

The causes, resolution and consequences of contests for space in Atlantic salmon (*Salmo salar* L.)

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For my family, with love and gratitude.

2017

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Declaration

I declare that this thesis is entirely my own composition and that I performed all the research described herein.

Kirstine I. O'Connor
August 1999

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There have been so many positive influences throughout my PhD that it is difficult to know where to start.

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Summary

The objectives of this thesis were firstly, to examine fighting behaviour in juvenile Atlantic salmon (*Salmo salar*) and to relate this to the natural situation under which these contests will occur; and secondly, to examine the factors that determine dominance and their consequences.

Analysis of the behaviour of contesting dyads of fish revealed a tendency for subordinate fish to darken in body and sclera colour during aggressive encounters with a dominant conspecific. Since this darkening accompanies a reduction in the aggressive behaviour of the dominant fish it is hypothesised that darkening signals submission to an opponent. This hypothesis is compatible with both the Sequential and Cumulative Assessment Models. These models predict that in deciding what strategy to employ at any time during a contest an individual should consider all the information it has obtained up to that point, including the cumulative damage it has incurred during the fight. Both of these models suggest that combatants will alter their behaviour as a fight progresses and end the contest once one combatant acknowledges its opponent's superiority. By darkening in colour a subordinate fish is recognising its opponent's superiority and avoiding a protracted fight. Since fighting is costly, natural selection will favour any mechanism such as submission signalling that leads to shorter and hence less costly fights.

When fights between familiar opponents were compared to those between unfamiliar opponents, there was a trend for subordinate fish to darken at lower fight intensities when fighting familiar opponents. It is suggested that, in this context, darkening is used as a signal of submission when an individual faces an opponent it knows to be of superior resource holding potential. In this way potentially costly escalated fights are avoided and a subordinate fish may avert a costly battle and conserve energy for a fight against a stranger where the outcome is less predictable.

The influences of asymmetries in standard metabolic rate (SMR), date of first feeding and prior residence upon dominance, territory acquisition and growth were examined. Contrary to previous work there did not appear to be a correlation between SMR and dominance or growth. However, when salmon fry were separated into Early First Feeders (EFF), Late First Feeders (LFF) and Intermediates (according to the amount of yolk remaining in their yolk sacs and thus their anticipated date of switching to exogenous food) and placed into a stream tank simultaneously there was a clear effect of first feeding date. EFF tended to have more stable territories and LFF tended to dart higher into the water column to intercept prey items. These results suggest that EFF have an intrinsic advantage over LFF, which means that they are more likely to establish and maintain feeding stations.

To examine the influence of prior residence on behaviour and growth performance, the residence of groups of salmon fry was manipulated so that one group arrived at a new habitat three days ahead of a second group. Although there did not appear to be any difference in the dominance rank of the two groups of fish, the first fish to arrive in the habitat fed at a higher rate and subsequently grew faster. These results suggested that the advantage of early emergence is not entirely attributable to intrinsic differences and the advantage is partly mediated through a 'prior residence' effect.

Although this study did not find any advantages of high SMR it is hypothesised that SMR, date of first feeding and prior residence are so interwoven that to analyse their individual effects masks the true extent of their influence upon dominance and consequently growth. Since fish with a high SMR would tend to exhaust their yolk sacs sooner they will have an earlier first feeding date than fish with low SMRs. In addition, their early switch to exogenous feeding means that they emerge from the redd sooner than low SMR fish and thus gain a prior residence advantage. In this way the indirect advantages of a high SMR may be stronger than its direct influence when it is examined out of the context of a natural stream environment.

As the stream environment is extremely heterogeneous and food supply unpredictable, the stability of SMR under conditions of food deprivation were examined. Fish reduced their SMR after a period of food deprivation. However, the reduction was not uniform, so that the ranking of SMR, and by inference the dominance hierarchy, changed. This suggests that fish differ in their ability to 'down regulate' their SMR and may subsequently vary in their ability to withstand periods of low food availability. This is particularly interesting as it suggests that the flexibility of SMR rather than its magnitude may be a more realistic predictor of dominance in salmon parr.

While this thesis focuses on the short-term consequences of dominance (e.g. initial growth rate and territory acquisition), an individual's position in the hierarchy may have long term repercussions through its effect on growth rate. Dominant fish will tend to secure the most profitable feeding stations and hence have higher growth rates. The size advantage established by dominant individuals will be reflected in the probability of them metamorphosing into smolts after just one year in the river. Hence the competitive ability of juvenile salmon in their first few months of life will ultimately determine their life history strategy through its effect on growth rates. Subordinate fish that fail to obtain the growth threshold that triggers maturation during the critical period will adopt the S2 strategy and defer smolting for a further year.

Chapter 1

General Introduction

This thesis examines contests for space in juvenile Atlantic salmon. The rationale for this study and the background surrounding the subject is discussed in five main sections within this introduction. First it addresses the causes of animal conflict throughout nature. In the second section it discusses how fights are resolved and the theories surrounding the fighting strategies that opponents use during combat. The third section discusses the consequences of fights and the associated costs, and the fourth section addresses the use of Atlantic salmon in studies of animal conflict. The last section provides a brief overview of the project itself and the issues addressed in each chapter.

What causes fights?

Intraspecific competition is ubiquitous throughout nature. Conspecifics occupying the same niche will tend to have similar needs and must compete to secure resources to meet those needs (Begon *et al.*, 1990). The causes of contests vary widely according to the competitor's species and age, though they can usually be attributed to competition for space, mates and food or other limited resources.

The benefits from winning contests may be direct, as seen in contests over food where the winner gains ownership of the food item. For example the winner in a pair of duelling aphids (*Astegopteryx minuta*) gains access to the leaf feeding site (Foster, 1996). Alternatively, benefits may be indirect as contests contribute to the formation of a hierarchy that subsequently determines access to limited resources (Walter & Seyfarth, 1987). An example of indirect benefits is seen in male racoons (*Procyon lotor*) which establish a hierarchy through direct conflict which is subsequently reflected in consortship success (Gehrt & Fritzell, 1999). By determining the order of access to limited resources the competitive ability of an animal will have a significant effect on its fitness (Huntingford & Taylor, 1987).

How are fights resolved?

Game theory (Maynard Smith, 1982) is a branch of applied mathematics that is used to calculate the relative benefits of different fighting strategies by examining their costs and benefits. As the costs and benefits of contests vary so do the fighting strategies adopted by combatants. For example, pied flycatchers (*Ficedula hypoleuca*) fight more intensely to defend their territories in deciduous forests than in coniferous forest, since deciduous forest territories are of greater value and yield a higher breeding density, number of eggs laid and number of fledglings (Silverin, 1998). Similarly the elevated cost associated with contests in hypoxic environments means that male shore crabs (*Carcinus maenas*) reduce their fight duration as oxygen tensions decrease (Sneddon *et al.*, 1999).

Two basic game theory models have been used to explain how non-strategic factors, such as resource value, kinship and fighting ability, affect the evolution of combat behaviour: the Hawk-Dove game and the War of Attrition. However, these models are

limited as they do not account for the dynamic nature of fights in which an animal may modify its behaviour during a contest according to its situation. In viewing combatants as having fixed roles they do not produce the sequences of behavioural patterns that would result from animals forming behavioural strategies based upon external and internal stimuli (Enquist *et al.*, 1990). Rather than assume roles, such as those predicted by the Hawk-Dove model, animals tend to follow strategies that result in behaviourally diverse fights.

The strategy that an animal follows will determine how it behaves in certain circumstances and ultimately the probability that it will secure the contested resource. The strategy followed by the majority of a population of animals will be stable and form the evolutionary stable strategy (ESS) if it has a higher payoff when played against itself and other strategies, than the payoff for any other strategy played against it (Maynard Smith & Price, 1973). Maynard Smith and Parker (1976) applied the concept of the ESS to asymmetric contests and proposed that contests are decided on the basis of three potential asymmetries: an asymmetry in payoff, where one contestant gains more by winning than the other contestant; an asymmetry in resource holding potential (RHP; Parker, 1974) where one individual is a better competitor than its opponent; and an asymmetry in some variable unconnected with a payoff or RHP that would not affect the likely result of an escalated contest if one occurred, for example prior ownership of a territory by one of the contestants.

The transmission of information pertaining to these asymmetries occurs during contests, and several models have been put forward to explain the modification of contestants' behaviour as they receive this information (Parker & Rubenstein, 1981; Enquist & Leimar, 1983, 1987; Leimar & Enquist, 1984). The best known of these is the Sequential Assessment Model (Enquist & Leimar, 1983, 1987, 1990; Leimar & Enquist, 1984) which predicts that in deciding what strategy to employ at any time during a contest, an individual should consider all the information it has obtained up to that point. An alternative to this model is the recently developed Cumulative Assessment Model (Payne, 1998), which suggests that the temporally-varied behaviour seen in contests is due to decisions based upon the cumulative damage incurred during the fight. Both of these models predict that combatants will alter their behaviour as a fight progresses and end the contest once one combatant acknowledges its opponent's superiority. Since fighting is costly (Sneddon *et al.*, 1999) natural selection will favour any mechanism that leads to shorter and less costly fights.

In many species the transmission of RHP information is mediated through ritualised contests in which animals avoid using potentially lethal weapons or behaviours in favour of less risky clues as to their fighting ability. For example, despite the fact that both rattlesnakes (*Crotalus crotalus*) and oryx (*Oryx gazella*) have lethal weapons, they do not use them during intraspecific competition. Instead they have a ritualised style of

fighting in which opponents push each other backwards or to the ground (McFarland, 1981).

The transmission of information during ritualised fights may either avert interference competition between unequally matched opponents, or once it has begun may cut it short and avoid unnecessary costs for the opponents. Ritualised fights typically begin with low risk behaviours rather than more agonistic behaviours which may cause injury or attract predators. For example, the cichlid fish *Nannacara anomola*, starts fights with low risk behaviour such as tail beating and lateral displays rather than mouth wrestling which decreases its escape distance (Brick, 1998). Another example of opponent assessment which leads to a reduction in the probability of fight escalation is seen in red deer (*Cervus elaphus*) in which stag perform a series of low cost behaviours conveying RHP information prior to the onset of physical battle (Clutton-Brock et al., 1979; Clutton-Brock & Albon, 1979). The conveyance of information in this way means that escalated fights are rare and most contests are settled before physical contact is necessary (Krebs & Davies, 1978) although, as with any accepted zoological theory, there are exceptions. For example, each year 5-10% of male musk ox die as a result of fights over females (Wilkinson & Shank, 1977; see also Enquist & Leimar, 1990 for an explanation of fatal fighting).

Generally, fighting opponents will have conflicting interests with respect to the contested resource (Huntingford & Turner, 1987) but share a common interest in the avoidance of injury (Geist, 1974; Enquist & Leimar, 1990; Hurd, 1997). This means that mutually beneficial, and hence co-operative, signalling between opponents that can be used in mutual assessment and the resolution of disputes with minimal risk of potentially costly injuries will be favoured (Hurd, 1997).

Once an individual has decided to abandon a contest it is crucial that this information is conveyed to its opponent to avoid any further costs associated with a prolonged contest (Parker, 1974). This information may be conveyed in several ways including a change in behaviour or appearance such as a submissive posture (for example, submissive spotted hyenas (*Crocuta crocuta*) flatten their ears against their head, place their tails beneath their body and arch their back (Drea et al., 1996)) or change in colour or pattern (for example, the loser in a pair of cichlid fish *Astronotus ocellatus* exhibits vertical bars on its body (Beeching, 1995)). Alternatively, submission may be a combination of these. For example it has been hypothesised that subordinate steelhead trout (*Oncorhynchus mykiss*) remain a dark colour and change their body posture in order to reduce attacks from dominants (Abbott et al., 1985).

What are the consequences of fights?

The concept of costs associated with contest in terms of a negative fitness is critical to current ecological theory (Krebs & Davies, 1978). There are various potential

costs resulting from fights including injury (Clutton-Brock *et al.*, 1979; Shuster & Caldwell, 1989), increased predation risk (Ellington, 1983; Jakobsson *et al.*, 1995), lost foraging opportunities (Grant, 1997), an increase in energy expenditure (Hack, 1997), depletion of energy reserves (Plaistow & Siva-Jothy, 1996) and the accumulation of potentially harmful respiratory by-products (Thorpe *et al.*, 1995; Sneddon *et al.*, 1999). In addition, defeat during a contest may affect the future aggressive behaviour of an animal and hence its competitive ability (Chase *et al.*, 1994; Hsu & Wolf, 1999;). For example, recent contests significantly affect the behaviour of the hermaphroditic fish *Rivulus marmoratus* (Cyprinodontidae) and its probability of winning in a subsequent contest (Hsu & Wolf, 1999).

All of these effects may decrease an individual's competitive ability and consequently its access to resources. Hence individuals of low competitive ability may have low growth rates as they cannot secure food, low fecundity as they cannot secure mates, and incur high predation rates as they cannot secure good territories in which to shelter and feed. Thus an individual's competitive ability will ultimately determine its fitness. Moreover, in species with plastic life histories an individual's fitness will be crucial in determining its life history strategy.

Why use Atlantic salmon when studying contests?

There are three main reasons for using Atlantic salmon in a study of intraspecific competition. Firstly, due to their economic importance and relatively easy husbandry, they have been extensively studied and there is an abundance of literature available on virtually all aspects of salmon life history (see Metcalfe, 1998, for a review). Secondly, because juvenile Atlantic salmon are generally quite small it is easy to re-create and manipulate their environment in the laboratory and so examine the influence of external factors on their behaviour. Thirdly, their life history is such that they will naturally have to compete with conspecifics during early life history stages and the competitive ability of individual fish will have far reaching consequences in the context of their long-term development.

Upon emerging from their gravel nests (redds) juvenile Atlantic salmon establish feeding stations (Kalleberg, 1958; Keenleyside & Yamamoto, 1962) from which they visually (Fraser & Metcalfe, 1997) locate prey items, such as invertebrates, that are either carried in the current or suspended in the water. Since salmon emerge from the redd in numbers that far outreach the carrying capacity of the environment (Elliott, 1994) there will tend to be a large number of individuals occupying the same niche competing for similar resources (Begon *et al.*, 1990). This results in fierce territoriality among these young fish (Dill, 1978; Fausch, 1984; Cutts, 1996) and the establishment of a social hierarchy, where dominant fish gain the most energetically profitable stream positions (Fausch, 1984). Subordinate fish may either assume less profitable feeding stations or be forced

downstream by the aggressive behaviour of those that have already settled (Chapman, 1962; Mason & Chapman, 1965; Backiel & Le Cren, 1978; Elliott, 1986). Asymmetries in RHP between individuals at this stage will be instrumental in determining which fish establish feeding stations and survive, and which are displaced downstream where they face an increased risk of mortality (Elliott, 1994).

Salmon are phenotypically plastic with highly variable life-history strategies (Schaffer & Elson, 1975; Thorpe 1977, 1989, 1994; Hutchings & Myers, 1994; Metcalfe, 1998). The size distribution of a group of sibling Atlantic salmon supplied with unlimited food during their first spring will be roughly Gaussian. However, by the autumn of that year the distribution will have bifurcated into a bimodal distribution (Thorpe, 1977; Metcalfe, 1998). The larger fish (Upper Modal Group) will continue feeding over the winter and metamorphose into smolts after one year in the river (S1 strategy), whilst the slower growing fish (Lower Modal Group) will become anorexic (Metcalfe *et al.*, 1988; Metcalfe & Thorpe, 1992a) and subsequently deplete their fat reserves (Bull *et al.*, 1996). These Lower Modal Group fish smolt after at least one more year in the river (S2 strategy).

The bimodality in size, growth rates and smoltification date occurs in both wild and hatchery conditions (Thorpe, 1977; Bailey *et al.*, 1980; Bagliniere & Maisse, 1985; Bagliniere & Champigneulle, 1986; Heggenes & Metcalfe, 1991; Nicieza *et al.*, 1991). The causes of these variations in early life history strategy have been extensively studied (see Metcalfe, 1998 for review) and are generally attributed to a combination of external environmental factors (Thorpe *et al.*, 1989; Saunders *et al.*, 1994 Metcalfe, 1998;) and an individual's physiology and behaviour (Metcalfe, 1998). The interplay of these variables will affect the relative dominance and competitive ability of juvenile Atlantic salmon in the first few months post-emergence and hence the selection of a life-history strategy through their effect on growth rates (Metcalfe *et al.*, 1989, 1990; Metcalfe, 1991). Poor competitors which are unable to acquire the resources necessary to attain the growth threshold that triggers maturation during the critical period will adopt the S2 strategy, whilst faster growing fish go on to smolt in their first year (Metcalfe, 1998).

For these reasons a study of intraspecific competition in Atlantic salmon, its causes, resolution and consequences, is not only applicable to the species, but may go some way in determining the forces that drive the evolution of variable life histories.

Thesis objectives and overview

The objectives of this thesis can be separated into two broad categories: firstly, to examine fighting behaviour in juvenile salmon and to relate it to the natural situation under which these contests will occur; and secondly, to examine the factors that determine dominance in juvenile salmon and their consequences.

Although body darkening of subordinate fish has been observed in Atlantic salmon (Keenleyside & Yamamoto, 1962), it has not been examined in the context of fighting behaviour. The second and third chapters of this thesis examine the occurrence of body darkening during contests and its possible role as a signal of submission. Since Atlantic salmon emerging from a redd will hold feeding stations in close proximity to their neighbours, the third chapter focuses on the effect of familiarity on the propensity of fish to darken their bodies during aggressive contests.

The fourth and fifth chapters examine the influence on behaviour and growth of two asymmetries that will naturally exist between fish emerging from a redd. The first of these is the variation in the time of switching to exogenous food and the second is the asymmetry in the date at which the young fish leave the redd and associated prior residence advantage that the first fish to emerge will gain. While these two chapters are primarily focused on the long-term effects of asymmetries, the next chapter (6) examines the immediate influence of prior residency on the fighting behaviour of contesting pairs of fish.

A further asymmetry that may exist between contesting fish is that of Standard Metabolic Rate (SMR) which has previously been linked with dominance (Metcalfe *et al.*, 1995) and aggression (Cutts *et al.*, 1998). Chapter 7 examines the stability of an individual's SMR during a period of food deprivation to address its significance in a naturally occurring heterogeneous environment where food is not always readily available. The final experimental Chapter (8) examines the relative influence of SMR, prior residence and social context on the growth of juvenile fish. Finally, in the last Chapter (9) the results of the experiments are integrated and their implications are discussed, in relation to both Atlantic salmon and other species.

