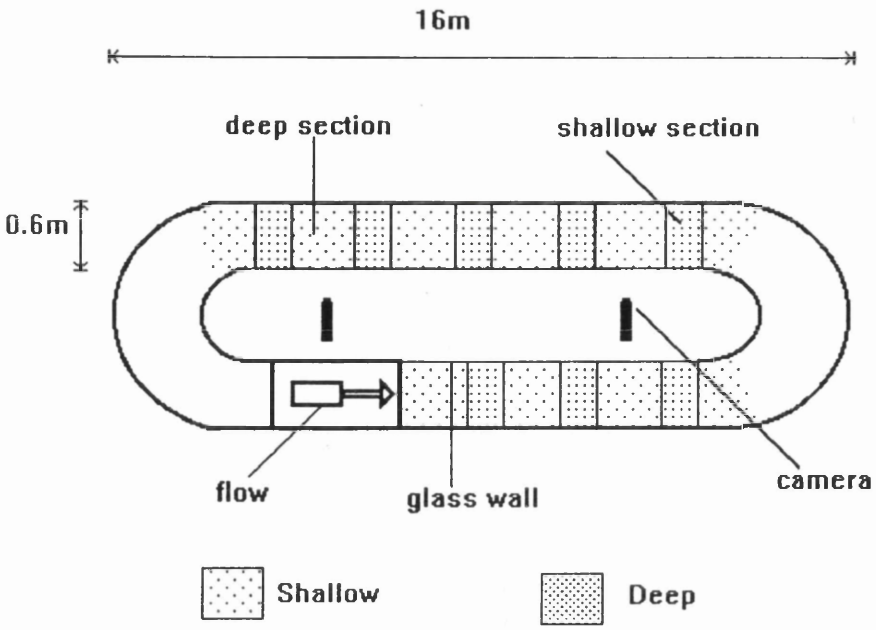
Experimental fish experienced the natural changes in light and photoperiod from November to March. Stream flow around the tank was provided by a Flygt mixer pump. This gave a velocity profile around the tank approximating to 9-10 cms^{-1} F and 1.5 cms^{-1} at the bottom (Figure 7.2). Freshwater was supplied (approx 12 l/min) to the flume up until the loch water supply failed on the 21/12/92.

Figure 7.1A

Top view of flume

Plate 5

Side view of 2 shelters and a deep section


16m
deep section
shallow section
0.6m
flow
glass wall
camera
Shallow
Deep

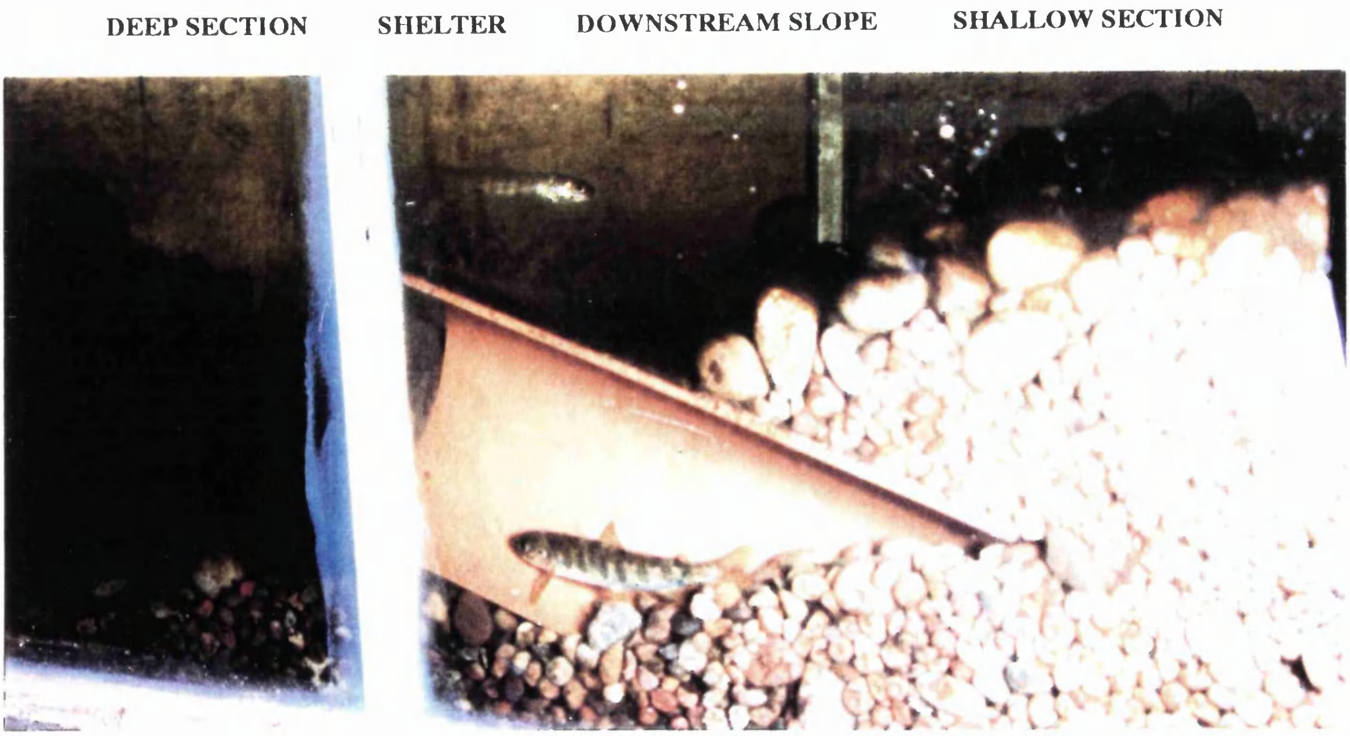
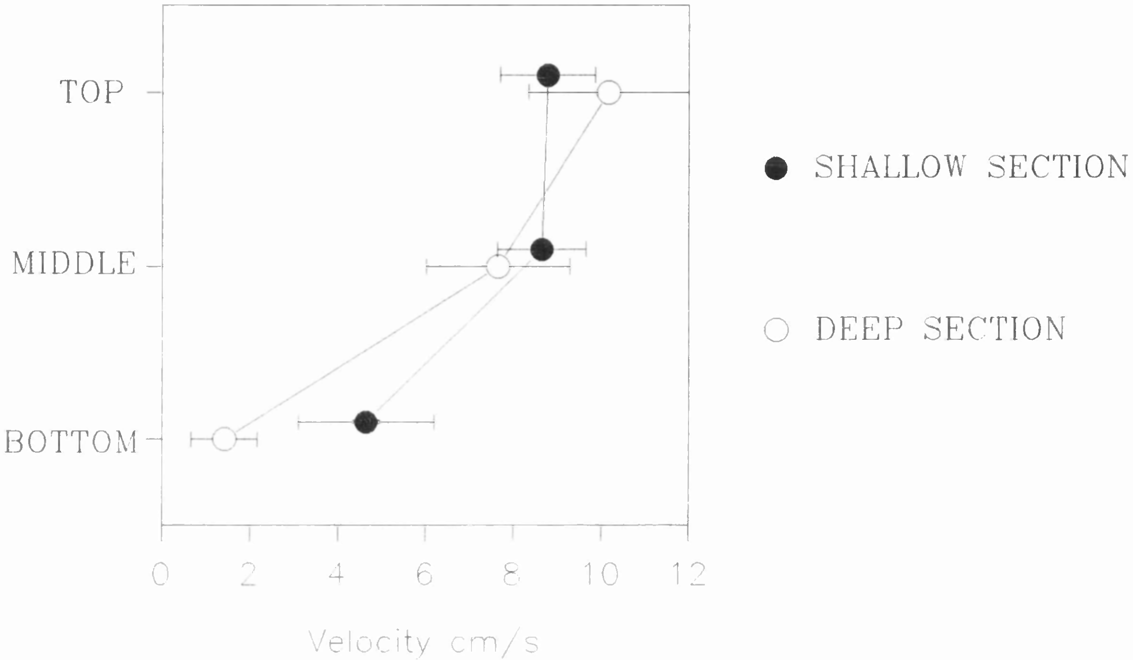