Each chapter is written as a journal paper. Chapters 2, 3 & 5 have been accepted for publication and chapters 4, 6 & 7 are currently being reviewed. Details of the accepted papers are as follows:

O'Connor, K. I., Metcalfe, N. B., and Taylor, A. C. 1999. Does darkening signal submission in territorial contests between juvenile Atlantic salmon (*Salmo salar*)? *Animal Behaviour*, in press.

O'Connor, K. I., Metcalfe, N. B., and Taylor, A. C. 2000a. Familiarity influences body darkening in territorial disputes between juvenile salmon. *Animal Behaviour*, in press.

O'Connor, K. I., Metcalfe, N. B., and Taylor, A. C. 2000b. The effects of prior residence on behavior and growth rates in juvenile Atlantic salmon (*Salmo salar*). *Behavioral Ecology*, in press.

Chapter 2

Does darkening signal submission in
territorial contests between juvenile
Atlantic salmon?

After O'Connor *et al.*, 1999

Abstract

Communication by means of visual signals occurs during the competitive, aggressive and sexual interactions of many animals. Some animals such as fish are able to change their body coloration rapidly, and there is evidence that this is used as a means of signalling. However, the precise meaning of such signals is rarely understood. The aim of this study was to examine (1) whether darkness in juvenile Atlantic salmon is associated with submission, and (2) whether changing to a darker colour could act as a signal to the opponent and hence induce a change in its behaviour. I found that both the sclera of the eye and the overall body coloration tended to darken in fish that were losing territorial encounters, while victors retained their original coloration. The darkening was rapid and usually occurred during a period of sustained attacks by the opponent; however, the aggression level immediately decreased once the losing fish had become darker. I suggest that the darkening of the losing fish was associated with submission and may result in a change in the behaviour of its opponent, so minimising the potential risk of injury during unnecessarily prolonged fights.

Introduction

Aggressive interactions are one of the commonest situations in which animals are assumed to engage in signalling. Several different types of information could be conveyed in this context, including the relative social rank of a contestant and cues indicating its intent. Signals indicating status (e.g. 'badges of status'; Rohwer, 1982; Roper, 1986) tend to remain stable over the period of a given encounter, whereas those conveying motivational state or intent are far more labile. Cues indicating intent allow combatants to continually assess their opponents in order to decide whether to abandon or continue a fight (Enquist & Leimar, 1983, 1987, 1990; Leimar & Enquist, 1984; Enquist *et al.*, 1990). While at first it might be assumed that transmission of such information to an opponent would be maladaptive, since individuals fighting over a resource have opposing interests as far as the outcome of the contest is concerned (Huntingford & Turner 1987), the contestants share a common interest in the avoidance of injury (Geist, 1974; Enquist & Lemar, 1990; Hurd, 1997). There is therefore the potential for mutually beneficial and hence co-operative signalling between opponents so as to resolve disputes with minimal risk of potentially costly injuries (Hurd, 1997). Other costs associated with escalated conflicts that may also be avoided include increased predation risk (Jakobsson *et al.*, 1995) and lost foraging opportunities (Grant, 1997). Although this strategy of avoiding excessive physical contact would potentially be open to cheating, honest signalling is likely to be the evolutionary stable strategy (van Rhijn & Vodegel, 1980).

Communication of intent in a quickly developing contest requires a graded signal that can be modified rapidly, and hence visual signals are often used in this context. While these commonly take the form of changes in body posture or movement patterns, some animal groups appear to use rapid changes in body coloration. Examples are those species of fish (such as cichlids) that have the capacity to modify both the colour and the visual pattern of areas of the body within very short time periods (Barlow, 1963; deMartini, 1985) by nervous and hormonal control of the expansion and contraction of thousands of pigment cells (chromatophores) (Waring, 1963; Fujii & Oshima, 1986; Nelissen, 1991; Hulscher-Emeis, 1992). Although visual signalling is often assumed to be a principal means of communication in fish, the vast majority of studies on colour pattern variation in fish have focused on cichlids (Nelissen, 1991; Hulscher-Emeis, 1992). Previous studies have integrated the ethological and physiological aspects of colour change in the actor (Barlow, 1963; Baerends *et al.*, 1986; Hulscher-Emeis, 1992), and several have suggested that visual signalling may modify the aggressive behaviour of the receiver (reviewed by Guthrie & Muntz, 1993).

The animals used in this experiment are juvenile Atlantic salmon (*Salmo salar*). In these young fish aggression is not associated with reproduction, but rather with the defence of a feeding territory. There is some indication that body darkening is associated with territorial defence, as territory-holding salmon have been recorded to become quite

pale in overall coloration while fighting, but darken between bouts (Keenleyside & Yamamoto, 1962). Aggressive fish have also been noted to develop vertical bands through each eye, and Keenleyside and Yamamoto (1962) proposed that it was possible to determine which was the most dominant fish in a tank since it was the one with the most pronounced vertical eye band. However, there has been no detailed investigation of either the factors that determine darkening, nor whether it is apparently being used as a signal. Therefore the goals of this study were to examine (1) whether darkening in juvenile Atlantic salmon is associated with submission, and (2) whether this darkening could act as a signal to the opponent and hence induce a change in its behaviour.

Methods

A batch of full-sibling eggs from sea run salmon caught in the River Almond, Perthshire were incubated at the Scottish Office Agriculture Environment and Fisheries Department Almondbank salmon rearing unit. The eggs were moved to the University Field Station at Rowardennan, Loch Lomond on 8 November 1996. Once hatched, the fish were kept under ambient photoperiod and temperature conditions in 1m diameter round tanks. These tanks received a continual turnover of water pumped from Loch Lomond and therefore rich in zooplankton. Once the fishes' yolk sacs were completely absorbed the fish diet was supplemented with commercial salmon food (Fulmar feeds, BOCM Pauls Ltd.), which they received *ad libitum* from automatic feeders.

On September 30th 1997 100 lower modal group fish (i.e. those that would delay seaward migration for at least a further 18 months, Thorpe 1977) were transferred to Glasgow University where they were kept in 1m wide square tanks. The fish were kept at 15°C under ambient photoperiod and hand fed bloodworm (chironomid larvae species) *ad libitum*. At this stage the fish had a mean forklength of 60.49mm ±0.75(SE) (N=80) and weighed an average of 2.32g ±0.09 (N=80).

To aid further identification each fish was given a unique combination of marks with alcian blue dye on its pectoral, pelvic, dorsal, anal and/or caudal fins. This marking technique has no effect on the behaviour or growth of first feeding salmon fry (Metcalfe *et al.*, 1992).

The experiments were carried out between 28th October and 9th December 1997 (i.e. 7-9 months after first feeding) and took place in an aquarium maintained at 15°C, with a 12L: 12D photoperiod.

Invasion Experiment

The tanks used for testing responses to territorial invasion were divided into two square halves (10x10cm) by an opaque partition, and had a water depth of 8cm. At the centre of the dividing partition was a circular door (6 cm diameter) which was initially kept shut. Three of the glass sides of the tank were coated in waterproof white paper leaving one side through which observations could be made. The substratum of each tank consisted of small marble chips (0.5cm diameter, Esmo, Rowebb) which produced a topographically natural but light coloured substratum against which the fish could easily be seen. Salmon parr in the wild will naturally come across patches of substratum of similar colour to the marble chips used in this experiment.

At 1500 hours at the start of each experimental run, fish were assigned to size matched pairs (mean percentage weight difference = 8.19±7.84%), and one fish was placed in each half of a tank. The fish placed in the left side of the tank is referred to as the 'resident', and the fish in the right side the 'intruder'. Both sides of the tank were identical in every respect, except that the side of the door facing the intruder was marked

with a red cross so that the intruder would be able to distinguish between its own familiar side of the tank and the side into which it was subsequently induced to invade (see below).

The fish were left for either 0,1,2 or 3 days in their respective sides of the tank before the experiment began. Prior residence time was varied to investigate the effect of the duration of residency on the nature and outcome of aggressive encounters with intruding fish; these analyses will be presented elsewhere (Chapter 6).

Quantification of body and eye coloration

Juvenile salmon are light brown on the dorsal and lateral surfaces down to approximately the lateral line. Below the lateral line they are light grey, shading to silver on the belly (Jones, 1959). Straddling the lateral line along each side of the body are a series of clearly defined oval dark patches called 'parr marks'. These vary in number from 7-12, with 11 or 12 being most frequent (Jones, 1959). Dorsal to the lateral line are numerous black or dark brown oval patches. These are scattered over the entire dorsal and dorso-lateral surfaces with concentrations in several irregular bands which straddle the mid dorsal line.

Three areas were identified and used to grade the colour of the fish (Figure 1). These were:

- 1 the parr marks
- 2 the spaces between the parr marks
- 3 the oval patches straddling the mid dorsal line of the fish

Each of these areas was assigned to one of three categories according to their colour (Table 1). Eye coloration was also scored. The eyes of the salmon have a central black pupil surrounded by a narrow brilliant yellow iris. Around this iris is the broader sclera which can vary in colour from light grey to black. The colour of the sclera was graded on a scale of one to three (Table 1). The intermediate sclera coloration occurred when expansion of the melanophores anterior and posterior to the pupil led to darkening of the sclera, while the sclera in front and behind the pupil remained light grey (Keenleyside & Yamamoto 1962). All colour scoring was done by me. In order to assess the objectivity of the colour grading, my scores were compared to those obtained by 5 independent fish biologists asked to colour grade the same 10 fish using the method described. There was an 80% agreement between my scores and those given by the 5 other scorers, with no consistent bias being evident. Since a total of 18 different colour grade combinations were identified during the experiment an 80% agreement constitutes a high level of concordance, and I therefore concluded that the method provided a sufficiently accurate and objective means of scoring the colour patterns of the fish.

Table 1.

Description of the colour changes and assigned scores for the eye and 3 areas of the

body of each fish (body areas are shown in Figure 1)

Body area 1	Body area 2	Body area 3	Sclera
light cream	grey/	cream/ white	light cream
slate grey	light grey	brown/	slate grey
dark black	grey/	slate grey	dark black

Both fish involved in each experiment were colour graded at 4, 2 and 0 minutes before the start of the simulated territory invasion. The door between the two sides of the testing tank was then opened and the intruder gently induced to move into the resident's side of the tank using a transparent Perspex rod. Once both fish were in the resident's side of the tank the door was closed. The behaviour of the two fish was then recorded continuously for two hours. The different behaviours of the fish were classified according to a modification of the scheme outlined by Keenleyside and Yamamoto (1962). In order to assign dominance within the pairs of fish, the classified behaviours that they exhibited were given point values and the fish that totalled the most points was classified as the winner of the contest. Points were assigned to behaviours as follows:

1 point for each lateral display, where the fish expanded all its fins maximally, tensed its body and arched its tail upwards, before beating its tail slowly, irregularly and with wide amplitude.

2 points for each charge, which is the most direct form of attack and involved one fish swimming directly and quickly towards its opponent.

3 points for each charge which culminated in the aggressor biting its opponent.

In conjunction with recording the behavioural interactions, the body and sclera colour of each fish was scored each minute over the two hour observation period. Unfortunately the observation time limitations meant that it was not possible to also record the body postures of the fish.

At the end of the observation period the fish were left for two hours, after which their colour was scored again. The fish were then fed bloodworm and left overnight in the same section of the observation tank. Next morning they were scored for colour again

before being removed and returned to the stock tank. A total of 40 replicate territorial invasions were performed, each with previously untested fish.

Ethical note: The experiment was carried out under licence from the UK Home Office. The procedure was such that the fish were continuously under observation during the period when the dominance status of the fish was established, so that it was possible to intervene and remove either fish immediately if contests ever escalated to a point where injury could occur. However this was never necessary, and interaction rates in salmon are low and rarely involve overt aggression once dominance hierarchies are established (Metcalfe *et al.*, 1989; see also Figure 4). None of the fish sustained physical damage during the contests.

Results

Patterns of darkening

Prior to the territorial invasion (two and four minutes before the partition door was opened) 75 out of 80 fish (94%) were assigned the palest possible body colour classification 1,1,1 and had a sclera colour grade 1. This pale coloration was therefore taken to represent the 'normal' condition. Any change in colour to a higher grade than that scored during the two pre-invasion measurements was deemed a darkening. Two fish darkened both body and eye colour the instant the intruder entered the resident's side of the tank. However, as no behavioural data had been collected by this time these fish were not included in the statistical analyses of the factors causing colour changes. Of the 40 contests that were staged, 22 resulted in both body and sclera darkening in at least one of the two fish which indicates a highly significant association between colour changes of the two areas (Chi-square: $\chi^2=21.78$, $P<0.001$). Two contests resulted only in a body darkening and two only in sclera darkening.

Four hours after the start of the territorial invasion, seven of the fish that had darkened their body colour had returned to their original pale coloration. Next morning twelve of the 24 were back to their normal pale body colour, while the rest were still dark.

Links between colour change and aggression

During six of the trials neither of the fish exhibited aggression, and in one trial both fish obtained the same aggression score and so could not be assigned to relative dominance categories. None of the fish involved in these seven trials darkened, and all seven trials were excluded from the statistical analyses of dominance. The mean difference in points between the winner and loser in the remaining trials was 65.42 (± 15.29 SE, $N=33$).

Nineteen of the 24 fish that developed a darker body colour were losers of the territorial contest while five were winners; thus fish winning a contest were significantly less likely to darken their body colour than those that lost (Chi-square: $\chi^2=12.83$, $P<0.001$). Of the five winners that darkened two returned to their original colour within the following twenty minutes, and the mean point difference between opponents was 28 (± 14.6), which is considerably less than the mean points difference between the opponents in the 19 contests in which the loser darkened (100.42 ± 23.18). The same trend for darkening to be associated with losing was shown with eye coloration: 19 of the 26 fish that changed sclera colour were losers while seven were winners (in one fight both the winner and loser changed), so fish that won contests were less likely to darken their sclera than those that lost (Chi-square: $\chi^2=9.14$, $P<0.01$).

The probability of an encounter resulting in a body or eye darkening increased with the total number of points scored in the contest (Logistic regressions: model χ^2 for body colour = 14.40, $P<0.001$; model χ^2 for eye colour = 20.77, $P<0.001$). The amount of

aggression a fish received significantly influenced the probability that it would darken in colour, since the more points that were scored against it the greater the likelihood that both body and sclera colour would darken (Logistic regressions: model χ^2 for body = 26.03, $P<0.001$; model χ^2 for sclera = 29.28, $P<0.001$; Figure 2). However, the number of attacks initiated by a fish had no effect on how likely it was to darken its body or sclera colour (Logistic regressions: model χ^2 for body = 3.08, $P=0.08$; model χ^2 for sclera = 0.27, $P=0.60$).

An index of body darkening throughout the experiment was calculated as the sum of the mean grades awarded for each of the body areas prior to the invasion at the start of the experiment subtracted from the sum of the grades at the end of the two hour period of observation. Therefore a fish that scored 1,1,1 at the start and 3,1,3 at the end would have an index of body darkening of four (i.e. 7-3). An aggression score was also calculated as the difference between the points scored by a fish and its opponent. The degree of darkening of losers was inversely proportional to the signed difference in the aggression scores of the two fish (Figure 3, Spearman rank correlation, $r_s = -0.67$, $N=33$, $P<0.001$). Hence the greater the extent to which a loser was attacked by the winner, the darker its final colour. However, there was no relationship between the difference in aggression points scored and the comparable index of body darkening in winners (Figure 3; Spearman rank correlation $r_s = -0.23$, $N=33$, $P=0.19$). Winners therefore tended to retain their initial coloration.

For those fish that darkened during the two hours of continuous observation, there was no relationship between the number of points scored against them up to the time of the darkening and the time at which the colour change took place (Linear regression: body: $r^2=0.04$, $F_{1,23}=0.97$, $P=0.34$; eye: $r^2=-0.03$, $F_{1,22}=0.95$, $P=0.34$). Thus the amount of aggression a fish was subjected to did not determine how quickly it darkened. There was also no relationship between the percentage weight difference of the two opponents and the time at which one of the fish darkened (Linear regression: body: $r^2=-0.03$, $F_{1,23}=0.37$, $P=0.55$; eye: $r^2=-0.04$, $F_{1,22}=0.10$, $P=0.76$). Hence the time of darkening was not mediated by a size asymmetry. However, there was a positive relationship between the time at which the sclera darkened and when the body darkened, indicating that the two areas tend to darken simultaneously (Spearman rank correlation, $r_s=0.91$, $N=24$, $P<0.001$).

In order to determine whether the darkening in losers acts as a signal to its opponent, or merely a reaction to the aggression it is subjected to, I examined the behaviour of the winner and loser relative to the time of the losing fish's colour change. To do this, the points scored by the winner during successive ten minute periods were calculated with respect to the time of the loser's first body or sclera darkening. The mean rate of aggression (points scored per 10 minute period) against the loser increased dramatically up until the point at which it first darkened body or eye colour (Figure 4; Spearman's rank correlation, body: $r_s=0.96$, $N=11$ time periods, $P<0.001$, eye: $r_s=0.87$,

$N=11$, $P<0.001$). However, after the initial darkening of colour the aggression rate dropped equally rapidly (Figure 4; Spearman's rank correlation, body: $r_s=-0.86$, $N=10$, $P<0.01$, eye: $r_s=-0.87$, $N=10$, $P<0.001$). This result suggests that there is an association between the darkening of the loser and the change in the aggressive behaviour of the opponent.

There was a trend for the mean rate of aggression (points scored per 10 minute period) by the loser to increase up to the time when it first darkened its body or eye colour (Figure 5; Spearman's rank correlation, body: $r_s=0.58$, $N=11$ time periods, $P=0.06$, eye: $r_s=0.56$, $N=11$, $P=0.07$). As the mean rate of aggression focused at the subordinate fish by the dominant fish is increasing up to the point when it darkens it may be under increasing pressure to defend itself. Thus the increase in mean aggression rate by the subordinate fish may be a direct result of an increase in encounter rate. However it should be noted that the mean aggression rate of the loser is consistently lower than the winning fish throughout the contest. The increase in aggression rate of the subordinate would seem to suggest that the change in behaviour of the dominant fish is in response to something other than a change in behaviour of the subordinate since at the time of its darkening it is becoming ever more aggressive.

Figure 1

Areas of the body of a juvenile salmon used for scoring colour.

- (1) the parr marks
- (2) the spaces between the parr marks
- (3) the oval patches straddling the mid dorsal line of the fish
- (4) the sclera of the eye

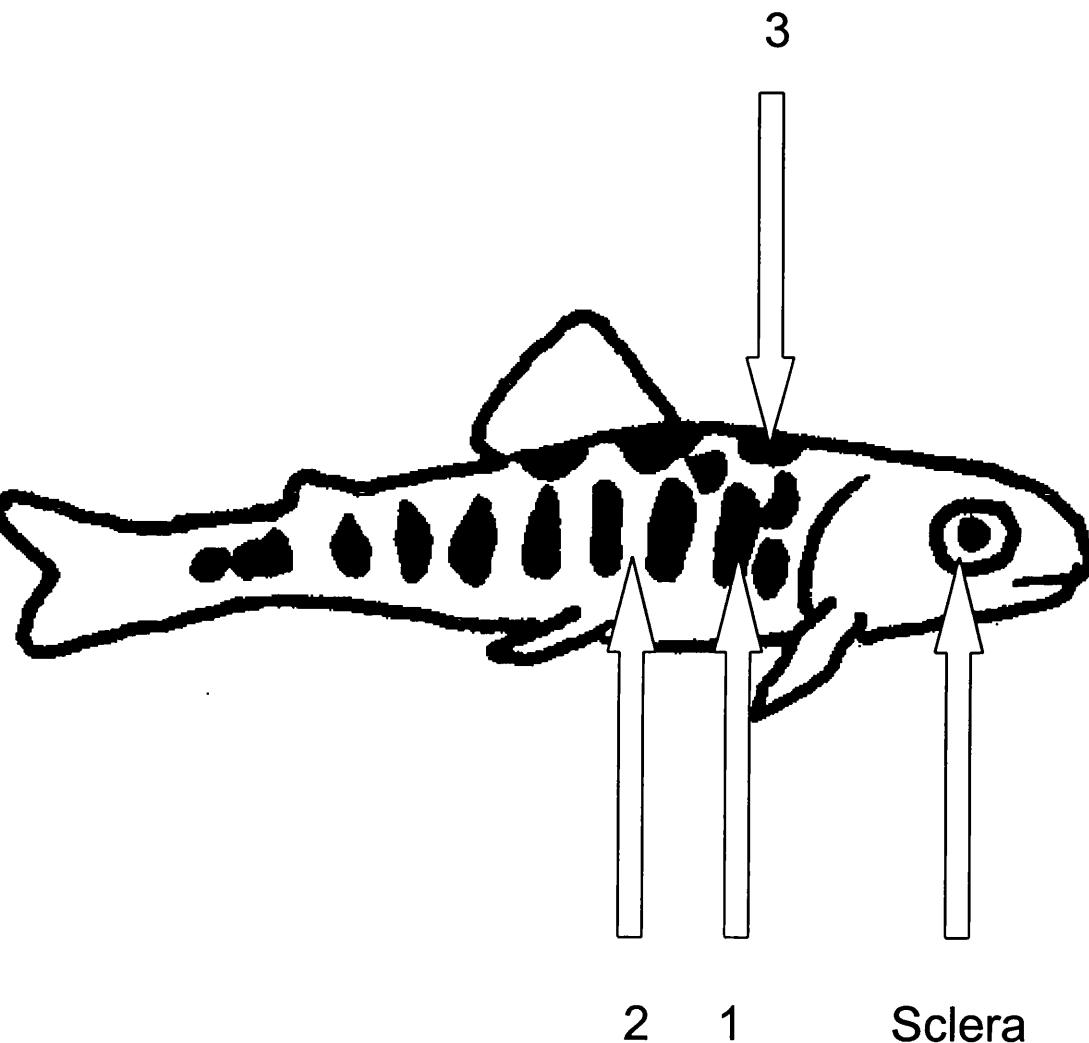


Figure 2

Relationship between points scored against a juvenile salmon and the likelihood of (a) the body and (b) the eye sclera darkening. Points scored against a fish were grouped together into 25 point bands so that the nine data points on the graph represent 33 fights.

Equations of the logistic regression lines are as follows (see text for statistical analysis):

Probability of body darkening = $a/(a+1)$, where $a = e^{(0.0315x-1.7593)}$

Probability of sclera darkening = $a/(a+1)$, where $a = e^{(0.0388x-1.7264)}$

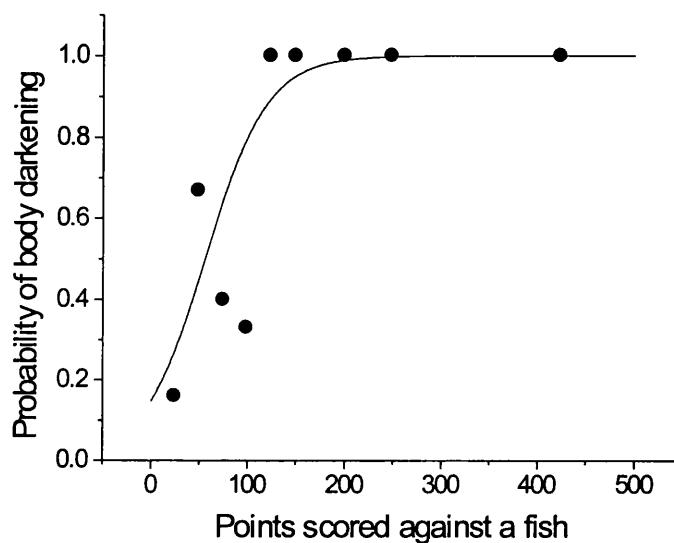
Points were awarded for aggressive behaviour as follows:

1 point for each lateral display

2 points for each charge

3 points for each charge culminating in a bite

a)



b)

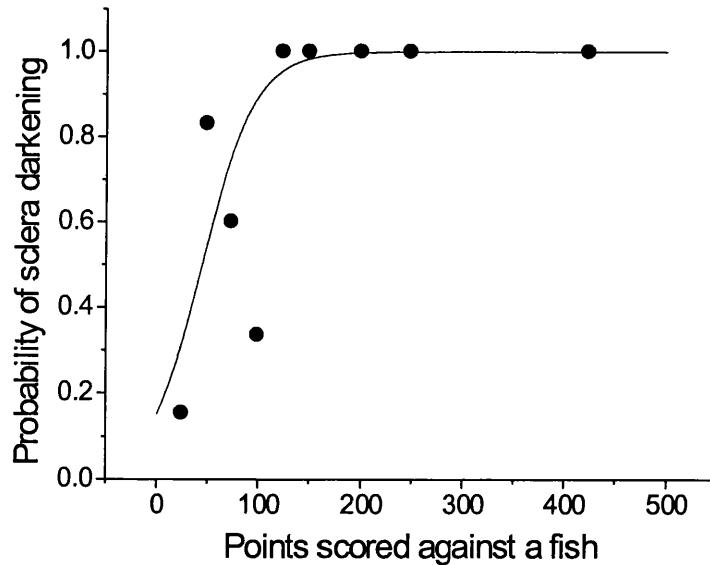


Figure 3

The relationship between net aggression score and index of the extent of body darkening in juvenile salmon. Closed symbol: losers; open symbol: winners. See text for statistical analysis.

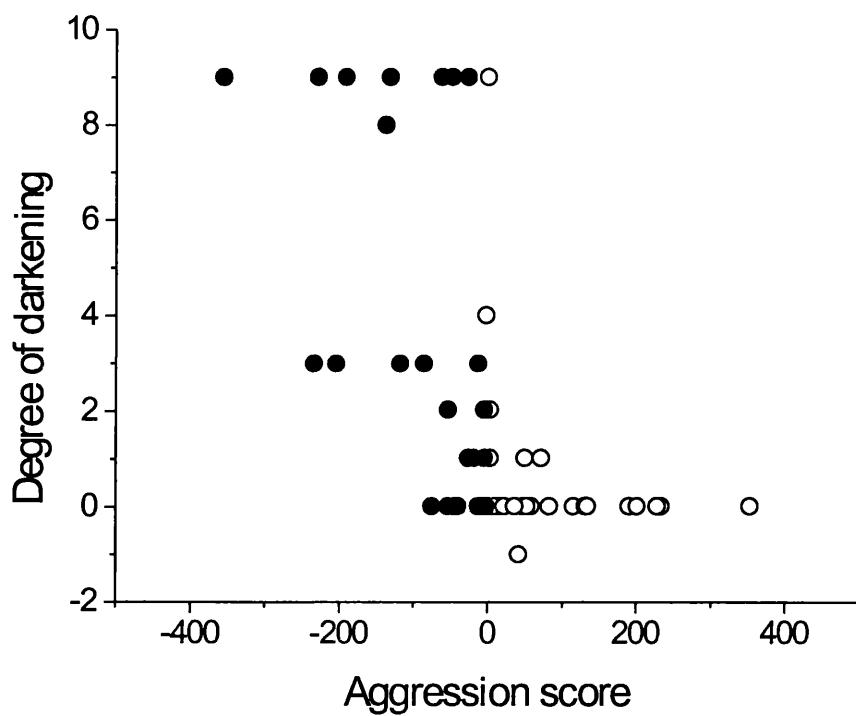
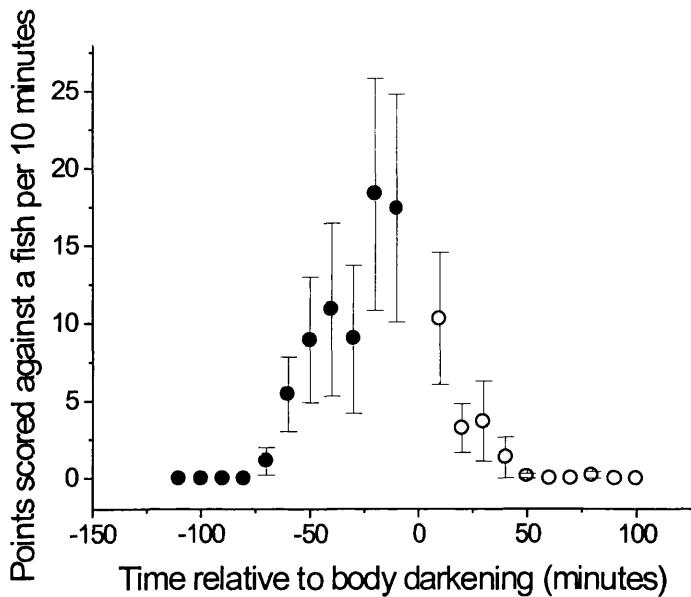


Figure 4

The relationship between the mean (\pm SE) rate of incurred aggression (points per 10 minutes) and time of first darkening in (a) the body and (b) the eye sclera of juvenile salmon losing territorial contests. Symbols as in figure 4.

a)



b)

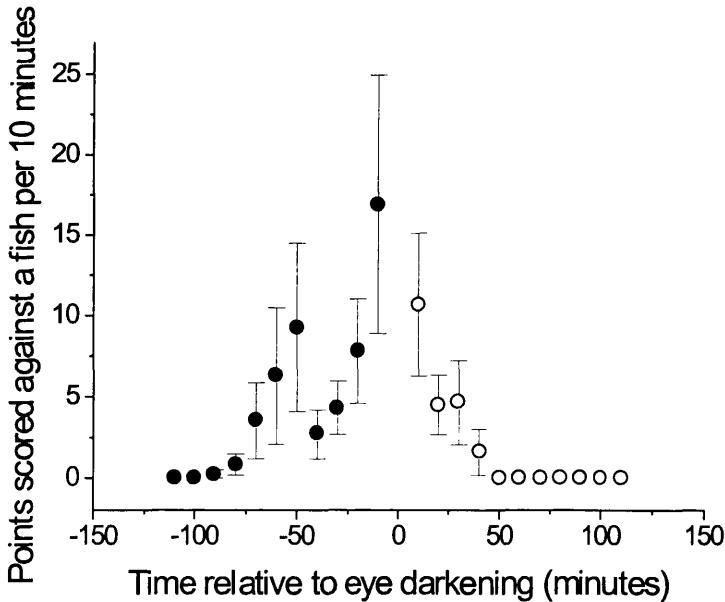
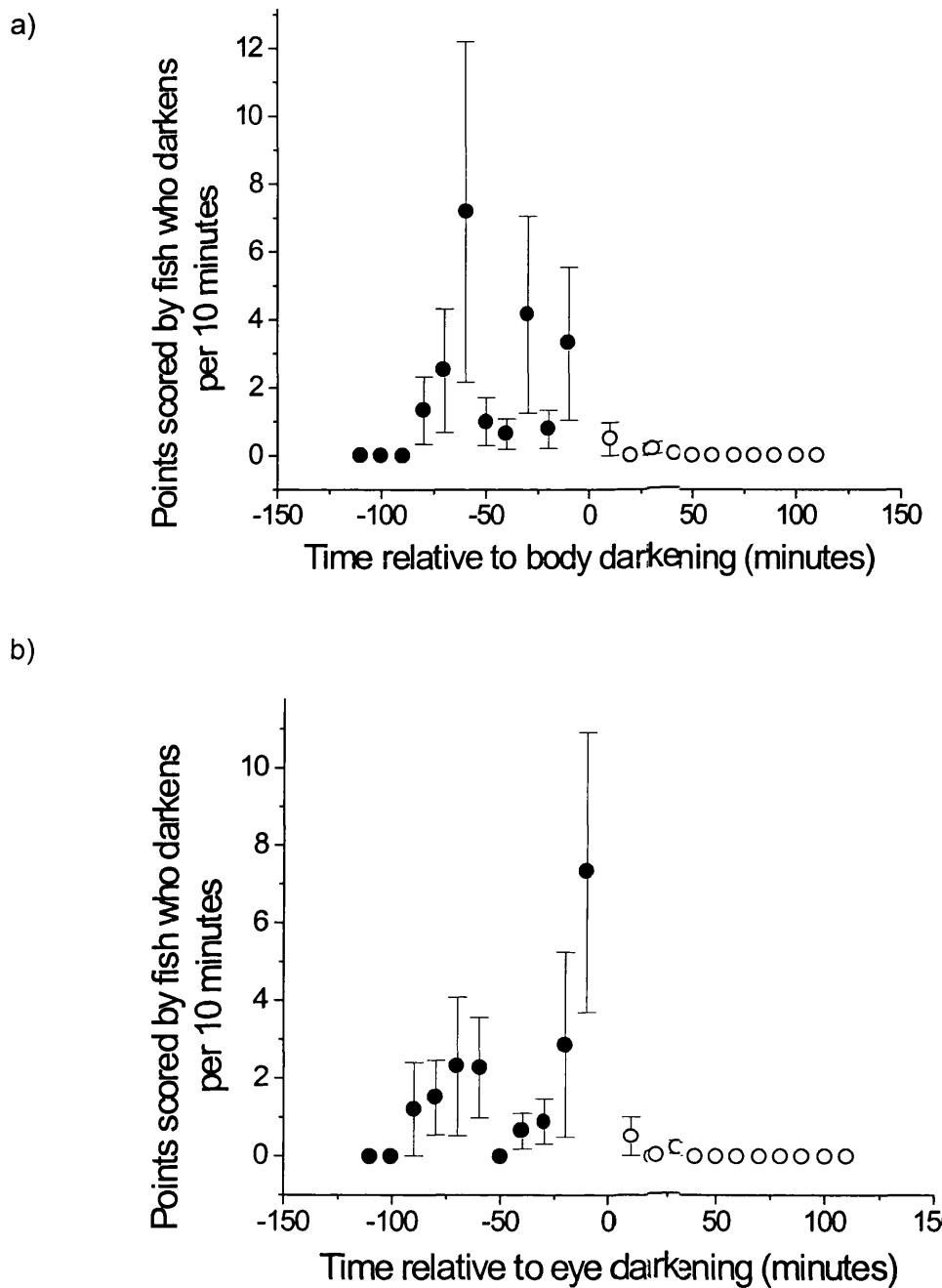


Figure 5

The relationship between the mean (\pm SE) rate of aggression (points per 10 minutes) by the fish who darkens and time of first darkening in (a) the body and (b) the eye sclera of juvenile salmon.



Discussion

The results indicate that juvenile Atlantic salmon parr typically adopt a uniformly pale coloration when on a light-coloured substrate, and that darkening of the body and sclera are associated with an aggressive encounter with a dominant fish. A relationship between temporary changes in body colour and dominance has been observed in several other species of fish (Baerends *et al.*, 1955; Okaichi *et al.*, 1958; Stacey & Chiszar, 1977; De Boer, 1980). In contests involving two salmon the subordinate fish was more likely to become darker than is the dominant, which usually retained its normal light coloration. The more intense the fight, the greater was the likelihood that one fish would darken, and the more aggression a fish received, the more likely it was to be the one that darkened. There did not appear to be a set threshold level of incurred aggression at which a darkening was triggered in the subordinate fish, but the greater the difference in aggression between the dominant and subordinate fish, the darker the subordinate became. Darkening of the sclera and body appear to be closely linked, since they almost always occurred simultaneously. It is unlikely that darkening simply indicates stress, since the fish became paler again while the stress of being subordinate persisted. Previous work on salmonids (Pickering & Pottinger, 1989) has shown that stress responses (i.e. elevated cortisol levels) persist for up to four weeks. Therefore if darkening was simply a stress response I would expect it to persist for the remainder of each trial.

All of the above trends suggest that the sudden change to a darker colour is linked to the moment when a fish loses an aggressive interaction and becomes subordinate to its opponent. This interpretation is supported by the fact that the behaviour of the more dominant fish changed abruptly once its opponent changed colour. As a result, the number of attacks on the subordinate rapidly decreased. The change in the dominant's behaviour is probably a result of the loser darkening rather than a response to a change in behaviour of the loser, since in the time leading up to the colour change the loser tended to become increasingly aggressive, and only reduced its aggression once it had changed colour and the dominant's behaviour had changed. These results suggest that the change in behaviour of the dominant is associated with darkening of the subordinate and not with a change in the aggressive behaviour of the loser.

There are two clear hypotheses to account for this effect: darkening either makes the subordinate fish less conspicuous to the aggressor (Rasa, 1969), or it is associated with, and may indeed signal, defeat. Reduced conspicuousness does not seem plausible since the substratum used in the experiment was very pale in colour. The second explanation therefore seems more likely: the darkening of the subordinate fish associated with submission and in this way may signal its defeat. Previous studies have shown that darkened subordinate rainbow trout (*Oncorhynchus mykiss*) also change their body postures when dominant fish are present (Abbott *et al.*, 1985). It is possible that body posturing may act in conjunction with body darkening to signal submission to the dominant fish, although I did not record postures in this study. In order to confirm the proposition

that darkening signals submission further research is needed. If either the colour of the fish, or their ability to darkening could be manipulated it would be possible to assess the impact of colour alone on the dominants behaviour and in this way tease apart the influence of colour and other variables such as body posture.

The social system of salmonids in streams is very stable. A minority of fish are mobile, but most maintain the same small home ranges for prolonged periods (Kalleberg, 1958). Within these small home ranges, some fish aggressively defend a territory while others adopt a floating strategy, avoiding conflict by living in the interstices between the sites occupied by more dominant individuals (Kalleberg, 1958; Bachmann, 1984; Puckett & Dill, 1985). Interactions between fish for feeding positions are therefore likely to be frequent. The balance between the value of the contested resource and the value of the future is an important factor influencing the frequency of death or severe injury during a fight (Enquist & Leimar, 1990). Although obtaining a feeding station is an important factor in determining early performance in salmonids (Elliott, 1994), fish should not invest too heavily in attempting to obtain or defend a particular feeding territory at this early stage of their life history. They should therefore avoid the dangerous fights seen between combatants when a major part of a contestant's lifetime reproductive success is at stake (Enquist & Leimar, 1990).