DEEP SECTION
SHELTER
DOWNSTREAM SLOPE
SHALLOW SECTION

Figure 7.2
Vertical flow profile of flume tank



Fortunately the pump inside the stream channel recirculated the water, and provided sufficient aeration for the fish. The loch water supply was not connected up again until late February but the experiment in the flume continued throughout. Therefore water temperature fluctuated more closely with air temperature for most of the experiment. Fish were fed once a day, at different times, with 100g of frozen bloodworms.

7.2.1 BEHAVIOURAL SCREENING

Behavioural surveys of the whole stream channel were carried out once a fortnight. The tank was surveyed as 2 main areas: sector A (upstream) and sector B (downstream). Within these two areas, 15 cm sectors were used to identify a fish's position to a small stretch of the tank. Screening involved recording flume section occupied, whether they were on the substrate and/or taking shelter, position in the water column (where appropriate) and the occurrence of aggression and feeding. All surveys were carried out before the fish were fed each day.

7.2.2 FILMING

Two CCTV cameras were set up to monitor areas of 1 metre in length in the upstream and downstream areas of the flume channel (Figure 7.1A). Each camera viewed two hides and one deep section. Recordings from each camera were made in daylight (10h00, 12h00, 15h00) and in darkness (19h00, 20h00, 4h00) every day for 2.5 minutes. During the day the full section of stream could be seen clearly by both cameras but at night the infra-red lights gave sufficient illumination for the shelters only to be visible. The infra-red lights were timed to come on immediately after the cameras so that the influence of illumination on behaviour could be seen. The video tapes were analysed to provide information on hide use by day and by night, aggression levels, feeding rates and position.

On the 22/3/93 the flume experiment was shut down after an outbreak of gas bubble disease. This problem was first recorded on the 11/3/93 and soon could be seen in the majority of the fish. At the end 28 fish were finally caught and weighed: 8 LMG (fork length 66.4 +/- 3.6 mm) and 20 UMG (fork length 105.1 +/- 1.55 mm). All UMG fish showed clear signs of smolting (silvery flanks and darkened fin edges). The results from the film work and surveys were then analysed to assess the changes in behaviour and habitat for each group of fish over the 5 months.

7.3 RESULTS

The disappearance of fish from each group (percentage of total remaining at end UMG = 40%; LMG = 76%) clearly occurred at different times. Most of the UMG fish appear to have died sometime in March, as evidenced by the high numbers of fish seen in the February surveys (32 of the original 33) (Figure 7.3.A). However, the very high mortality rate of LMG fish could have occurred at any time over the winter (Figure 7.3B). In all surveys fewer LMG than UMG fish were observed, but the difference in numbers of fish seen in each group did not change significantly over the five months ($X^2 = 6.14$, d.f. = 4, $P > 0.05$, see Table 7.1).

7.3.1 BEHAVIOURAL SCREENING

Data on position were amalgamated into a 5 x 2 contingency table of month by sector (upstream vs downstream) for each modal group. A chi-square test was then used, for each modal group, to assess whether there were any significant changes in the use of upstream and downstream positions with time (Table 7.2 and 7.3).

In UMG fish there was a significant change in position during the 5 month period ($X^2 = 18.432$, d.f. = 4, $P < 0.001$). To identify where these differences came from, an *a posteriori* partitioning procedure was carried out, with an adjusted critical value of $P < 0.01$ (Siegel and Castellan, 1988). This showed that there were no differences in the number of UMG fish seen in either the upstream or downstream sectors for the first three months (Table 7.2). However in February 1993 there were significantly more UMG fish in the upstream sector ($X^2 = 14.469$, d.f. = 1, $P < 0.001$). From the observations carried out at the time it was clear that the change in position in February resulted in the formation of a shoal of UMG fish in a very small section of the upstream arm (Figure 7.4A). This shoaling behaviour by the UMG was also reflected in a gradual shift into midwater over the five months (Figure 7.5A). Significantly more UMG fish were to be found in midwater after February compared to previous months (Partitioned $X^2 = 46.12$, d.f. = 1, $P < 0.001$).

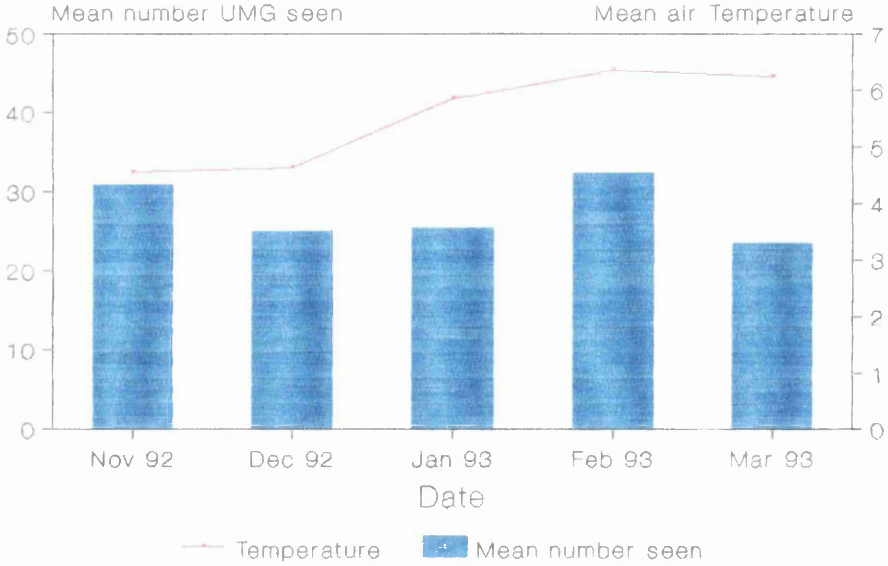
There was no significant change in the position of LMG fish over the 5 month period ($X^2 = 0.641$, d.f. = 4), see Table 7.3. More LMG fish were found in the upstream

Figure 7.3A

Mean number of UMG fish seen in each month in relation to mean air temperature. Total numbers seen in the stream channel were unrelated to temperature (Spearman rank = 0.0630, n= 24, p >0.05).

Figure 7.3B

Mean number of LMG fish seen in each month in relation with mean air temperature. Total numbers seen in the stream channel were unrelated to temperature (Spearman rank = 0.1707, n= 24, p >0.05).


Mean number UMG seen
Mean air Temperature
50
40
30
20
10
0
7
6
5
4
3
2
1
0
Nov 92
Dec 92
Jan 93
Feb 93
Mar 93
Date
Temperature
Mean number seen

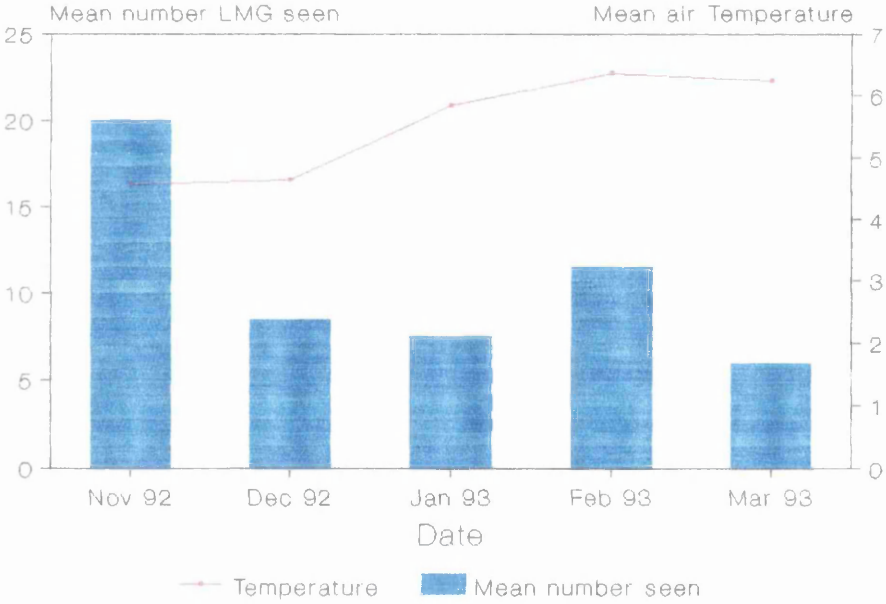

Mean number LMG seen
Mean air Temperature
25
20
15
10
5
0
7
6
5
4
3
2
1
0
Nov 92
Dec 92
Jan 93
Feb 93
Mar 93
Date
Temperature
Mean number seen

Table 7.1.

Average number of UMG and LMG fish seen in each month for the downstream and upstream sectors during surveys ($X^2 = 6.14$, d.f. = 4, $P > 0.05$).

Month	UMG	LMG	Partitioned X^2
Nov / 92	30.5	19.5	(D.F = 1)
Dec / 92	25	8	2.25
Jan / 93	27	7.5	1.64
Feb / 93	37.5	10.5	1.106
Mar / 93	23	5	1.153

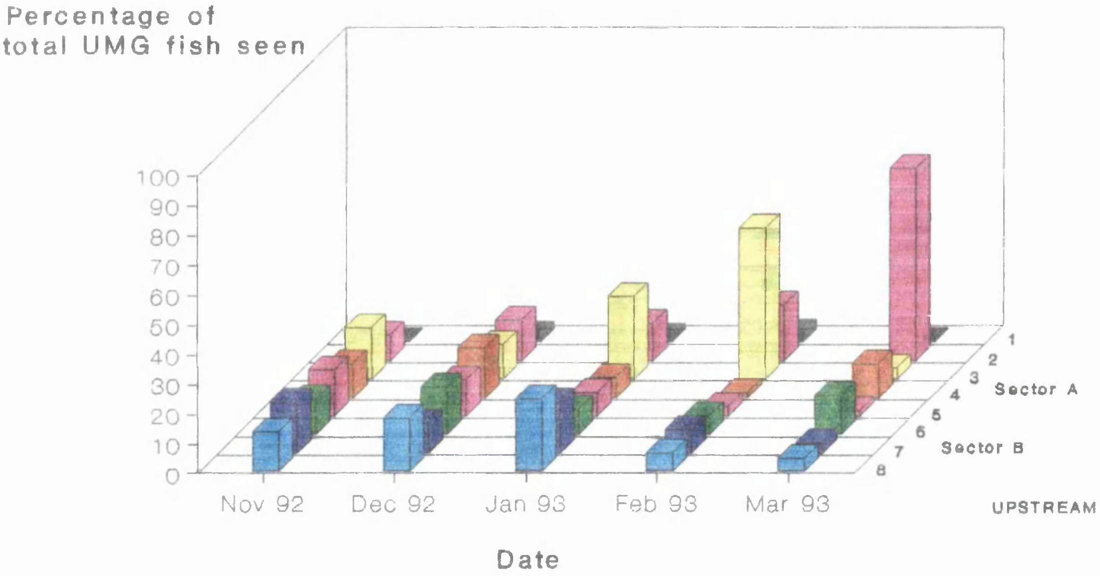
Significantly more fish observed: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Figure 7.4A