In this situation, rapid communication is paramount to avoid unnecessary and potentially costly fights. The status-signalling hypothesis proposed by Rohwer (1975) suggests that superior fighters benefit from distinctive colour markings ('badges of status') because these reduce the number of aggressive contests that are needed to maintain their dominance status, while subordinates benefit by avoiding interactions with superior individuals (Rohwer, 1982; Senar & Camerino, 1998). However, in salmon darkening, which could be a signal, is a trait of subordinates rather than dominants, and it does not appear to prevent the onset of aggression, rather it accompanies defeat. It is likely that darkening in subordinates receiving frequent attacks may be a result of extreme stress, which also indicates subordination to the opponent. Since subordinates did not maintain their darker coloration after the initial contest, it is possible that this may carry an associated cost, such as increased conspicuousness and hence risk of predation (see Morris *et al.* (1995a) for discussion of costs of vertical bars in swordtail fish *Xiphophorus multilineatus*).

Classical models of animal conflicts such as the Hawk-dove war of attrition (see Maynard Smith, 1982 for review) are probably less appropriate to contests between salmon than the sequential assessment model (Enquist & Leimar, 1983, 1987, 1990; Leimar & Enquist, 1984; Enquist *et al.*, 1990). This model assumes that there is an assessment process that occurs during fights such that individuals perform behaviours that provide information to their opponents as to their fighting ability. As the fight proceeds the combatants build up an increasingly accurate profile of their opponent's capabilities as they assess asymmetries such as differences in size or strength. Eventually one

contestant will judge the other to be stronger and will give up, thereby avoiding any (further) injury. The abandonment of the fight was then accompanied, and possibly signalled, by the darkening in skin and eye colour.

The sequential assessment model predicts that subsequent fights between the same contestants will be shorter if they can remember their opponent's fighting potential. The majority of disputes among salmon over territories will be between long-term neighbours. Recent work has shown that salmonids apparently have the capacity for individual recognition, in that they exhibit less aggression to familiar opponents (Johnsson, 1997). It would be interesting to test whether darkening during a conflict varies according to the familiarity of the opponents, since it is possible that fish signal their submission to a familiar and more dominant individual by darkening before they have incurred the cost of being subjected to aggressive attacks (see Whitfield, 1987 for a discussion of the relative roles of the 'Individual Recognition' and 'Status Signalling' hypotheses').

Chapter 3

Familiarity influences body darkening in territorial disputes between juvenile salmon.

After O'Connor *et al.*, 2000a

Abstract

Escalated contests between animals are potentially costly due to increased energy expenditure and risk of predation or injury. Hence I would expect selection to favour any mechanism that avoids unnecessary prolonged fighting.. One such means of avoiding escalated fights could be the use of information gained through individual recognition. Previous work (O'Connor *et al.* 1999a; Chapter 2) has shown that a darkening of the body colour is closely associated with submission in contests between juvenile Atlantic salmon and it has been hypothesised that it may act as a visual signal to the opponent. I tested the hypothesis that body darkening is used to reduce the cost of contests between familiar fish such that losers should darken quicker when faced with familiar rather than unfamiliar opponents. In contests between unfamiliar fish, submissive darkening tended to occur after more highly escalated contests in which the loser incurred more aggression, whereas the opposite occurred when familiar fish were in conflict. In addition there was a trend for familiar fish to either submit quickly or engage in protracted conflicts in which neither fish signalled submission, whereas in unfamiliar fish contests were of intermediate duration regardless of whether either fish darkened. I suggest that body darkening is used by familiar fish to signal submission to familiar dominants in order to avert a costly escalated fight, but familiarity can lead to escalation without submission if perceived competitive asymmetries are finely balanced.

Introduction

Escalated fights are potentially costly, since they result in increased energy expenditure and a greater risk of predation or injury (Abbott & Dill, 1985; Puckett & Dill, 1985; Enquist *et al.*, 1990; Jakobsson *et al.*, 1995). I would therefore expect selection to favour any mechanism that reduces the need for unnecessary prolonged fighting. One such means of avoiding escalated fights could be the use of information on the likely outcome of a contest gained through individual recognition. Familiar individuals could use prior knowledge of their opponent's Resource Holding Potential (RHP) to either curtail, or avert costly escalated fights with more dominant individuals. According to the asymmetric war of attrition model (Parker & Rubenstein, 1981), the degree of fight escalation should depend on the familiarity of the contestants, with familiar opponents settling fights with relatively little aggression (Ydenberg *et al.*, 1988). For animals living in stable groups, the cost associated with the formation of a dominance relationship can thus be recouped by the subsequent avoidance of repeated escalated fights (Senar *et al.*, 1990; Pagel & Dawkins, 1997).

In order for familiarity to be beneficial individuals must possess the cognitive ability to not only recognise opponents, but to recall their social status and/or fighting ability relative to their own. The ability to distinguish between conspecifics is widespread (Magurran *et al.*, 1994), and animals of many different species have been shown to decrease their levels of aggression as they become familiar with one another (Chase, 1985). This reduction in aggression may be mediated through tolerance to territorial intrusion in familiar conspecifics (see Ydenberg *et al.*, 1988 for a review) and has been termed the 'dear-enemy' effect (Fisher, 1954).

While all of these studies confirmed that increased familiarity results in a decrease in aggression levels between opponents, the mechanism behind this decrease has remained elusive. As familiar contestants will tend to have a more comprehensive knowledge of their opponent's RHP, the sequential assessment model (Enquist & Leimar, 1983) predicts that they should be able to ascertain the probability of defeat earlier in the fight, and so be able to cut short an encounter with a more dominant opponent. However, recognition of relative social status alone may be insufficient to avert fight escalation, as dominance relationships are not set in stone and a dominant individual cannot be certain that a subordinate will not try to challenge its position. Hence opponents may need to signal motivational state in order to reaffirm dominance relationships. Although a cessation of violence by one opponent may indicate its present motivational state, a signal of submission may be required to avert further attacks from a dominant.

In a recent study of contests between juvenile Atlantic salmon (*Salmo salar*) I observed a strong association between body darkening of the subordinate fish and a reduction in the aggressive behaviour of the dominant fish (O'Connor *et al.*, 1999; Chapter 2). Often in staged fights one individual suddenly darkened in body colour, and this led to

a rapid decrease in aggression from its victorious opponent, I hypothesise that in this way body darkening in salmon may act as a visual signal of submission.

In this study I examine the influence of familiarity on body darkening in territorial disputes between salmon and whether this potential visual signal works in conjunction with familiarity to avoid fight escalation. Juvenile Atlantic salmon tend to show high fidelity to particular areas of their home stream (Armstrong *et al.*, 1997), which produces a relatively stable social structure where the probability of meeting a familiar conspecific is high. Individual recognition has been documented in several fish species, including salmonids (Zayan, 1974; Beaugrand & Zayan, 1985; Johnsson, 1997), as has the effect of familiarity on fight intensity (pygmy swordtails, *Xiphophorus nigrensis* and *X. multilineatus*: Morris *et al.*, 1995b; rainbow trout, *Oncorhynchus mykiss*: Johnsson, 1997; green swordtails, *Xiphophorus helleri*: Beaugrand, 1997; sea trout, *Salmo trutta*: Höjesjö *et al.*, 1998). I therefore predicted that losers of contests would be quicker to darken (i.e. at a reduced level of escalation) when faced with familiar rather than unfamiliar opponents and that, if darkening is a signal, its occurrence signifies the acknowledgement of an opponent's dominance.

Methods

A batch of full-sibling eggs from sea run salmon caught in the River Shin, Perthshire were incubated at the Scottish Office Agriculture Environment and Fisheries Department Almondbank salmon rearing unit. The eggs were moved to the University Field Station at Rowardennan, Loch Lomond on 5 February 1998. Once hatched, the fish were kept under ambient photoperiod and temperature conditions in 1m diameter circular tanks with a water depth of 30cm. Once the fishes' yolk sacs were completely absorbed, the fish diet was zooplankton in the water supply (pumped from Loch Lomond) supplemented with commercial salmon food (Fulmar feeds, BOCM Pauls Ltd.) which they received *ad libitum* from automatic feeders.

On 23 April 1998, 300 fish were transferred to Glasgow University where they were randomly separated into two equal groups and kept in two 1m wide square tanks (tanks A and B). The fish were kept at 15°C under ambient photoperiod and hand fed a mixture of commercial salmon food and bloodworm (chironomid larvae species) *ad libitum*.

The experiments were carried out between September 13 and December 13 1998 (i.e. 6-9 months after first feeding) and took place in an aquarium maintained at 14°C, with a 12L: 12D photoperiod. At this stage the fish had a mean forklength of 51.34mm \pm 0.79 (SE) and weighed an average of 1.37g \pm 0.06 (N=118).

Familiar group establishment

On day 0, eight fish were randomly selected from each of the two stock tanks and separately placed into two smaller tanks (30x60cm) with a water depth of 25cm. These smaller tanks meant that there was an increased probability of any two fish coming into contact with each other and hence an increased level of familiarity. The substratum of each tank consisted of small marble chips (0.5cm diameter, Esmo, Roweb) which produced a topographically natural but light coloured substratum, against which the fish could easily be seen. Salmon parr in the wild will naturally come across patches of substratum of similar colour to the marble chips used in this experiment. Whilst in these two tanks the fish received bloodworm *ad libitum*.

On day 8 the fish were removed from their tanks, anaesthetised with 5ml/l of a solution of 10g/l benzocaine (ethyl-p-aminobenzoate) in 95% ethanol, and given unique combinations of marks with alcian blue dye on their pectoral, pelvic, dorsal, anal and/or caudal fins. This marking technique has no effect on the behaviour or growth of first feeding salmon fry (Metcalfe *et al.*, 1992). Once marked, the fish were assigned to pairs to form the following combinations;

Both fish from tank A

Both fish from tank B

One fish from each tank (i.e. A and B).

Each pair of fish was size matched as closely as possible (mean percentage weight difference = $6.65 \pm 0.68\%$, mean percentage length difference = $3.24 \pm 1.56\%$) and any fish not assigned a partner was not used in the experiment and placed in a new stock tank. The two members of each pair were placed on either side of a partitioned experimental tank (see below), the fish placed in the left side of the tank was referred to as the 'resident', and the fish in the right side the 'intruder'. Approximately twice as many 'mixed' pairs (A+B) were created as single source pairs, so that near equal numbers were obtained of the four possible combinations (AA, BB, AB, BA). Where the resident and intruder were from the same original stock tank, they were familiar with each other (i.e. AA, BB), and where the two fish were from different stock tanks (i.e. AB, BA) the fish were considered to be unfamiliar having been separated at first feeding, 6-9 months earlier.

Invasion Experiment

The experimental tanks used for testing responses to territorial invasion were divided into two square halves (10x10cm) by an opaque partition, and had a water depth of 8cm. At the centre of the dividing partition was a circular door (6 cm diameter) which was initially kept shut. Three of the glass sides of the tank were coated in waterproof white paper leaving one side through which observations could be made. As in the familiarity tanks, the substratum of each experimental tank consisted of light coloured marble chips. Both sides of the tank were identical in every respect, except that the side of the door facing the intruder was marked with a red cross so that the intruder would be able to distinguish between its own familiar side of the tank, and the side into which it was subsequently induced to invade.

The fish were left for 2 days in their respective sides of the tank before the experiment began in order to give the resident a 'prior resident advantage' (Krebs & Davies, 1987) in the subsequent contest (see below). Previous work had shown that 2 days prior residence in juvenile Atlantic salmon is sufficient for the resident to behave in a territorial manner, usually attacking any invader into its territory, whereas shorter durations of residence may result in the resident ignoring the presence of an intruding fish (Cutts *et al.*, 1999a; Chapter 6).

Quantification of body colour

Juvenile salmon are light brown on the dorsal and lateral surfaces down to approximately the lateral line. Below the lateral line they are light grey, shading to silver on the belly (Jones, 1959). Straddling the lateral line along each side of the body are a series of clearly defined oval dark patches called 'parr marks'. These vary in number from 7-12, with 11 or 12 being most frequent (Jones, 1959). Dorsal to the lateral line are numerous black or dark brown oval patches. These are scattered over the entire dorsal and dorso-

lateral surfaces with concentrations in several irregular bands which straddle the mid dorsal line.

Three areas were identified and used to grade the colour of the fish according to the scheme outlined by O'Connor *et al.* (1999a; Chapter 2)). This scoring method has been found to be repeatable (O'Connor *et al.*, 1999; Chapter 2)) and all colour scoring was done by me.

Previous work (O'Connor *et al.*, 1999; Chapter 2)) has shown that subordinate fish may darken in any of the areas described above as a result of aggression received from another fish. This darkening is closely associated with submission during a contest and may act as a signal to the dominant fish as it is correlated with a decrease in the amount of aggression focused on the subordinate fish.

Both fish involved in each experiment were colour graded at 4, 2 and 0 minutes before the start of the simulated territory invasion at 0900hrs. The door between the two sides of the experimental tank was then opened and the intruder gently induced to move into the resident's side of the tank using a transparent Perspex rod. Once both fish were in the resident's side of the tank the door was closed. The behaviour and colour of the two fish was then recorded continuously for two hours using the same scoring system as O'Connor *et al.*, (1999a; Chapter 2)). In brief, in order to assign dominance within the pairs of fish, the classified behaviours that they exhibited were given point values and the fish that totalled the most points was classified as the winner of the contest. Points were assigned to behaviours as follows:

1 point for each lateral display, where the fish expanded all its fins maximally, tensed its body and arched its tail upwards, before beating its tail slowly, irregularly and with wide amplitude.

2 points for each charge, which is the most direct form of attack and involved one fish swimming directly and quickly towards its opponent, but without touching it.

3 points for each charge which culminated in the aggressor biting its opponent.

At the end of the observation period the fish were left in the residents' side of the tank for a further two hours during which their colour was scored twice at 3 and 4h since the territorial invasion. The fish were then removed and placed in a separate stock tank. Each fish was only used in a single trial. The entire procedure of placing 8 new fish from each stock tank to the familiarity tank, then creating familiar and unfamiliar pairs, then observing the results of a territorial invasion, was repeated a total of fifteen times. This resulted in a total of 57 territorial invasions, 30 between unfamiliar fish (i.e. AB or BA) and 27 between familiar fish (AA or BB).

Ethical note: The experiment was carried out under licence from the UK Home Office. The procedure was such that the fish were continuously under observation during the period when the dominance status of the fish was established, so that it would have been

possible to intervene and remove either fish immediately if contests ever escalated to a point where injury could occur. However this was never necessary, and interaction rates in salmon are low and rarely involve overt aggression once dominance hierarchies are established (Metcalfe *et al.*, 1989). None of the fish sustained physical damage during the contests.

Results

All 57 staged territorial invasions resulted in at least some aggression (mean total number of points scored by a pair of fish = 58.47 ± 7.33 (SE) ($N=57$)). In 56 of the territorial invasions one fish scored more points than its opponent and this fish was one referred to as the winner of the contest. In the contest in which both fish scored the same number of points both scored just one point. In 98% of the contests the resident made the first aggressive behaviour. The vast majority (54 out of 56) of contests were won by residents. Of the 57 invasions, 38 resulted in at least one of the pair of fish changing body colour (i.e. a change in score for one or more of the three body areas scored for colour during the two hours of continuous observation). All but two of these changes were to a darker colour, which is thought to be a signal of submission (O'Connor *et al.*, 1999; Chapter 2)). All of the fish that darkened were the losers of the contest, since they scored fewer points than their opponents (mean difference in score = 61.25 ± 9.73 points). Of the 36 fights resulting in darkening, 18 occurred in situations where the staged fight was between two unfamiliar fish (i.e. AB or BA) and the other 18 were between two familiar fish (i.e. AA or BB). It was the invader who darkened in 35 of the 36 occasions, a result that was thus independent of familiarity. There was no difference between familiar and unfamiliar fish in the amount of aggression received (i.e. points incurred) by a losing fish (*t* test assuming equal variances: $t_{54}=0.21$, $P=0.83$). Thus familiarity *per se* did not lead to a reduction in aggression incurred by a losing fish.

There was no apparent difference in the propensity of fish to darken between familiar or unfamiliar dyads (Chi-square test: $\chi^2 = 0.27$, $P=0.60$), and no difference between familiar and unfamiliar pairs in the level of aggression seen during a contest (i.e. total number of points scored by both fish; *t* test assuming equal variances: $t_{57}=0.26$, $P=0.80$). Likewise, in contests where darkening occurred, familiarity had no effect on the amount of aggression (i.e. number of points) received by the loser before it darkened (*t* test assuming equal variances: $t_{34}=0.87$, $P=0.39$) or in the time at which the darkening took place, whether this is measured from the moment the intruder entered the residents' side of the tank, or from the onset of aggression (*t* test assuming equal variances: $t_{34}=0.82$, $P=0.42$, and $t_{34}=0.72$, $P=0.48$ respectively).

There was however, an interaction between familiarity, intensity of aggression and the occurrence of darkening. In contests between unfamiliar fish, darkening was associated with more escalated contests (i.e. more points were scored in total in the interaction), whereas the pattern was the other way around in contests between familiar fish (Figure 1; two way ANOVA, interaction between familiarity and occurrence of darkening: $F_{1,53}=4.57$, $P<0.05$; both main effects were non significant). Thus the more aggression that a loser received from an unfamiliar opponent, the more likely it was to darken (logistic regression of probability of darkening against intensity of aggression received: $\chi^2 = 4.48$, $P<0.05$, Figure 2). However when fights were between familiar fish

there was no significant relationship between aggression received by the loser and the propensity to darken (logistic regression: $\chi^2=1.28$, $P=0.26$), and in fact the trend was in the opposite direction (Figure 2).

Contest duration was calculated as the time between the first and last aggressive behaviours (i.e. lateral display, charge or nip) observed during the two hours of observations. There was no relationship between the contest duration, familiarity and the occurrence of darkening (two way ANOVA, effect of familiarity: $F_{1,53}=0.01$, $P=0.93$; effect of occurrence of darkening: $F_{1,53}=1.68$, $P=0.20$; interaction between familiarity and occurrence of darkening: $F_{1,53}=3.00$, $P=0.09$). However, when the two fish were familiar, contests were shorter when one of the contestants darkened than when neither fish darkened (*t* test assuming equal variances: $t_{25}=2.18$, $P<0.05$; Figure 3).

Figure 1

The relationship between fight intensity and whether or not one of the dyad darkened. Encounters between unfamiliar opponents in which one fish turned dark (solid bars) were more escalated than those in which neither fish darkened (open bars). Conversely, when opponents were familiar, darkening tended to occur after low intensity rather than escalated contests. Data presented as means \pm S.E.; see text for statistical analysis.

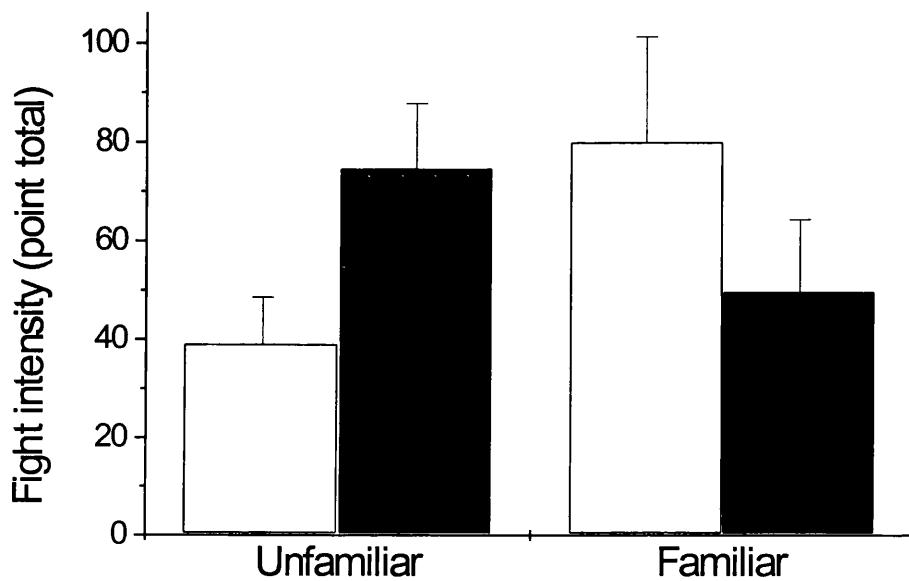


Figure 2

Relationship between the amount of aggression received by the ultimate loser and the likelihood that it would darken its body. Encounters between 30 pairs of unfamiliar fish are represented by open circles, while those between 29 pairs of familiar opponents are represented by filled circles; the data are grouped into 25-point bands along the abscissa for ease of representation. The equation of the logistic regression line curve for unfamiliar fish is given by:

Probability of darkening = $a/(a+1)$, where $a = e^{(0.0194x-0.6364)}$ and x = amount of aggression received. See text for statistical analysis.

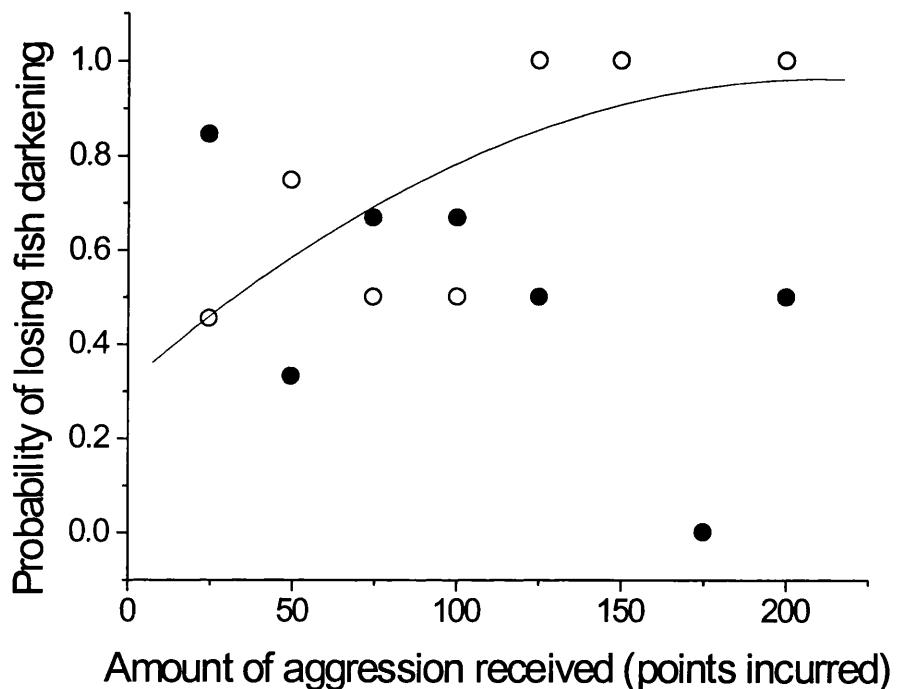
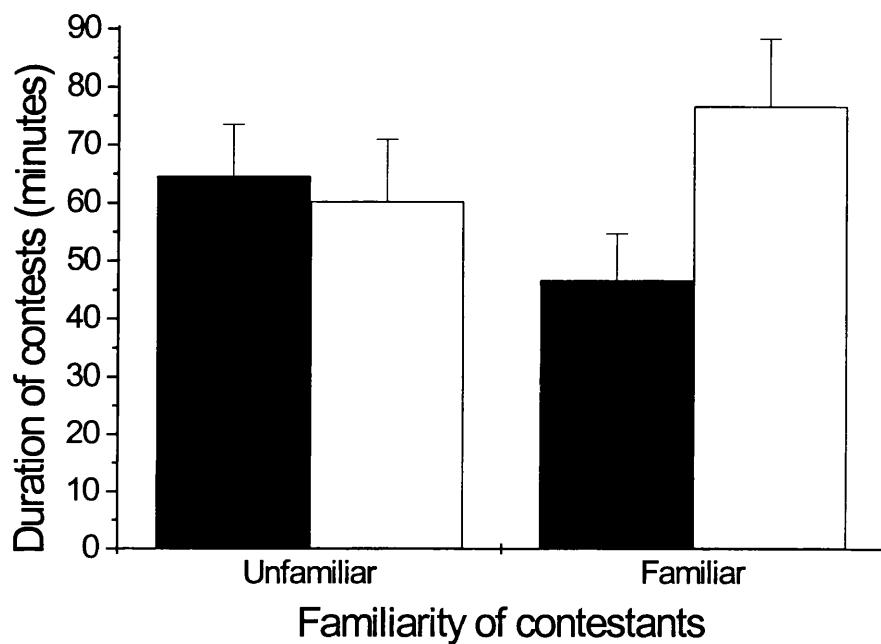


Figure 3

The relationship between the duration of the contest (i.e. time between first and last aggressive interaction) and whether or not one of the dyad darkened. Although there was no difference in the duration of contests between unfamiliar fish whether one fish darkened or not, encounters between familiar opponents in which one fish turned dark (solid bars) were shorter than those in which neither fish darkened (open bars). Data presented as means \pm S.E.; see text for statistical analysis.



Discussion

The results of this experiment offer further support for the hypothesis that darkening in juvenile Atlantic salmon acts as a signal of submission during aggressive encounters (O'Connor *et al.*, 1999; Chapter 2)). By darkening in body colour, subordinate fish are able to avert potentially costly escalated fights. In addition, the results of this experiment suggest that fish familiar with their opponents may darken their bodies at low fights intensities in order to reduce the probability of escalation. Although familiarity had no effect on the overall likelihood of one of the dyad darkening during an encounter, it significantly influenced the context in which darkening occurred. In encounters where the two fish were unfamiliar, the incidence of darkening increased with the amount of aggression incurred by the loser, so that the signalling of submission tended to occur when fights became escalated. In contrast, encounters between familiar fish in which the loser darkened, tended to involve less aggression than those in which no darkening took place. One possible explanation for this phenomenon is that familiarity provides extra information that changes the optimal strategies of contestants. However, I found that familiarity with the eventual victor only resulted in the loser receiving less aggression if it darkened. If the loser did not darken it incurred the same amount of aggression as an unfamiliar fish, suggesting that familiarity only led to a reduction in the cost of the conflict if one fish signalled submission by darkening.

Recognition of the opponent potentially allows fish to ascertain their relative social status and RHP. The use of such information has been shown in sea trout, where initiators of conflicts were more likely to win against a familiar fish than against an unfamiliar fish (Höjesjö *et al.*, 1998), which suggests that an individual will only start a conflict with a familiar opponent if it expects to win. In female guppies, *Poecilia reticulata*, 12 days living in groups of six is sufficient for fish to recognise their tank-mates (Griffiths & Magurran, 1997). In my experiment 8 days in small groups resulted in the fish becoming familiar with one another (since they behaved differently to fellow group members than to unfamiliar fish), and the interactions that took place in these small groups would likely have led to the establishment of some form of dominance hierarchy (Fausch, 1984; Metcalfe *et al.*, 1989). Information on the relative status and RHP of other group members could have been gleaned from direct conflicts or from observation of fights between other fish. The use of information derived from witnessing a contest between a future possible opponent and a previous opponent is termed observational learning and is vital in the formation of hierarchies (Rowell, 1974). The adaptive value of observational learning is obvious: observers gain information about potential opponents so that they can avoid conflict with individuals with greater RHP or submit earlier (Slater, 1986; Zayan, 1987; Cheney, 1990; Hogue, 1996). Johnsson & Åkerman (1998) showed that rainbow trout were capable of observational learning in this context, since fish that had observed

conflicts involving their future opponents were quicker to either submit or commence an attack.

I found that escalated fights only tended to result in the loser darkening if the contestants were unfamiliar. This is in agreement with a previous study of fights between unfamiliar fish that showed that as the aggression level increased the probability that one of the two fighting fish would signal submission by darkening also increases (O'Connor *et al.*, 1999; Chapter 2)). In contrast, familiar fish tended to show the opposite trend, as submissive darkening was associated with less aggressive contests. Johnsson and Åkerman (1998) suggest that in fights between familiar fish, relative status is settled faster and costly fights are avoided when compared to fights between strangers. This would correspond to the contests that I observed between familiar fish where the loser quickly signalled submission by darkening before incurring much aggression. In other contests it may have been the case that prior asymmetry in social status was offset by the residency asymmetry (Maynard Smith & Parker, 1976), such that the increased value of the territory to a resident led to a greater motivation to fight with an otherwise more dominant opponent. The opposing asymmetries would then lead to a more equal (and therefore escalated) contest, with a reduced motivation for either contestant to signal submission. However, as residents nearly always initiated the contest and in the majority of contests the darkening fish was the intruder it is probable that the motivation to fight associated with territory ownership is stronger than any previously established dominance relationship. Thus I suggest that in contests between familiar fish, darkening intruders would tend to have been fish that were previously subordinate to the resident. As the intruder recognised the resident to be more dominant it darkened early on in the contest and in this way avoided a potentially costly escalated battle. However, if the intruder was previously dominant to the resident, the fight tended to escalate as the resident fought to defend its territory and the intruder to assert its dominance; in this situation neither fish darkens.

Previous work has shown that RHPs of the contestants may be affected by factors relating to the history of the contestants other than simply their familiarity (Beaugrand *et al.*, 1996). Thus prior dominance (Beaugrand *et al.*, 1996), experience of contests in that area (Cloitier, 1995), prior residence (Cutts *et al.*, 1999a), or interactions between these variables (Beaugrand *et al.*, 1996) can all influence the outcome of social conflict. A clear example is seen in green swordtails, where male fish are handicapped by prior subordination experience, and must be at least 40% bigger than a previously dominant opponent in order to be the likely winner of a conflict (Beaugrand *et al.*, 1991). Were it not for the prior resident asymmetry it is likely that there would have been a lower overall level of aggression in contests between familiar than unfamiliar fish in my experiment (as found by Johnsson (1997) in rainbow trout).

An interesting feature of the contests studied here is that there was no immediate gain for the winner, as there were no resources available within the territory. Thus fights

were primarily to establish territorial ownership and/or a dominance relationship, which could later be used to determine future access to resources. Contests over future rather than current resources have also been seen in domestic hens (Pagel & Dawkins, 1997).

In the wild, juvenile salmon defend territories, which allow them exclusive access to a limited food source (Dill, 1977), typically invertebrates that are drifting downstream or living in the benthos (Puckett & Dill, 1985). Salmonids frequently have stable home ranges (Bachman, 1984) and thus familiar neighbours (but see also Gowan & Fausch, 1996). This familiarity lends itself to the formation and maintenance of a dominance hierarchy (Jenkins, 1969; Fausch, 1984). However, kin selection may add a further dimension to the situation. Intruders into a fish's territory will belong to one of the four possible combinations of familiar or unfamiliar fish that are either kin or non-kin. Although previous laboratory based studies have shown that kin show reduced aggression to each other in Atlantic salmon and rainbow trout, and that groups of kin have more even growth rates than non kin groups (Brown & Brown, 1996), this may have little relevance to wild fish since kin do not necessarily occupy adjacent territories (Fontaine & Dodson, 1999). In fact the ability to recognise familiar neighbours may be far more valuable in terms of averting contests than kin recognition. Tolerance to familiar individuals will increase an animal's direct fitness as repeated escalated fights are avoided through recognition and acknowledgement of dominants (Whitfield, 1987). Whereas recognition between kin may be mediated through water borne chemosensory cues or other phenotypic characteristics (Brown & Brown, 1992, 1996), recognition and status acknowledgement between familiar non-kin conspecifics may rely upon signals. By signalling submission a subordinate fish may avert a costly battle and reserve energy for a fight against a stranger where the outcome is less predictable.

Chapter 4

The effects of date of first feeding
on behaviour and growth rates in
juvenile Atlantic salmon.

Abstract

This is a study of the effects of date of first feeding on feeding behaviour and growth performance of dispersing Atlantic salmon fry (*Salmo salar*). Atlantic salmon fry were separated into Early First Feeders (EFF), Late (LFF) and Intermediate, according to the amount of yolk remaining in their yolk sacs and the anticipated date at which they would switch to exogenous food. In replicated sections groups of six fish (3 EFF and 3 LFF) were introduced into identical sections of a semi-natural stream tank. Standardised behavioural observations were made on each fish over the following 14 days, after which all fish were removed and measured. Initially EFF tended to be larger than LFF, though their growth rates throughout the study were not significantly different. There was no difference in the rate of feeding, aggressive encounters or subsequent dominance between EFF and LFF. EFF exhibited a higher degree of site fidelity and LFF darted higher into the water column to intercept prey items. These results suggest that EFF have an intrinsic advantage over LFF that means that they are more likely to establish and maintain feeding stations. Although previous studies have shown that EFF are more dominant than LFF in the short-term no such difference was found in rates of aggression over this two week study.

Introduction

Asymmetries in competitive ability during vulnerable life history stages will be instrumental in determining which animals survive and which do not. In the absence of advantages associated with territory ownership (the 'prior resident's effect'; see O'Connor et al., 2000b; Chapter 5)), variation in resource holding potential (Parker, 1974) must arise from intrinsic differences between individuals. Such variation is especially pertinent to animals that are attempting to establish themselves in an environment. Animals dispersing from their natal site incur a cost of emigration that will generally increase with distance travelled from their natal site (Plissner & Gowaty, 1996). As the distance from the natal site increases, individuals face increasing mortality risks associated with unfamiliar habitat, passage through areas of high predator density, and the physiological costs associated with extensive movement (Plissner & Gowaty, 1996). Dominant individuals tend to be more sedentary and move only short distances provided resources are available, whilst subordinate individuals often disperse even in the absence of severe population pressure, as they are displaced or excluded by dominants well before food resources become limited (Gauthreaux, 1978). Given the costs of dispersal, unequal competitive ability leading to unequal resource partitioning will thus ultimately affect individual survival (Elliott, 1994).

The Atlantic Salmon is an ideal species for a study of the individual asymmetries that contribute to differential dispersal, since the fry emerge from the nest (redd) in numbers that far exceed the limits of their natal habitat's carrying capacity (Giles, 1994). Thus the differences that exist between individuals will be instrumental in determining their success in the ensuing inevitable dispersal.

After hatching, the fry remain in the gravel substratum of their natal stream for a variable period while obtaining nutrients from their yolk sac (Kalleberg, 1958). Once this endogenous food supply is absorbed, they exhibit a normally distributed temporal pattern of emergence and dispersal from the spawning ground (Godin, 1982; Brännäs, 1987). The peak of emergence is highly synchronised both in natural (Gustafson-Marjanen & Dowse, 1983) and artificial redds (Godin, 1982; Brännäs, 1987). Following emergence, the fish establish and defend territories (Gustafson-Greenwood & Moring, 1990, Kalleberg, 1958). Competition for food and space during the post-emergence period is fierce (Keenleyside & Yamamoto, 1962), and if a population exceeds the carrying capacity of the habitat, some fry will be forced downstream by the aggressive behaviour of those that have already become established (Chapman, 1962; Mason & Chapman, 1965; Le Cren, 1973; Backiel & Le Cren, 1978; Elliott, 1986; Beall et al., 1994). Hence the period following the switch to exogenous food will be pivotal in salmonid life histories, as it is the time of greatest mortality (Elliott, 1986) when up to 85% of emerging fry may be taken by predators (Peterman & Gatto, 1978). Asymmetries that exist between emerging conspecifics will be crucial in determining which fry manage to secure and defend a feeding station.

The size variation of eggs from a single female is negligible (Thorpe *et al.*, 1984), and since initial fry size is dependent on egg size the size variation among first feeding fish is also small (Thorpe *et al.*, 1984). However, the size variation increases rapidly over time (Metcalfe *et al.*, 1992), as dominant fish that can secure more food soon establish and enhance a size advantage (Huntingford *et al.*, 1990, Metcalfe *et al.*, 1992). Since the age at which a fish turns into a smolt and migrates to sea is largely determined by its growth rate during the preceding summer (Thorpe *et al.*, 1992), the factors determining growth during this early stage may be instrumental in deciding a fish's life history strategy.

Several studies have indicated that the earliest salmon to emerge from a redd may have an advantage in subsequent competition for feeding sites over those emerging later (Mason & Chapman, 1965, Chandler & Bjornn, 1988, Brannas, 1988). The advantage to early emerging fish appears to be two-fold: firstly, early emergers establish their territories before late emergers arrive and therefore gain a prior residence advantage in contests over that area (Cutts *et al.*, 1999a, O'Connor *et al.*, 2000b; Chapter 5); secondly, early emerging fish appear to be intrinsically dominant over later emerging fish (Metcalfe & Thorpe, 1992b). Some studies have suggested that this intrinsic difference is due to variation in the Standard Metabolic Rate (SMR) of individuals, since early first feeders tend to have higher SMRs than later first feeders (Metcalfe *et al.*, 1995, Cutts *et al.*, 1998). Fish with higher SMRs are more aggressive (Cutts *et al.*, 1998) and hence more dominant (Metcalfe *et al.*, 1995, Yamamoto *et al.*, 1998). However, a previous analysis of the relative dominance of first feeding fish (Metcalfe & Thorpe, 1992b) used pairs of fish in small bare tanks, very different from the natural environment experienced by wild fish. The aim of this experiment was therefore to test experimentally for the effect of date of first feeding on the behaviour and growth of underyearling salmon in a more realistic habitat and social environment.