Percentage of total UMG fish seen in each month in each sector. Both downstream and upstream sectors are divided up into four subsectors. This clearly shows a strong site specificity of positioning in February and March for the UMG.

Figure 7.4B

Percentage of total LMG fish seen in each month in each sector. Both downstream and upstream sectors are again divided up into four subsectors. No temporal change in positioning is evident but there is a clear preference for the upstream sectors throughout the 5 month period.


Percentage of total UMG fish seen
100
90
80
70
60
50
40
30
20
10
0
Nov 92
Dec 92
Jan 93
Feb 93
Mar 93
Date
1
2
3
4
5
6
7
8
Sector A
Sector B
UPSTREAM

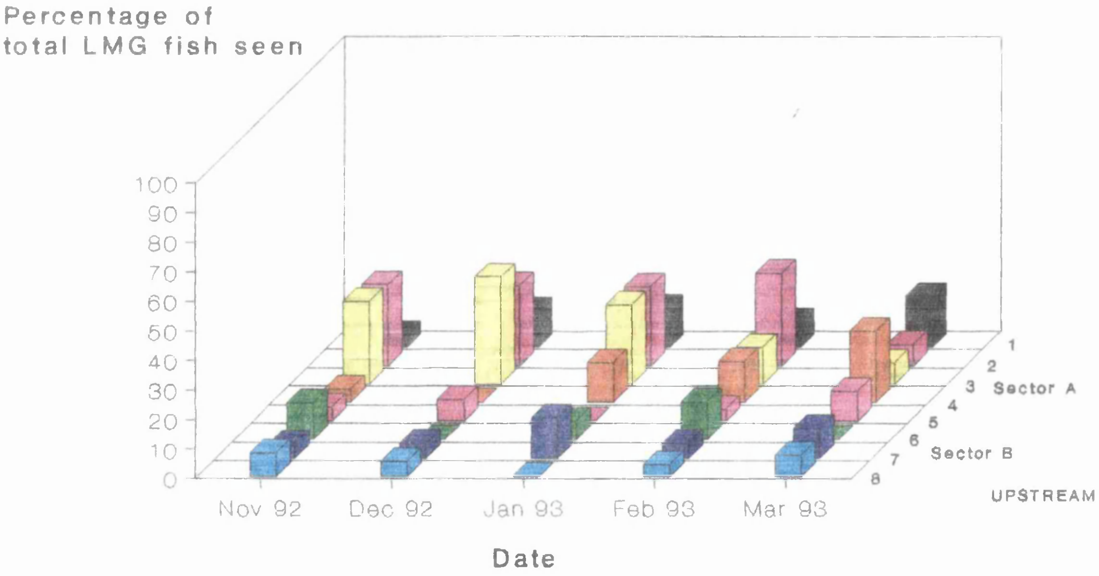

Percentage of total LMG fish seen
100
90
80
70
60
50
40
30
20
10
0
Nov 92
Dec 92
Jan 93
Feb 93
Mar 93
Date
1
2
3
4
5
6
7
8
Sector A
Sector B
UPSTREAM

Table 7.2.

Average number of UMG fish seen in each month for the downstream and upstream sectors during surveys ($X^2 = 18.432$, d.f. = 4, $P < 0.001$).

Upper Modal Group	Upstream A	Downstream B	Partitioned X^2
Nov / 92	12	18.5	(D.F = 1)
Dec / 92	11	14	0.122
Jan / 93	12.5	14.5	0.176
Feb / 93	30	7.5	14.469***
Mar / 93	17.5	5.5	3.665

Significantly more fish observed: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Table 7.3.

Average number of LMG fish seen in each month for the downstream and upstream sectors during surveys ($X^2 = 0.641$, d.f. = 4, $P > 0.05$)

Lower Modal Group	Upstream A	Downstream B	Partitioned X^2
Nov / 92	13.5	6	(D.F = 1)
Dec / 92	6.5	1.5	0.418
Jan / 93	6	1.5	0.159
Feb / 93	7.5	3	0.034
Mar / 93	3.5	1.5	0.03

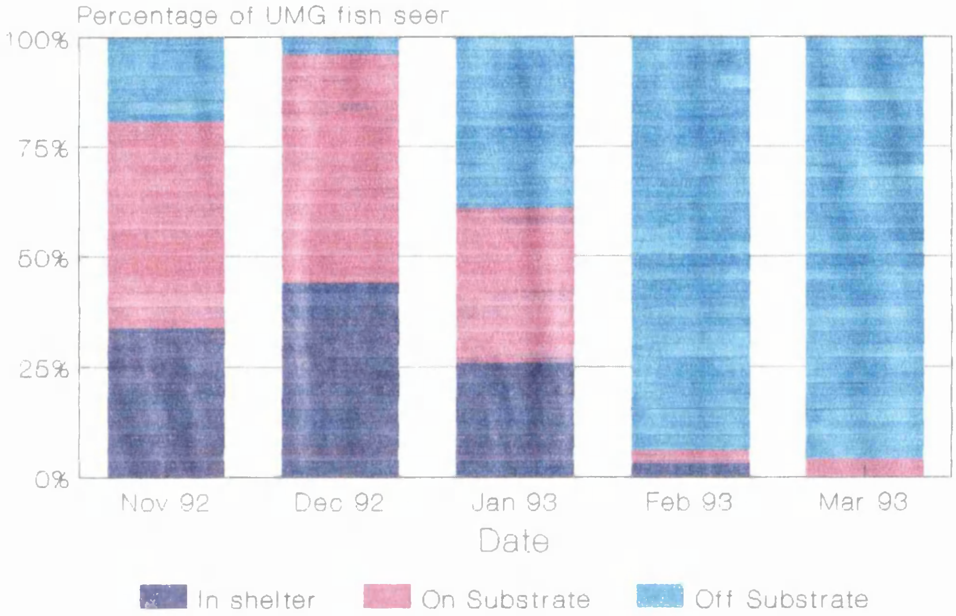
Significantly more fish observed: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