Methods

A batch of full-sibling eggs from sea-run salmon caught in the River Almond, Perthshire were incubated at the Scottish Office Agriculture Environment and Fisheries Department, Almondbank salmon rearing unit. Because Atlantic salmon emerging from a redd in the wild would at least share the same mother, it was decided that full-siblings should be used as this would best mimic the competitive situation faced by fry dispersing from redds in the wild. The fish were moved to the Glasgow University Field Station at Rowardennan on Loch Lomond on 8th November 1996, where they were kept under ambient photoperiod and temperature conditions in 1m square tanks. These tanks received a continual turnover of water pumped from Loch Lomond and were therefore rich in zooplankton.

On 8th April 1997 approximately 300 of the fish were sorted into three groups according to how much of their yolk sacs still remained (following Metcalfe & Thorpe, 1992b). Fish with the least amount of yolk remaining were referred to as 'Early First Feeders' (EFF) since they were likely to switch to exogenous feeding sooner than those with a large amount of yolk remaining (referred to as 'Late First Feeders' (LFF)). Fish with an intermediate amount of yolk remaining were not used in this study. These groups were then kept separately in 1m width square tanks and once their yolk sacs had been completely absorbed the fish diet was supplemented with commercial salmon food (Fulmar feeds, BOCM Pauls Ltd.), which they received *ad libitum* from automatic feeders.

The experiment was carried out between 2nd June and 16th June 1997 (i.e. 8-10 weeks after first feeding), in sections of an artificial stream tank that had a glass side wall to allow behavioural observations. Salmonids of this age are in the critical period for survival that follows emergence, and in natural streams experience intense competition for space and high mortality rates (Elliott, 1994). The stream tank also received a continual turnover of water pumped from Loch Lomond rich in zooplankton, which provided ample food for the salmon fry.

The artificial stream tank was divided into seven replicate sections numbered 1-7, 1 being furthest upstream. Each section of the stream tank measured 50 cm long by 30 cm wide with a water depth of 15 cm. The barriers between neighbouring sections were made of plastic mesh which allowed a flow of water but prevented the movement of the fish. A water pump created the flow through the sections (mean water velocity at the midpoint of the sections and 9 cm below the surface=0.02ms⁻¹ ±0.001(SE)). During the course of the experiment the average water temperature was 16 °C ± 0.41 (SE). Each section had a layer of gravel mixed with marble chips (Esmo, Rowebb) to produce a topographically natural but light coloured substratum against which the fish could easily be seen. Salmon parr in the wild will naturally come across patches of substratum of similar colour to the marble chips used in this experiment. Sections were divided into five 10 cm long zones along their length, with zone number 1 being the furthest upstream.

Six fish (three from each of the tanks containing early and late first feeders) were used in each of the replicate sections that were run simultaneously in the seven sections of the stream tank. On day 1 of the experiment six fish (three EFF and LFF) were randomly selected from the stock tanks and anaesthetised with 5ml/l of a solution of 10g/l benzocaine (ethyl-p-aminobenzoate) in 95% ethanol and given unique combinations of marks with alcian blue dye on their pectoral, pelvic, dorsal, anal and/or caudal fins. This marking technique has no effect on the behaviour or growth of first feeding salmon fry (Metcalfe *et al.*, 1992). Whilst anaesthetised their weights and fork lengths measured (to the nearest mm and 0.01g respectively). Once fully recovered from the anaesthetic (i.e. after 1 hour) the six fish in each group were introduced into a single section of the stream tank. These fish were then left to settle for three days. The resulting high density of fish within each section (40 fish/m²) approximated the wild situation where Atlantic salmon fry emerge from the redd in numbers that far outstrip the natural carrying capacity of the natal site.

Observational data were then collected on days 4, 6, 8, 11 and 13. On each of these days each fish was observed twice (for 2 minutes at each time), with the two observations being approximately 1.5 hours apart. During each 2 minute observation the number of feeding attempts made by the fish was recorded, along with its location in the stream section (zone 1-5), mean height maintained off the bottom and the maximum height in the water column to which it swam in order to intercept a prey item. Both height measurements were made to the nearest 0.5 cm using a 15 cm transparent Perspex ruler placed against the glass wall of the tank. In addition to this any aggressive interaction with another fish (i.e. lateral display, charge or nip, as described by Keenleyside and Yamamoto (1962)) during the 2 minutes was recorded. On day 15 all six fish were removed from each section of the stream tank, anaesthetised and their final weight and fork lengths recorded.

Individual Specific Growth Rates for weight and length were calculated as $100(\ln(\text{Final measurement}) - \ln(\text{Initial measurement}))/\text{duration of experiment in days}$, following Ricker (1979). In order to control for the effect of body size on growth rates, these values were then regressed against the initial weight and length of the fish, and the equation of the resulting line used to calculate the expected Specific Growth Rate for each fish, given its initial size. The difference between the expected and observed Specific Growth Rate (adjusted Specific Growth Rate) was used in subsequent analysis of growth rates. Using the weight (W) and fork length (L) measurements, an index of each fish's condition (Condition factor, K) was also calculated as $K = 10^5(W/L^a)$, where a is the slope of a regression of $\log_{10}(\text{weight})$ on $\log_{10}(\text{length})$ following Bolger and Connolly (1989).

Data from each fish have been used as individual experimental units in the statistical analysis.

Results

Initial size and condition

Since there were a total of seven sections each containing six fish the sample size for all analysis of both early and late first feeders (EFF or LFF) was 21 unless otherwise stated. Although initially early first feeders (mean weight = 0.20 ± 0.01 g (SE)), fork length = 29.61 ± 0.39 mm) tended to be larger than late first feeders (LFF) (mean weight = 0.13 ± 0.004 g (SE)), fork length = 26.86 ± 0.24 mm), there was no difference in the size of fish between sections (two-way ANOVA, effect of sections number on initial weight: $F_{6,28}=0.95$, $P=0.47$; development category (i.e. EFF/LFF): $F_{1,28}=30.90$, $P<0.001$; effect of section number on initial fork length: $F_{6,28}=1.40$, $P=0.25$; development category : $F_{1,28}=36.77$, $P<0.001$). Despite the tendency for EFF to be larger than LFF, there was no overall difference in their condition factor (K), and condition factor did not vary between sections (two-way ANOVA, effect of section number on initial K: $F_{6,28}=0.58$, $P=0.74$; development category : $F_{1,28}=0.55$, $P=0.46$). Hence the relationship between length and weight was the same for both EFF and LFF.

Spatial positions, feeding behaviour and aggression

The position of individual fish within the stream tank was relatively stable such that an average of $58.33\% \pm 3.44\%$ (SE) of observations of a given fish were from a single zone. Since analyses of growth rate showed that fish in sections further down stream grew slower (see below), suggesting a disparity in suitable food abundance, section number was used as a covariate in an analysis examining the effect of development category on "zone fidelity", where zone fidelity is defined as the number of times a fish was observed in its most frequently used zone as a percentage of the total observations. Hence, zone fidelity is an indication of the propensity of a fish to remain in one zone rather than move between zones. Analyses revealed that there was no difference in the slope of the regression line of zone fidelity against section number between EFF and LFF (ANCOVA, interaction between section number and development category: $F_{1,38}=0.12$, $P=0.74$). When the interaction term was removed from the ANCOVA the results indicated that there was a significant difference in the intercept of the two regression lines (ANCOVA, effect of development category on zone fidelity: $F_{1,39}=10.89$, $P<0.01$) but no trend between section and zone fidelity (ANCOVA, effect of section number: $F_{1,39}=0.53$, $P=0.47$). Thus, EFF tended to have higher zone fidelities ($68.57\% \pm 3.8$) than LFF ($48.1\% \pm 4.86$), but there was no significant difference between sections. This indicates that EFF spend a greater proportion of their time in one zone and that LFF show a greater propensity to move between zones.

There was no significant difference in the mean height maintained above the substratum between EFF and LFF (Mann-Whitney $U=171$, $P=0.21$, mean for EFF = 0.41 ± 0.08 cm, LFF = 0.80 ± 0.25 cm). However, there was a trend for LFF to swim to a

greater height in order to intercept prey items than EFF (Mann-Whitney $U=144.5$, $P=0.05$, mean for EFF=2.86±0.74cm, LFF= 5.05±0.86cm, Figure 1).

A dominance score was calculated as the number of successful aggressive interactions involving a focal fish (i.e. when the opponent was displaced) during the total observation time, minus the number of times it lost an interaction; positive values therefore indicate a more dominant fish. EFF did not have significantly different dominance scores to LFF (t-test assuming equal variances: $t_{40}=1.51$, $P=0.14$, mean for EFF= 0.24 ±0.23, mean for LFF= -0.24 ±0.22). Despite the tendency for fish to grow at slower rates the further down stream their section (see below), there was no trend for aggression to increase or decrease between the sections (Spearman rank: $r_s=0.07$, $P=0.65$).

There was no difference in the total number of attacks initiated by the two development categories (Mann-Whitney $U=167$, $P=0.11$, mean for EFF=0.76±0.23 per 20 min, LFF= 0.33±0.14 per 20 min). Nor was there a difference in the number of attacks they initiated against the opposite development category (Mann-Whitney $U=189$, $P=0.22$, mean for EFF=0.38±0.18 per 20 min, LFF= 0.14±0.10 per 20 min) or the same development category (Mann-Whitney $U=180.5$, $P=0.18$, mean for EFF=0.38±0.13 per 20 min, LFF= 0.19±0.11 per 20 min). There was also no difference in the number of successful attacks that a fish made between the development categories (Mann-Whitney: $U=20$, $P=0.30$). There was no evidence that aggression levels were related to food availability, since the mean rate of attacks in a section did not correlate with the mean number of feeding attempts (Spearman rank: $r_s=0.59$, $n=7$, $P=0.16$).

Dominance was neither related to initial length or weight (Linear regression: initial length: $r^2=0.02$, $n=42$, $P=0.19$; initial weight: $r^2=-0.02$, $n=42$, $P=0.73$). There was no relationship between a fish's dominance score and its feeding rate (Linear regression: $r^2=0.01$, $n=42$, $P=0.22$), and the feeding rates of the fish neither varied with development category nor section (two-way ANOVA, effect of section number: $F_{6,28}=1.31$, $P=0.28$; development category : $F_{1,28}=0.94$, $P=0.34$).

Growth rates

The effects of the dominance score, development category and section number on adjusted SGR of weight of the fish over the experiment were analysed using an ANCOVA in which development category and section number were factors and dominance score was a covariate. The analysis was then repeated to examine the influence of these variables on adjusted SGR of length and change in condition factor (Table 1a, b and c). The results of these analyses indicated that adjusted SGR of weight and length of the fish over the experiment was significantly affected by section number, such that fish in sections furthest from the inflow to the stream tank grow less than those upstream (Figure 2).

To examine whether the influence of section number was masking any effect of dominance or development category, the average SGR of weight and length was calculated for each section and subtracted from the adjusted SGR of weight or length for each fish in the section. This new value is referred to as residual adjusted SGR since it is the difference between the fish's actual SGR (corrected for body size) and the mean of all the fish in that section. Hence fish with positive residual adjusted SGRs would have been growing faster than other fish in their section and those with negative values would have been growing slower.

Analyses revealed that there was no difference in the slope of the regression of residual adjusted SGR of weight against dominance score between EFF and LFF (ANCOVA, interaction between of dominance score and development category: $F_{1,38}=2.42$, $P=0.13$). When the interaction term was removed from the ANCOVA, the results indicated that there was no difference in the intercept of the two regression lines (ANCOVA, effect of development category on SGR of weight: $F_{1,39}=0.04$, $P=0.85$) and that there was no trend between dominance score and SGR of weight (ANCOVA, effect of dominance score: $F_{1,39}=1.82$, $P=0.19$). Likewise, analysis of SGR of length data revealed that there was no difference in the slope of the regression of residual-adjusted SGR of length against dominance score between EFF and LFF (ANCOVA, interaction between of dominance score and development category: $F_{1,38}=1.03$, $P=0.32$). When the interaction term was removed from the ANCOVA the results indicated that there was no difference in the intercept of the two regression lines (ANCOVA, effect of development category on SGR of weight: $F_{1,39}=0.34$, $P=0.56$) and that there was no trend between dominance score and residual adjusted SGR of length (ANCOVA, effect of dominance score: $F_{1,39}=2.08$, $P=0.16$).

Unlike their effect on growth rates, section number and development category did not affect the change in condition factor during a section (Table 1c). However, the dominance score did affect the change in condition factor (Table 1c) such that fish with lower dominance scores tended to have a greater change in their condition factor over the course of the experiment (Linear regression: $r^2=0.09$, $n=42$, $P<0.05$, Figure 3). The final condition factor of the fish did not vary between sections or development categories (two-way ANOVA, effect of section number on final K: $F_{6,28}=1.17$, $P=0.35$; development category : $F_{1,28} =0.22$, $P=0.64$).

Table 1

Results of ANCOVAs investigating the influence of development category (Feeding cat., EFF or LFF), Section number (Section, 1-7) and dominance score (Dom.) on the growth and condition of fish kept in groups of 6 (3 EFF and 3 LFF) in replicate sections of a stream tank. Effects on (a) the change in SGR of weight (% per day); (b) SGR of length (% per day); (c) change in condition factor (K).

(a)

	df	F	P
Dom.	1	1.54	0.22
Development cat.	1	0.03	0.86
Section	6	15.30	<0.001
Residual	33		

(b)

	df	F	P
Dom.	1	1.82	0.19
Development cat.	1	0.27	0.60
Section	6	14.59	<0.001
Residual	33		

(c)

	df	F	P
Dom.	1	6.39	0.02
Development cat.	1	2.54	0.12
Section	6	0.90	0.51
Residual	33		

Figure 1

Mean (\pm SE, n=21) maximum height swum to intercept prey items by EFF (i.e. early first feeders) and LFF (i.e. late first feeders) juvenile Atlantic salmon fry kept in groups of 6 (3 EFF and 3 LFF). See text for statistical analysis.

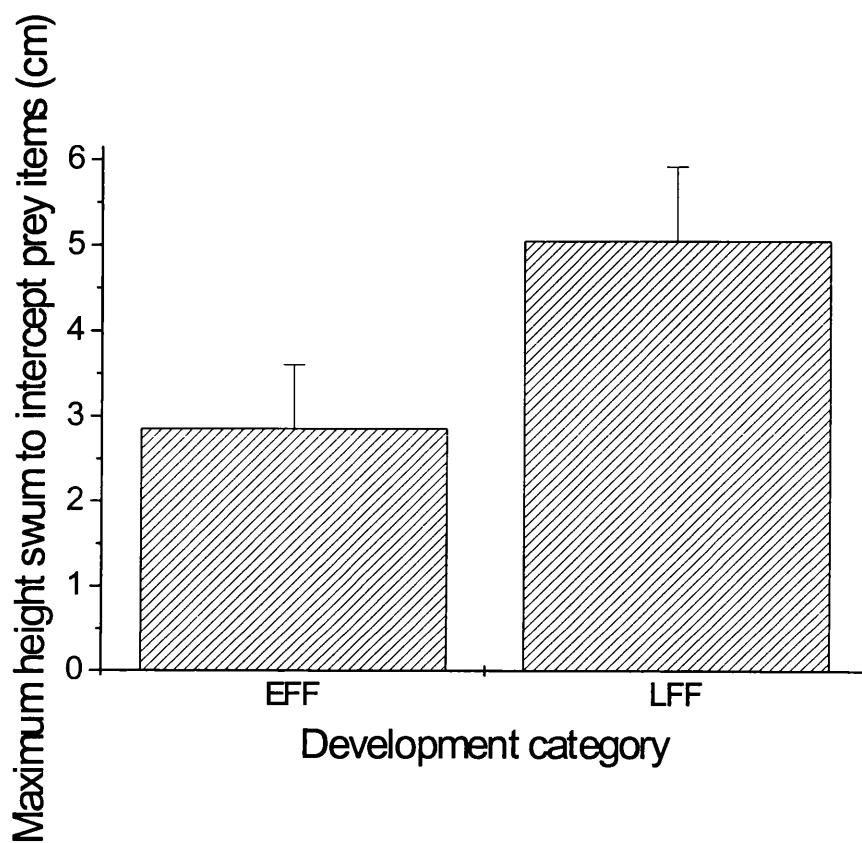
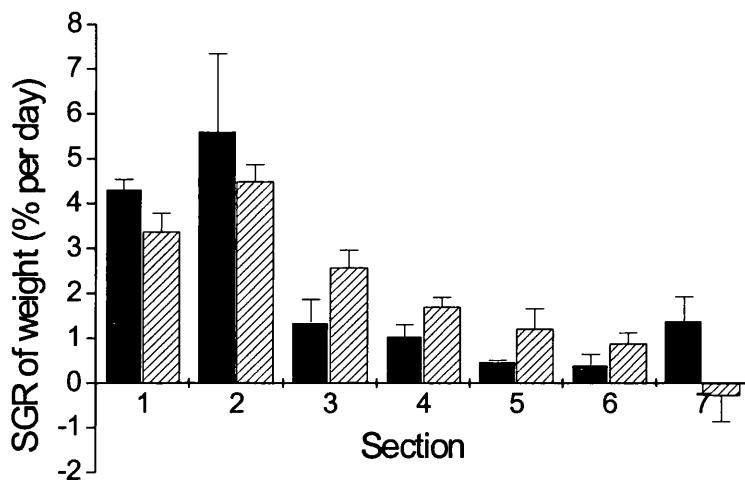


Figure 2

The SGR of a) weight and b) length (% per day) of EFF (represented by solid bars) and LFF (represented by hatched bars) juvenile Atlantic salmon fry in relation to section number; each section included 3 EFF and 3 LFF. Values are means (\pm SE). See text for statistical analysis.

a)



b)

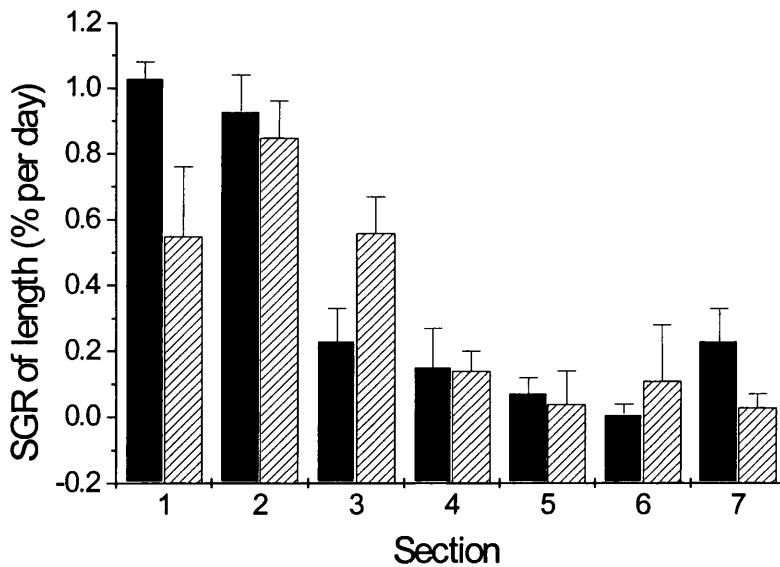
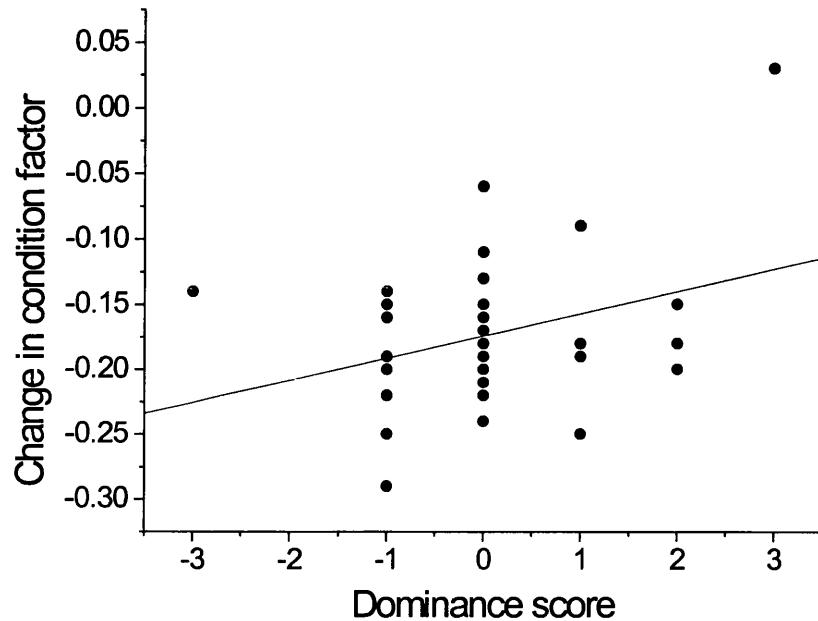


Figure 3

The relationship between the change in condition factor and dominance score in Atlantic salmon fry.