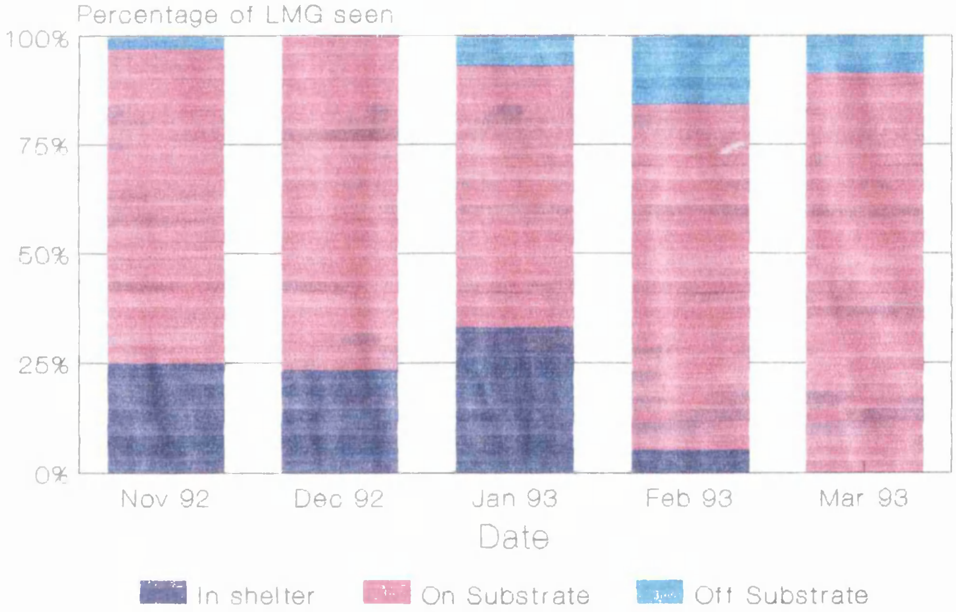
Figure 7.5A

The proportion of total UMG fish seen sheltering, touching the bottom and in midwater. No significant correlations, for the three behaviours were found with temperature or date.

Figure 7.5B

The proportion of total LMG fish seen sheltering, touching the bottom and in midwater. Fewer LMG fish were found off the substrate at lower temperatures (Spearman rank correlation = 0.9446, n = 5, $p < 0.01$).


Percentage of UMG fish seer
100%
75%
50%
25%
0%
Nov 92
Dec 92
Jan 93
Feb 93
Mar 93
Date
In shelter
On Substrate
Off Substrate


Percentage of LMG seen
100%
75%
50%
25%
0%
Nov 92
Dec 92
Jan 93
Feb 93
Mar 93
Date
In shelter
On Substrate
Off Substrate

sectors throughout the study, see Figure 7.4B (Wilcoxon, n = 5, $T^{+} = 15$ $p < 0.05$). Similarly there was no significant shift to midwater in the spring (Figure 7.5B), most LMG choosing to remain close to the substrate throughout the 5 month period. Fewer LMG fish were found in midwater at lower temperatures (Spearman rank correlation = 0.9446, n = 5, $p < 0.01$)

A stepwise multiple regression was carried out to determine the most important predictor of aggressive behaviour, with the number of aggressive interactions per exposed fish as the dependent variable and average air temperature, date, time of day and total number of exposed fish as the independent variables. No significant predictors of aggressive behaviour were found. Using the same independent variables a further stepwise multiple regression was carried out on feeding behaviour. Once again no significant predictors were found.

7.3.2 FILM

The video film provided substantial information only on the behaviour of UMG fish. Very few LMG fish were seen regularly throughout the 5 months which made group comparisons impossible. In addition, by March virtually all fish had moved upstream and out of view of the cameras.

For the UMG fish there was a clear use of shelters by day but not by night throughout the 5 months (Fig 7.6.A). A few fish stayed in shelters at night during November, December and January but by February and March no fish were seen sheltering by night (Figure 7.6.A). A stepwise multiple regression was carried out to determine the most important predictor of daytime sheltering behaviour, with mean number of fish exposed by day as the dependent variable and average air temperature, date and time of day as the independent variables. Date was the only important predictor of daytime sheltering behaviour ($F_{1,119} = 80.75$, $r^2 = 0.40$, $p < 0.001$).

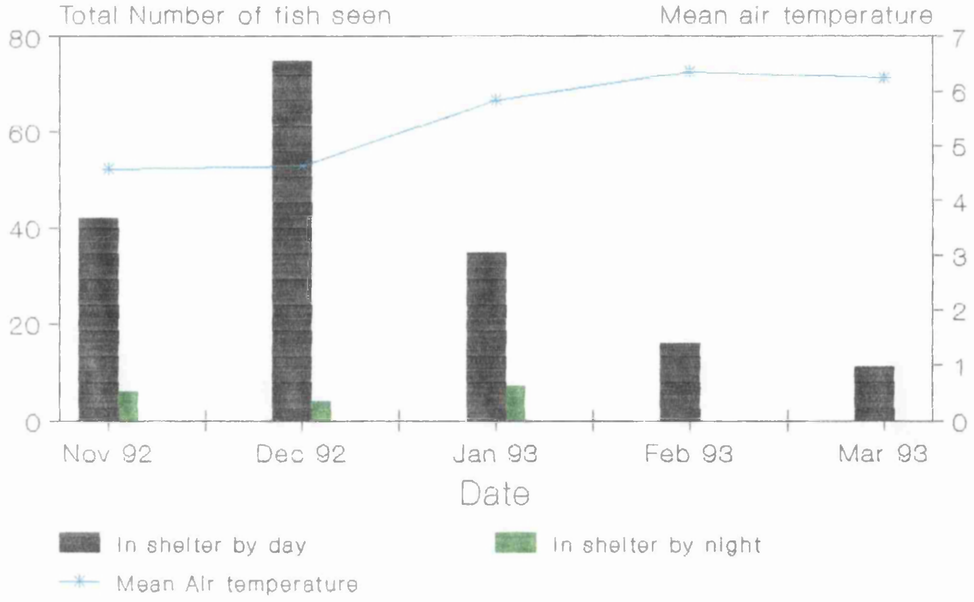
Figure 7.6.B shows that there was a significant tendency for remaining close to the substrate in December and January (partitioned $X^2 = 57.956$, d.f. = 2, $p < 0.001$), whilst in February a clear shift to midwater by the UMG was seen (partitioned $X^2 = 58.907$, d.f. = 2, $p < 0.001$). This midwater activity of UMG fish lasted until the end of the experiment and during this time loose shoals of UMG fish could be seen on the video recordings. To evaluate the most important influence on positioning for exposed fish, position was regressed on average air temperature, date and time of day.

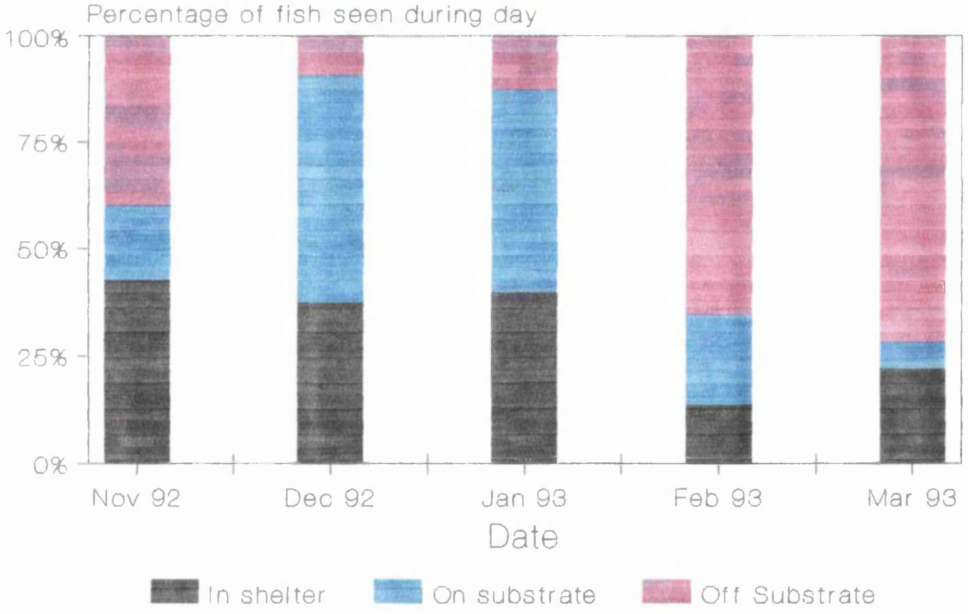
Figure 7.6A

The total number of UMG fish seen on film sheltering by day and by night in each month (Number of days sampled in each month = 14). Below 5°C there was a significant correlation between number of fish sheltering and temperature (Spearman rank correlation = -.343, n = 57, $p < 0.01$).

Figure 7.6B

The proportion of total UMG fish seen on film sheltering, touching the bottom and off the substrate.


Total Number of fish seen
Mean air temperature
80
60
40
20
0
7
6
5
4
3
2
1
0
Nov 92
Dec 92
Jan 93
Feb 93
Mar 93
Date
In shelter by day
In shelter by night
Mean Air temperature


Percentage of fish seen during day
100%
75%
50%
25%
0%
Nov 92
Dec 92
Jan 93
Feb 93
Mar 93
Date
In shelter
On substrate
Off Substrate

This showed that the only significant predictor of whether a fish was on ($F_{1,119}$ = 9.499, $P < 0.01$) or off the substrate ($F_{2,118}$ = 10.27, $P < 0.001$) by day was date. A final comparison between daily air temperature extremes and positioning at equivalent sampling times showed no significant correlations.

A stepwise multiple regression was carried out to determine the most important predictor of daytime feeding behaviour, with mean number of feeds per exposed fish as the dependent variable and average air temperature, date, time of day and total number of exposed fish as the independent variables. The only significant predictor of the amount of daytime feeding was the total number of fish exposed ($F_{1,113}$ = 8.15, r^2 = 0.067, $p < 0.001$). However, a similar stepwise multiple regression carried out for the number of aggressive interactions per exposed fish showed that date was the most important predictor of aggression ($F_{1,113}$ = 13.17, r^2 = 0.104, $p < 0.001$) followed by the total number of fish exposed ($F_{1,113}$ = 11.05, r^2 = 0.16, $p < 0.001$). This latter result reflects the shift to the midwater shoaling behaviour seen in both the survey and film records of early spring when the aggression rates were clearly lower, see Table 7.4.

Table 7.4.

Average number of UMG feeding attempts and aggressive interactions per exposed fish seen in each month.

Month	Number of feeds per exposed fish	Number of aggressive interactions per exposed fish
Nov / 92	0.38	0.32
Dec / 92	0.48	0.12
Jan / 93	0.33	0.11
Feb / 93	0.24	0.06
Mar / 93	0.32	0.07

7.4 Discussion

The most striking difference between UMG and LMG fish was the midwater shoaling behaviour. A few UMG fish were first seen shoaling on the 19/11/92 in the downstream area of the tank. However by the 5/2/93 a large (*circa* 20) shoaling group of UMG fish had moved forward into the upstream section of the tank. The film results also indicated that there was a clear decline in aggression over this spring period (Table 7.4). Interestingly LMG fish failed to take advantage of this sibling shoal of larger fish for protection against predation.