(Change in condition factor = (0.017* dominance score)-0.18; $r^2 = 0.09$, $F_{1,40} = 4.81$, $P < 0.05$).



Discussion

The similarity of the fishes' initial body proportions between sections was as expected since all of the fish were full siblings of the same age. Within sections the tendency for early first feeders (EFF) to be larger than late first feeders (LFF) could be due to the difference in duration of exogenous feeding. The EFF would have exhausted their yolk sacs sooner than the LFF and presumably had been feeding on zooplankton and commercial food for a longer period of time than LFF. Although previous studies have found no difference between the initial size of EFF and LFF (Metcalfe & Thorpe, 1992b), the fish used in the present study were older and if EFF were dominant to LFF, as suggested by Metcalfe and Thorpe (1992b), they would have had longer in which to establish a size advantage. An alternative hypothesis for the difference in size is that EFF have higher growth rates than LFF (possibly due to their higher SMR, Metcalfe *et al.*, 1995). Although there was no difference in growth rates between development categories (EFF/LFF) in this experiment, it is possible that the duration of the experiment (2 weeks) was insufficient to detect a growth difference.

Despite the similarity between development categories in the height maintained above the substratum, LFF tended to dart to a greater height in order to intercept prey items and had a lower level of zone fidelity i.e. less stable spatial position. One possible hypothesis for these differences in behaviour is that EFF had secured the most profitable feeding stations and the poor feeding stations available to LFF meant that they had to be more mobile in order to meet their energetic costs. Although this experiment found that neither the aggressive behaviour, nor the dominance score of the fish differed between development categories or sections, previous studies have shown that EFF tend to be more aggressive than LFF (Cutts *et al.*, 1999a) and hence more dominant (Metcalfe & Thorpe, 1992b), as they have higher Standard Metabolic Rates (SMR) (Metcalfe *et al.*, 1995; Cutts, 1996). If EFF were indeed dominant to LFF they would have acquired the best feeding stations. Juvenile salmon are 'sit and wait' predators with well defined feeding stations from which they emerge to intercept prey items (Stradmeyer & Thorpe, 1987); if the EFF had secured high quality feeding stations they would remain fairly sedentary and wait for the food to come to them (Kalleberg, 1958; Fausch, 1984). However, if the LFF had not secured good feeding stations they would have had to move between poorer sites in order to meet their energetic costs. In addition, they may have been forced to swim higher into the water column in order to intercept prey items. This behaviour may be risky, as it will make them more conspicuous to predators (Martel & Dill, 1995). In this experiment it is possible that the aggression associated with establishing territories may have occurred during the two days immediately following introduction into the stream tank, and that the low level observed may have merely served to enforce an already established hierarchy. In order to investigate this further it would be necessary to

repeat the experiment recording the behaviour of the fish immediately following introduction into the stream tank.

Despite the tendency for fish in upstream sections to grow at a faster rate than those in downstream sections there was no difference between sections in the aggressive behaviour of the fish. In addition the frequency of aggressive interactions did not differ either between or within development categories. Thus neither development category focused attacks at members of the same or opposite category. This is contrary to work by Chandler and Bjornn (1988) with juvenile steelhead trout (*Oncorhynchus mykiss*) which found that attacks tended to be more frequent between EFF. Although there was no difference in feeding rate between sections, the fish in sections furthest upstream grew the fastest in terms of both weight and length. It is possible that the fish in upstream sections had a greater choice of food types and were able to select the most profitable items. Fish in sections further downstream would thus have had less choice as the largest/most profitable food items would have been removed by fish in upstream sections. Since there was no difference in feeding rate, this depletion of optimal food items would mean that the growth of fish in downstream sections was nutritionally constrained. It is interesting to note there was no difference between the sections in the level of zone fidelity, suggesting that feeding station mediated an advantage independent of food quality (assuming that fish in upstream sections removed the optimal food items). Other studies have also shown that juvenile salmon will defend a territory in the absence of food (Chapter 6).

Although neither development category nor dominance score influenced growth rates, more dominant fish tended to have a greater increase in condition factor than more subordinate fish. Condition factor could indicate subtle changes in the relationship between weight and length that are not evident from direct analysis of growth data. It is possible that although dominant fish did not feed at a faster rate than subordinate fish they were acquiring the most profitable food items and consequently had a greater increase in condition factor. This is despite the negligible effect of dominance score on growth in terms of weight and length. Despite the difference in rate of change in condition factor there was no difference between the development categories in their final condition factor.

This experiment indicates that there is an intrinsic advantage associated with early emergence that leads to EFF establishing and maintaining stable feeding stations. Although it was not possible to quantify the quality of the feeding stations, the high level of zone fidelity suggests that they confer an advantage. As 'sit and wait' predators juvenile Atlantic salmon are likely to remain sedentary unless disturbed or food becomes limited, hence the low zone fidelity seen in LFF, and the propensity to dart up higher into the water column to intercept prey items, suggests that the quality of feeding stations available to them is less than those accessible to EFF. The intrinsic advantage of EFF that mediates the difference in feeding station quality will be further strengthened by the prior residence

advantage resulting from EFF leaving the redd first (Cutts *et al.*, 1999a; O'Connor *et al.*, 2000b; Chapter 5).

The advantages of early emergence must be balanced against the benefits of synchronous emergence (Pulliam & Curaco, 1984). By emerging together the young fish would benefit from a 'dilution effect' (Daan & Tinbergen, 1979), whereby the increased prey availability means that the individual's mortality risk decreases as the predator becomes satiated or limited in its handling capacity (Begon & Mortimer, 1986). Natural selection has favoured synchronous emergence as both early and late emergers will be subject to high mortality risks: EFF because they are present in low numbers and suffer a high predation risk and LFF because they are unlikely to secure territories and will be displaced downstream (the fish which are displaced downstream tend to be subordinates in poor physical condition who generally die (Elliott 1994)). There is a delicate balance between the risks associated with predation and downstream displacement, and the advantages of early emergence and the 'dilution effect'. The optimum strategy will ultimately increase the likelihood of smolting in the first year (Thorpe *et al.*, 1992) and asymmetries, such as intrinsic differences between EFF and LFF, which contribute to this decision, will be pivotal in determining a fish's life history strategy.

Chapter 5

The effects of prior residence on
behaviour and growth rates in juvenile
Atlantic salmon.

After O'Connor et al., 2000b

Abstract

It is well documented that prior residence confers advantages in territorial disputes. However, its impact on other aspects of behaviour and fitness is less understood. Here I test how prior residence influences the subsequent feeding behaviour and growth performance of dispersing Atlantic Salmon fry (*Salmo salar*), using experimental manipulations of residence in a semi-natural stream tank. In replicated trials, groups of seven 'Primary' fish were released into the stream tank 3 days ahead of seven 'Secondary' fish. Standardised behavioural observations were made on each fish over the following 14 days, after which all fish were removed and measured. Primaries and Secondaries were initially the same size and body condition, and exhibited the same degree of site fidelity. However, Primaries darted higher into the water column to intercept prey items, fed at a higher rate and subsequently grew faster. Larger fish (in terms of body length) tended to be more dominant, and dominants grew faster than subordinates. However, there was no difference in dominance between Primaries and Secondaries. These results suggest that the well-documented advantage of early emerging salmon fry over late cannot be completely attributed to intrinsic differences, and that the advantage is partly mediated via a 'prior residence' effect. Furthermore, prior residents gain foraging advantages without necessarily becoming more dominant.

Introduction

It is generally accepted that animals dispersing from their natal site incur a cost of emigration that will generally increase with distance travelled from their natal site (Plissner & Gowaty, 1996). Dispersing individuals face increasing mortality risks associated with unfamiliar habitat, passage through areas of high predator density, and the physiological costs associated with extensive movement (Plissner & Gowaty, 1996).

Environmental dispersal, that is “the movement that an animal makes away from its birthplace in response to crowded conditions” (Howard, 1960), is a common phenomenon in nature, and will tend to occur when a population is living at or close to its carrying capacity (see “density responsive emigration” (Lidicker, 1962), “saturation dispersal” (Lidicker, 1975)). Dominant individuals tend to be more sedentary and move only short distances provided resources are available, whilst subordinate individuals disperse even in the absence of severe population pressure, as they are displaced or excluded by dominants well before food resources become limited (Gauthreaux, 1978). Given the costs of dispersal, unequal competitive ability leading to unequal resource partitioning will thus ultimately affect individual survival (Elliott, 1994).

The Atlantic Salmon is an ideal species for a study into the individual asymmetries that contribute to differential dispersal, as the fry emerge from the nest (redd) in numbers that far exceed the limits of their natal habitat’s carrying capacity (Giles, 1994). Thus the individual differences that exist between individuals will become instrumental in determining their success in the ensuing inevitable dispersal.

After hatching, the fry remain in the gravel substratum of their natal stream for a variable period while obtaining nutrients from their yolk sacs (Kalleberg, 1958). Once this endogenous food supply is absorbed they exhibit a normally distributed temporal pattern of emergence and dispersal from the spawning ground (Godin, 1982; Brännäs, 1987). The peak of emergence is highly synchronised both in natural (Gustafson-Marjanen & Dowse, 1983) and artificial redds (Godin, 1980; Brännäs, 1987). Competition for food and space is fierce (Keenleyside & Yamamoto, 1962), and if a population exceeds the carrying capacity of the habitat, some fry will be forced downstream by the aggressive behaviour of those that have already settled (Chapman, 1962; Mason & Chapman, 1965; Backiel & LeCren, 1978; Elliott, 1986;).

The Prior Residence effect, whereby interactions between residents and intruders are more commonly won by the resident (Maynard Smith & Parker, 1976; Leimar & Enquist, 1984), has been well-documented in a variety of animals (Huntingford & Turner, 1987; Archer, 1988,). In semi-natural stream channels, early emerging salmon fry have a better chance of establishing a feeding site than late emerging fry (Chapman, 1962; Mason & Chapman, 1965; Fausch & White, 1986; Chandler & Bjornn, 1988; Metcalfe & Thorpe 1992b; Brännäs, 1995). This apparent advantage of early first feeding could be the result of an intrinsic quality common to early first feeding fish. For example, fish with

higher Standard Metabolic Rates (SMR) will tend to use up their yolk sacs sooner than those with low SMRs and so will emerge earlier. Since fish with high SMRs tend to be dominant over fish with lower SMRs (Yamamoto *et al.*, 1998; Metcalfe *et al.*, 1995) the true extent of the advantage of prior residence is difficult to assess.

Recent experimental work on older salmon suggests that territory ownership *per se* may be more important than differences in Resource Holding Potential (RHP) between fish, as pilot data from a single trial indicated that intrinsically dominant individuals were unable to displace, and consequently grew slower than, subordinates that already held territories (Huntingford & De Leaniz, 1997). In this paper I test whether this is also true at the fry stage when there is greatest competition for resources. In a series of replicated trials I examine how prior residence influences the behaviour and growth performance of salmon fry, using experimental manipulations of residence in order to control for confounding effects.

Methods

A batch of full-sibling eggs from sea run salmon caught in the River Almond, Perthshire were incubated at the Scottish Office Agriculture Environment and Fisheries Department, Almondbank salmon rearing unit. As Atlantic salmon emerging from a redd in the wild would at least share the same mother, it was decided that full-siblings should be used as this would best mimic the competitive situation faced by fry dispersing from redds in the wild. The egg fish were moved to the Glasgow University Field Station at Rowardennan on Loch Lomond on 8th November 1996. The fish were kept under ambient photoperiod and temperature conditions in 1m square tanks. These tanks received a continual turnover of water pumped from Loch Lomond and therefore rich in zooplankton. Once the fishes yolk sacs were completely absorbed the fish diet was supplemented with commercial salmon food (Fulmar feeds, BOCM Pauls Ltd.), which they received *ad libitum* from automatic feeders.

The experiment was carried out between 1st June and 30th July 1997 (i.e. 7-11 weeks after first feeding), in sections of an artificial stream tank that had a glass side wall to allow behavioural observations. Salmonids of this age are in the critical period for survival which follows emergence, and experience intense competition for space and high mortality rates (Elliott, 1994). This tank had a continual turnover of water pumped from Loch Lomond and therefore rich in zooplankton, which provided ample food for the salmon fry. In order to ascertain the exact levels of plankton in the water, samples were collected by placing fine mesh plankton nets in the water column at three different locations in the stream tank for twenty minute periods. These samples were collected on 4th June, 16th and 30th July at 1300hrs. The contents of the nets were then dried and weighed to the nearest µg. Over the duration of the experiment the mass of plankton collected during a twenty minute period did not vary (one-way ANOVA, effect of date: $F_{2,6}=0.18$, $P=0.84$).

Each section of the stream tank measured 100 cm long by 30 cm wide with a water depth of 15 cm. During the course of the experiment the average water temperature was 16°C (± 0.4). The upstream and downstream barriers between neighbouring sections were made of plastic mesh. A water pump created a flow through the sections (mean water velocity at the midpoint of the sections and 9 cm below the surface=0.03ms⁻¹ ± 0.01 (SD)). Each section had a layer of gravel mixed with marble chips (Esmo, Rowebb) to produce a topographically natural but light coloured substratum against which the fish could easily be seen. Salmon parr in the wild will naturally come across patches of substrate of similar colour to the marble chips used in this experiment. Sections were marked into ten 10 cm long zones along their length zones along their length, with zone number 1 being the furthest upstream.

Fourteen fish randomly chosen from a stock tank were used in each of the five replicate trials. The fish were anaesthetised with 5ml/l of a solution of 10g/l benzocaine

(ethyl-p-aminobenzoate) in 95% ethanol and given unique combinations of marks with alcian blue dye on their pectoral, pelvic, dorsal, anal and/or caudal fins. This marking technique has no effect on the behaviour or growth of first feeding salmon fry (Metcalfe *et al.*, 1992). On day 1 of each trial seven fish were randomly selected from each group of fourteen and introduced into a single section of the stream tank. These fish were then left to settle for three days and are referred to as 'Primaries' as they were the first fish to be released into the stream tank. In the morning of day 4 the Primaries were removed, anaesthetised, and their weights (to the nearest 0.01g) and fork lengths (to the nearest 0.1mm) recorded. Although all of the fish recovered from the anaesthetic and were able to swim in a normal manner within 2-3 minutes of being placed in fresh aerated water, they were left for a further hour before they were returned to the same section of the stream tank. In the evening of day 4 the remaining seven fish were anaesthetised and their weights and lengths recorded. Once these fish had fully recovered they too were placed in the same section of the stream tank. These fish are referred to as 'Secondaries'. The resulting high density of fish within each section (47 fish/m²) approximated the wild situation where Atlantic salmon emerge from the redd in numbers that far outstrip the natural carrying capacity of the natal site.

Observational data were then collected on days 6, 8, 11 and 13. On each of these days each fish was observed twice (for 2 min at each time), with the two observations being approximately 1.5 hours apart. During each 2 min observation the number of feeding attempts made by the fish was recorded, along with its location in the stream section (zone 1-10), mean height maintained off the bottom and the maximum height in the water column to which it swam in order to intercept a prey item. Both height measurements were made to the nearest 0.5 cm using a 15 cm transparent Perspex ruler placed against the glass wall of the tank. In addition to this any aggressive interaction (i.e. lateral display, charge or nip, as described by Keenleyside & Yamamoto (1962)) with another fish during the 2 min was recorded. On day 15 all fourteen fish were removed from each section of the stream tank, anaesthetised and their final weight and fork lengths recorded. Three Primaries and two Secondaries died during the course of the trials; the data collected for these individuals were omitted from the analyses.

Individual Specific Growth Rates for weight were calculated as $100(\ln(\text{Final measurement}) - \ln(\text{Initial measurement}))/\text{duration of experiment in days}$, following Ricker (1979). In order to control for the effect of body size on growth rates, these values were then regressed against the initial weight of the fish and the equation of the resulting line used to calculate the expected Specific Growth Rate for each fish, given its initial weight. The difference between the expected and observed Specific Growth Rate (adjusted Specific Growth Rate) was used in subsequent analysis of growth rates. Weight was used for these calculations as length did not change greatly over the two week period. Using the weight (W) and fork length (L) measurements, an index of each fish's condition

(Condition factor, K) was also calculated as $K = 10^5(W/L^a)$, where a is the slope of a regression of $\log_{10}(\text{weight})$ on $\log_{10}(\text{length})$ following Bolger and Connolly (1989).