Shoaling behaviour can be seen in streams at this time of year in smolting groups of fish, which often congregate in deeper pools (personal observations). However, in the wild smolting fish would be expected to move downstream and not up. This unnatural behaviour may have been caused by two factors : 1) the food supply came from the upstream end of the tank and 2) the stream channel was a closed system. Other work done on smolting salmonids in enclosed systems similarly suggests that unnatural migratory movements may occur (Hoar, 1958).

A further interesting behaviour seen in UMG fish in the early part of the winter was the night/day shift in sheltering behaviour. This movement out of shelters by night would not appear to be related to the nocturnal activity often associated with salmonid downstream migrations (Hoar, 1958), as the majority of migrations occur in early spring, not the middle of winter. Recent work would suggest that the amount of daytime sheltering behaviour would be closely correlated with temperature (chapter 5) However only daily mean air temperatures could be used in the statistical analysis of present data which may not have been a very accurate measure of flume water temperature.

The other main result from this work was the very low number of LMG fish found at the end of the winter. Although there was a protective bird net over the whole stream channel, endothermic predators could have forced their way through to the stream. It is unlikely though that there was any selective predation by such a predator, e.g. a mink (Mustela vison), because these endotherms are known to preferentially select larger sizes of fish (Kruuk et al., 1993). Furthermore there was no evidence of predation (i.e. fish remains). It is more likely that the LMG fish either : 1) starved to death or 2) were somehow in a position, such as deep in the gravel, where a change in oxygen concentration was lethal or 3) they were unable to find suitable overwintering habitat (streambed refuges, plate 4).

Whatever the reason for this mortality, the implications are still the same. If LMG fish do not survive the winter in great numbers then it is unlikely that they will survive in a stream up till smolting stage. Hence the LMG group found in hatchery tanks might not be seen in the wild, but the behaviour associated with this hatchery tank life history (LMG) may be an example of the kind of sacrifices most non-smolting salmonids have to make during winter.

CHAPTER 8

GENERAL DISCUSSION

8.1 INTRODUCTION

The objective of this thesis was to investigate behaviour exhibited by juvenile Atlantic salmon that might be predominantly controlled by either light or temperature. This led to a series of studies on a variety of behaviour patterns exhibited during two key phases of a juvenile Atlantic salmon's life history, namely the first movements away from the redd and the first winter. This final chapter brings together the main findings of these studies in relation to the two key times originally chosen.

8.2 MOVEMENTS AWAY FROM THE REDD

8.2.1. EFFECT OF LIGHT INTENSITY ON NIGHTLY MOVEMENT

Light levels have often been implicated as a possible releasing factor triggering the movement of alevins away from the redd. In Chapter 2 this relationship was investigated and a clear correlation was found between nightly activity and light level, with fewer alevins moving away from the redd as light levels increased. This simple relationship was interpreted as a negative photokinesis, since the frequency of movement was dependent on the intensity of the stimulation. It was concluded that this behaviour could therefore be the result of a simple photoresponse or retinal developmental differences between alevins (less developed alevins becoming temporarily disorientated and hence move away from the redd because the ambient night-time incident light is still below their threshold level) (Ali, 1961; Manteifel, 1978). This movement of alevins away from the redd appears to be predominantly controlled by light level, but the exact underlying mechanism behind this behaviour is not yet clear. To investigate this further fine scale patterns of behaviour during movement were investigated in Chapter 3.

8.2.2. TIMING AND METHOD OF MOVEMENT AWAY FROM THE REDD

Filmed alevin behaviour (Chapter 3) showed that nightly movements were temporally clumped and that peak dispersal time was in the first half of the night, which is in agreement with other studies. In addition, it was very clear that fish were moving away from the redd at two different levels in the water column; close to the substrate and in midwater. This behaviour was very similar to that described by a recent study (Garcia de Leaniz et al., 1993b), and so further work was done to investigate the different methods of movement observed. Undergravel trapping results revealed that a small proportion of alevins from all the redds were choosing the gravel of the stream bed as a medium for movement. Therefore, it would appear that alevins are able to control the timing and method of movement away from the redd which goes against the traditional view that movement of alevins away from the redd is the result of displacement due to a temporary disorientation (Bardonnet et al., 1993).

8.2.3. DAILY ACTIVITY PATTERNS AFTER MOVEMENT AWAY FROM THE REDD

In the natural environment the nocturnal movement of alevins away from the redd continues for a number of nights and alevins may move up to 200 metres or more in total. Once they have settled into a first feeding site they quickly adapt to a diurnal lifestyle. The exact sequence of these events and their timing are not known. In Chapter 4 this problem was investigated for two groups of newly dispersed alevins kept at different temperatures. The first group of alevins shifted slowly to a diurnal lifestyle over a period of one week whilst the other group adopted a diurnal lifestyle immediately. This difference in timing could be explained by a difference in developmental stage between the two groups or alternatively it could have been a temperature dependent effect similar to that found in Chapter 5. Another interesting aspect of this study was the dramatic influence of an accidentally increased flow on the shelter seeking behaviour of one group of alevins. This behaviour is not unusual and has been reported for other salmonids (Hoar, 1958). Hiding at high flow is clearly a safety response which would help prevent young alevins being displaced and is further evidence that young alevins are capable of making a controlled dispersal away from the redd. Interestingly the nocturnal activity of alevins was completely suppressed over the two days of high flow, which implies that a dispersing alevin may try to seek shelter under the gravel as flow increases both by day and by night. Hence the streambed is a natural safety zone which can be used to avoid predators and high water velocities. Competition for this shelter may also influence movement up and downstream of alevins in early Spring.

8.3. THE FIRST WINTER

8.3.1 DETERMINANTS OF DIURNAL-NOCTURNAL SWITCHING IN FORAGING SALMON

During winter some salmonids are known to adopt a nocturnal lifestyle which involves hiding in streambed refuges by day and emerging into the water column by night. This behaviour has only recently been reported in the literature and so no studies had been done to determine the underlying influences behind the reported seasonal change to nocturnalism. In Chapter 5 it was demonstrated that this switch to nocturnalism can be induced in individuals during any season (i.e. it is independent of life history strategy) by manipulating water temperature. Parallel changes occur in the retinae of juvenile salmonids, so making the fish more dark adapted at low temperatures (Allen & Munz, 1983); both behaviour and sensory physiology have therefore evolved in tandem. Three possible functional explanations, which may not be mutually exclusive, for this shift in behaviour were put forward, namely restricted food availability , avoidance of competition and avoidance of predation. Furthermore a putative relationship between temperature, activity and light level was outlined. 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 and sensory effects on foraging efficiency within the same species. Future research may reveal how the relative costs and benefits of such variables as feeding efficiency and predation risk may influence this behavioural switch.

8.3.2 THE EFFECT OF TEMPERATURE ON BURST SWIMMING PERFORMANCE

Another behaviour related to overwintering nocturnalism is burst swimming performance. In Chapter 6 the burst swimming performance of juvenile Atlantic salmon was found to be significantly reduced at low temperatures. This is to be expected for an ectothermic animal and has been found many times before. However, differences in performance were evident for groups of juvenile Atlantic salmon adopting different life history strategies. The burst swimming performance, in terms of absolute distance, of a LMG fish was more impaired by a temperature decrease then that of an UMG fish. Hence there is an increased risk associated with activity for both groups of juvenile Atlantic salmon at low temperatures. In addition the risk of capture by a predator for a LMG fish is significantly higher which may explain the known behavioural differences between the two groups.

8.3.3 OVERWINTERING BEHAVIOUR IN AN ARTIFICIAL STREAM

Up till this point the work undertaken on juvenile Atlantic salmon behaviour had been carried out entirely inside closely controlled environments, so a final study in a flume tank was used to investigate the overwintering behaviour of juvenile Atlantic salmon in relation to life history strategy. Fish from both modal groups exhibited the shift to daytime sheltering behaviour and activity at night in early winter. Towards February a large shoaling group of UMG fish had congregated in a small area of the tank. This change in social behaviour from an aggressive animal to a relatively unaggressive shoaling one, is associated with the downstream migration to the sea of UMG fish as smolts. No LMG fish exhibited such behaviour, so by February there was a marked habitat segregation between the two modal groups with the LMG defending small home areas and remaining in close association with the substrate whilst the UMG shoaled in midwater and showed limited aggression to conspecifics.

So for juvenile Atlantic salmon adapting to life at low temperatures has forced them to use daytime shelters in the substrate of the streambed and shift to a nocturnal foraging pattern. Temperature is a controlling factor for this behaviour and it is now essential to investigate how other changes in the physical environment from one day to the next (e.g. night-time light intensity and stream water depth) can influence the cost/benefit ratio of different foraging options. The flexibility in foraging shown by salmon makes them not only an excellent behavioural model for pure science research but also could influence the aquaculture industry since the standard practice in salmon farms is to feed the fish only during the daylight hours.

8.4 FISHERIES MANAGEMENT CONSIDERATIONS

The specific behaviour patterns outlined in this thesis and their steering components are closely related to survival in the natural environment. Many of the behaviours observed clearly give fish flexibility at times of year when their chances of survival are poor (Garcia de Leaniz, 1990). A clear example of this is the overt behavioural adaptations made by salmonids to feed and survive in the winter stream environment. This flexible mode of foraging, described in chapter 5, is thought to maximise feeding efficiency in summer but reduce predation risk in winter. This shift in priorities may occur due to changes in the relative costs and benefits of different foraging options. Such diverse foraging patterns require fisheries managers to consider the availability of sufficient overwintering habitat and more importantly to correct daytime electrofishing estimates of abundance according to water temperature. For example, in glacial streams it has now been shown that juvenile Atlantic salmon will remain nocturnal throughout the summer (Fraser et al., in prep). Similarly estimates of abundance may also have to be corrected for fry dispersal.

8.5 FISH FARMING IMPLICATIONS

In the past 25 years the increasing importance of the salmon farming industry has led to an upsurge in the number of studies on the behaviour of artificially reared salmon. Many of these studies have concentrated on the feeding behaviour of the freshwater and sea water stages of the salmon. At present, the diel rhythm of activity in farmed fish is not that far removed from the wild salmon with both groups undergoing similar shifts in activity at certain times in their life history, though attempts have been made to manipulate these shifts in artificially reared salmon (Thorpe, 1981). Therefore, a lot of these shifts in activity of captive salmon strains are still adaptations originating from the natural environment. This has resulted in the 'ghost' of the wild fish still remaining in many of the captive strains of salmon. Therefore in order to understand what cues a salmon uses to time activity it is necessary to have a thorough knowledge of the natural environment in which these animals evolved. However the current approach of the farming industry is to try and force the salmon's endogenous feeding rhythm into a convenient and productive time and place.

Food intake and growth are closely related in salmonids. The most important controlling factors behind these variables are thought to be water temperature and size. Farmed fish will not grow as well at very low or high temperatures as at intermediate ones because appetite is reduced. At present salmonids are fed by day on land and sea based farms according to temperature, daylength, fish size and fish health. No attempt is made to manipulate the natural environmental cues available to the fish and so the activity of fish changes with the daily and seasonal changes in natural light and temperature. In Spring and early summer salmonids are normally active around dawn and dusk whilst in late Summer and early Autumn salmonids feed mostly during the day. In the winter there is increasing evidence that the preferred feeding time of many salmonids is at night (Adron et al., 1973; Landless, 1976; Fraser et al., 1993; Heggenes et al., 1993).

Fish farming feeding techniques should accommodate for any possible shifts in daily behaviour with season. This is important because although there is enough evidence to suggest that fish can learn at what time to expect food (Adron et al., 1973), there appears to be no evidence that they will switch their diel activity pattern in response to food availability. The clearest way of expressing this is simply to say fish feed because they are active, and are not active because they are feeding (Swift, 1964; Andreasson, 1969; Eriksson & Alanärä, 1990). Fish farming is now a matured industry and yet it still has many immature unprofitable practices one of which is the feeding regimes used at present. Hopefully future research will reveal the influence of environmental cues on feeding activity. This may help farmers to increase feeding efficiency and reduce the release of nitrogenous waste products.

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