Data from each fish have been used as individual experimental units in the statistical analysis.

Results

Initial size and condition

Initial (i.e. day 4) weights and lengths of the fry varied significantly between trials as fish had grown larger by the onset of later trials. However, there was no overall difference in the initial size of Primary (mean weight=0.53±0.05g (SE) (n=32), fork length =37.54±1.37mm (32)) and Secondary fish (weight=0.54±0.05g (33), fork length =37.35±1.19mm (33); two-way ANOVA, effect of trial number on initial weight: $F_{4,55}=71.30$, $P<0.001$; Primary/Secondary residence: $F_{1,55}=0.22$ $P=0.64$; effect of trial number on initial fork length: $F_{4,55}=103.41$, $P<0.001$; Primary/Secondary residence: $F_{1,55}=1.51$, $P=0.22$).

The initial condition factor (K) of the fish also varied with trial but not with the resident category (two-way ANOVA: effect of resident category: $F_{1,55}<0.001$, $P=0.97$; trial: $F_{4,55}=4.47$, $P<0.001$), fish in later trials having lower K values than those in earlier trials.

Spatial positions, feeding behaviour and aggression

The position of individual fish within the stream tank was relatively stable, such that an average of 49.2±2.5% (SE) of observations of a given fish were from its most frequently occupied of the 10 zones. There was no difference in this measurement of 'zone fidelity' between Primaries and Secondaries (Mann-Whitney $U=470.5$, $P=0.89$, mean for Primaries=47.6±3.2%, Secondaries=50.8±4.0%). There was also no difference in mean height maintained off the stream substrate (Primary fish=1.2±0.3cm (32), Secondary fish=1.0±0.3cm (n=32); Mann-Whitney $U=432$, $P=0.21$). However, when swimming upwards to intercept prey items, Primary fish tended to dart to a greater maximum height above the substrate than Secondary fish (Primary fish=5.1±0.7cm (32), Secondary fish=3.0±0.8cm (32), Mann-Whitney $U=383.5$, $P=0.05$).

While the feeding rates of the fish varied between the trials (with fish in later trials feeding more intensively), there was a consistent and significant trend within trials for Primary fish to feed more frequently than Secondary (Primary fish=2.71±0.29 feeding attempts per min (32), Secondary fish=1.52±0.22 (32), two-way ANOVA, effect of resident category: $F_{1,55}=13.09$, $P<0.001$, trial: $F_{4,55}=4.10$, $P<0.001$, Figure 1).

A dominance score was calculated as the number of successful aggressive interactions made by a focal fish (i.e. when the opponent was displaced) during the total observation time, minus the number of times it lost an interaction; positive values therefore indicate a more dominant fish. Primary fish did not have significantly different dominance scores to Secondary fish (t-test assuming equal variances: $t_{63}=1.00$, $P=0.32$, mean for Primaries=0.50 ±0.62, Secondaries=-0.48 ±0.62).

There was no difference between Primary and Secondary fish in the number of attacks they initiated in total (mean for Primaries=1.03 ±0.33 attacks per minute, Secondaries=0.61 ±0.22, Mann-Whitney: $U=482$, $P=0.51$). Nor was there a difference in the number of attacks they initiated against the opposite resident category (mean for

Primaries=0.55 \pm 0.21 attacks per minute, Secondaries=0.29 \pm 0.11, Mann-Whitney: U=498.5, P=0.62) or the same resident category (mean for Primaries=0.47 \pm 0.15, Secondaries=0.32 \pm 0.13, Mann-Whitney: U=475.5, P=0.41). There was also no difference in the number of successful attacks that a fish made between the resident categories (Mann-Whitney: U=106, P=0.61). There was no evidence that overall aggression levels were related to food availability, as the mean rate of attacks in a trial did not correlate with the mean feeding rate (Spearmans rank r_s = 0.1, P= 0.87). Since fish weight and length varied between trials the two variables, standardised values (z scores) were calculated for each fish in relation to the size of the other fish in its trial. Dominance appeared to be dependent on both standardised length and weight, with relative length providing the strongest relationship (Figure 2; quadratic regression based on relative length: r^2 = 0.19, N=64, P<0.001). However, relative weight had an additional minor effect explaining a further 2% of the variation (overall multiple regression, r^2 = 0.21, N=64, P<0.05). In order to test whether this relationship was similar for both residence categories of fish, residual dominance scores were calculated as the difference between the observed dominance score and the score predicted from the quadratic equation (Figure 2). As these residuals did not differ significantly between Primary and Secondary residents (t-test assuming equal variances: $t_{63}=1.313$, P=0.19) I can assume that the relationship between relative length and dominance is the same for both categories of fish.

Growth rates

In order to investigate the effect of dominance status on growth, the fish were split into two groups on the basis of their dominance scores ('dominant' fish, with dominance scores greater than zero, and 'subordinate' fish with dominance scores zero or less). A three way ANOVA revealed that the trial to which a fish belonged had a strong effect on adjusted Specific Growth Rate (Table 1). This is probably due to fish being larger in later trials, so that although the absolute level of food supply was stable (see Methods), the relative food supply per unit weight of fish decreased through the season. More interestingly, dominance and residence category also affected adjusted Specific Growth Rate (Table 1): dominant fish typically grew faster than subordinates (Figure 3), and independent of dominance, Primaries grew faster than Secondaries (Figure 4).

Table 1

Results of a three-way ANOVA investigating the influence of dominance category (DOM, dominant or subordinate), residence group (RESID, Primary or Secondary) and trial number on adjusted Specific Growth Rate (% increase in weight per day)

		df	F	Sig.
Main Effects	DOM	1	10.90	<0.01
	Trial	4	4.22	<0.01
	RESID	1	8.66	<0.01
2-Way Interactions	DOM * Trial	4	0.26	0.90
	DOM * RESID	1	2.50	0.12
	Trial * RESID	4	1.17	0.34
3-Way Interactions	DOM * Trial * RESID	4	0.64	0.64
Model		19	3.62	<0.001
Residual		45		
Total		64		

RESID, residence category; DOM, dominance category.

Figure 1

Mean (\pm SE) feeding rates of Primary (i.e. prior resident, filled circles) and Secondary (i.e. later immigrant, open circles) Atlantic salmon fry in five replicate trials. See text for statistical analysis.

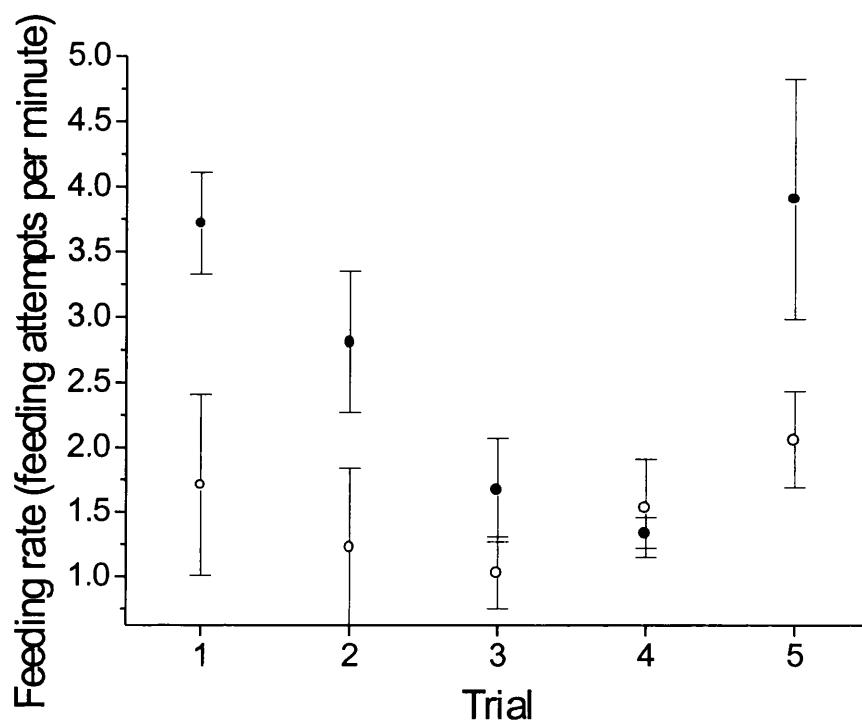


Figure 2

Standardised fork length (z score) against dominance score in Atlantic salmon fry.

(Dominance Score = $-0.61 - (1.58 \times \text{relative length}) + (0.67 \times \text{relative length}^2)$; $r^2 = 0.19$, $F_{2,62} = 8.33$, $P < 0.001$).

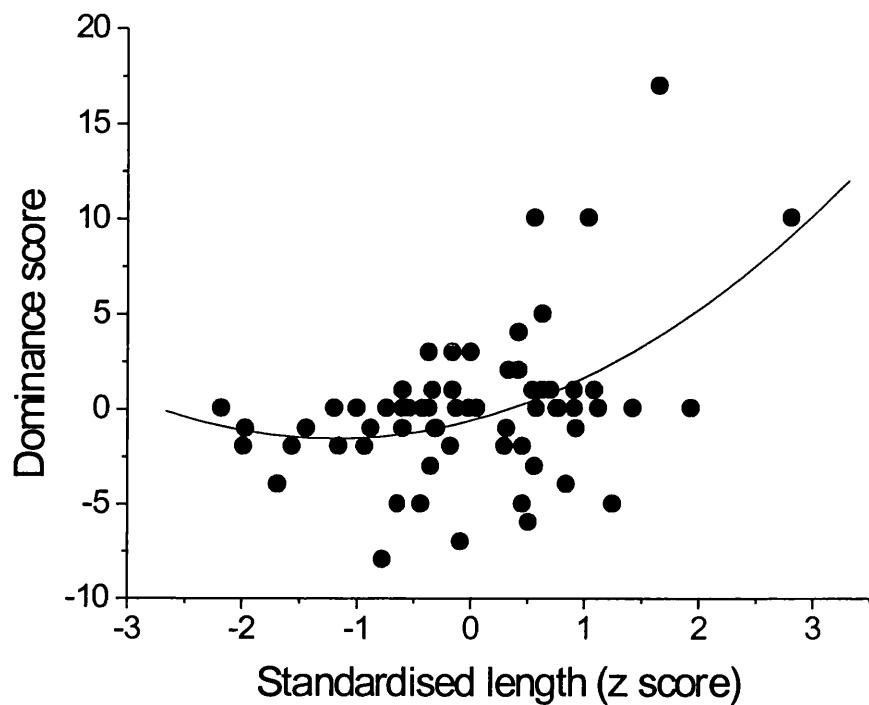


Figure 3

Comparison of mean (\pm SE) adjusted Specific Growth Rates (% increase in weight per day) between dominant (filled circles) and subordinate (open circles) Atlantic salmon fry in both residence categories.

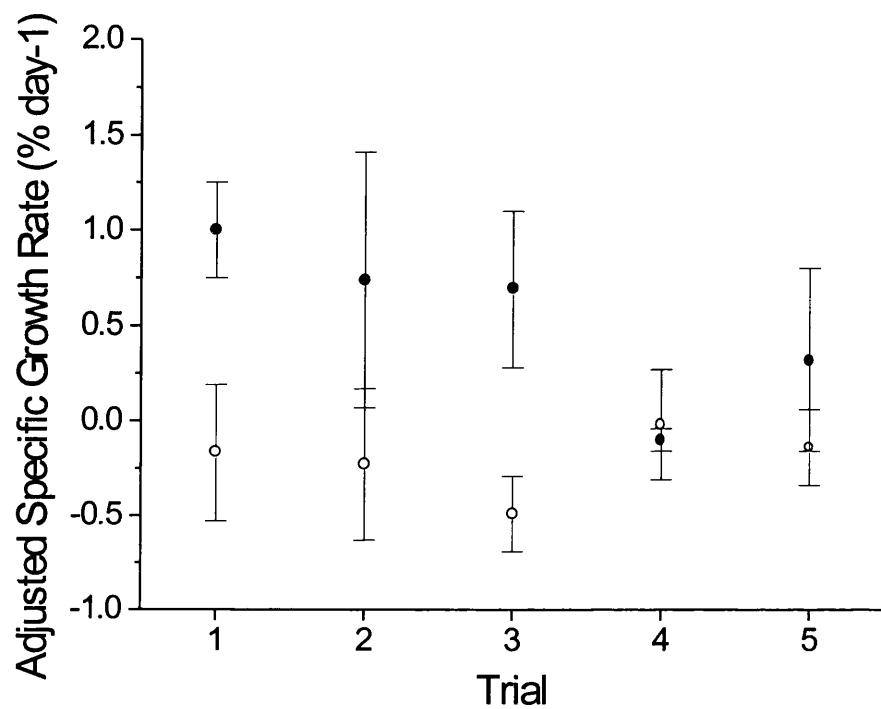
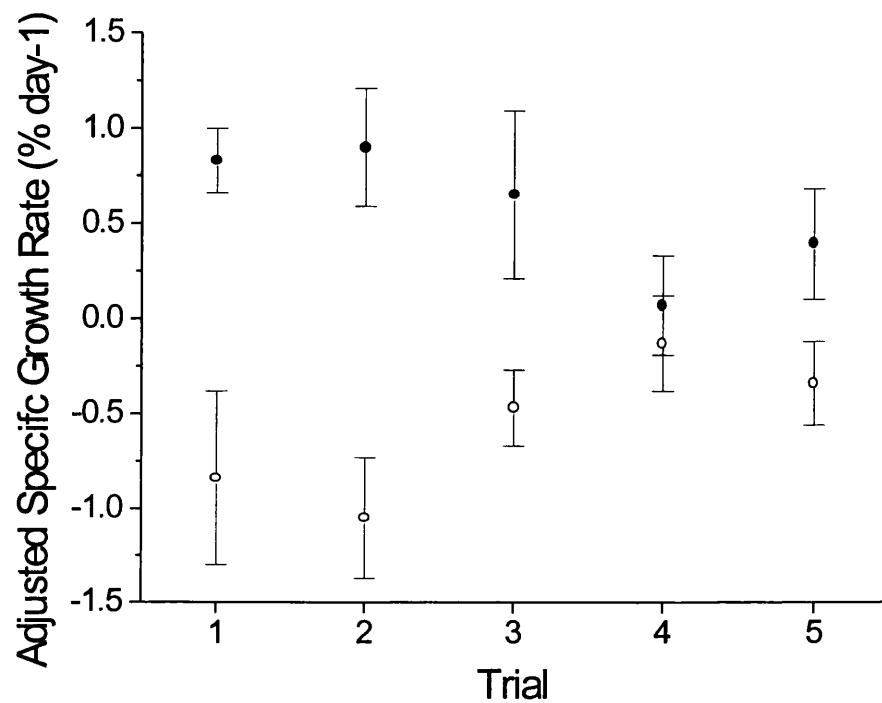


Figure 4

Comparison of mean (\pm SE) adjusted Specific Growth Rates (% increase in weight per day) between Primary (filled circles) and Secondary (open circles) Atlantic salmon fry in replicate trials. See text for statistical analysis.



Discussion

Despite the absence of any apparent differences in body size or condition, the first fish to establish themselves in the stream tank fed at a greater rate and subsequently had higher rates of growth than those introduced later. These differences in performance arose despite there being no significant differences between the residence categories in their spatial distribution or dominance status. Primary fish may have suppressed the feeding activity of the later animals without there having been any major differences in their levels of aggression. For example it is possible that Secondary fish did not dart as high into the water column as Primaries as their feeding activity was suppressed. Alternatively, this difference in darting height could reflect differences in the quality of their feeding stations, with prior residents having access to more drift food. However, it should be noted that the exact cause of differences in darting height is unclear (see page 63 for an alternative explanation) and further experiments examining darting behaviour are required.

The high feeding rate and growth rate of Primary fish seen in this experiment indicates that the previously documented advantage of early over late emergence in salmon fry (Chapman, 1962; Mason & Chandler, 1965; Fausch & White, 1986; Chandler & Bjornn, 1988; Brännäs, 1995) is partly due to a prior residence effect. The tendency for the first animals to arrive at a territory to win any subsequent disputes over the territory with intruders is well documented (Maynard Smith & Parker 1976; Leimar & Enquist, 1984; Huntingford & Turner, 1987; Krebs & Davies, 1987; Archer, 1988; Alcock, 1993), and has been examined in a variety of animals including juvenile salmonids (Maynard Smith & Reichert, 1984; Stamps & Krishnan, 1995; Tobias, 1997; Cutts *et al.*, 1999b; Johnsson *et al.*, 1999). The present study shows that prior residents gain foraging benefits even without having excluded later arrivals from a territory.

While this experiment controlled for any intrinsic differences between residence categories, the first fish to emerge (and therefore become prior residents) may be intrinsically more dominant. Metcalfe and Thorpe (1992) found that the first fish to emerge and begin feeding were dominant over later feeding fry from the same family in experiments that controlled for prior residence. It was later found that this superiority was due to differences in Standard Metabolic Rate (SMR), early feeding fry having relatively higher SMR values, the date of first feeding having no influence on dominance interactions once SMR was taken into account (Metcalfe *et al.*, 1995). The effect of date of first feeding arises because fish with a relatively high SMR will tend to have exhausted their yolk sacs sooner than fish with low SMRs and will have emerged from the redd and begun feeding sooner. Thus fish with a high SMR potentially have a double advantage: they are intrinsically dominant, and emerge earlier and so obtain a prior resident advantage over later feeding fry.

However, it should be noted that early emergence is not without its costs. Young animals and those at vulnerable stages in life are more likely to avoid predation if their period of dispersal or habitat shift is synchronised (Pulliam & Caraco, 1984). This is partly due to the 'dilution effect' (Daan & Tinbergen, 1979), whereby the probability of predation decreases as the potential prey's group size increases. The benefit of early emergence (i.e. a prior residence advantage) may thus be counterbalanced by the risk of predation. Fry are highly vulnerable to predation from piscivorous birds and other fish, and stand a better chance of survival if they emerge synchronously (Godin, 1982; Brännäs, 1995). Later emergers are afforded protection by large numbers, i.e. as prey number increases predator satiation decreases the individual risk of predation (Peterman & Gatto, 1978; Begon & Mortimer, 1986).

In a single trial using older salmon, Huntingford and Garcia De Leaniz (1997) found that the probability of settlement (as opposed to emigration downstream), and growth rates following settlement, were significantly higher in the first fish to be released into a stream tank. They also found that the probability of a fish settling decreased as its dominance rank increased. The similarity between the scaling of Metabolic Rate (slope of regression line $b=0.87$; Steingrimsson & Grant, 1999) and territory size ($b=0.86$; (Grant & Kramer, 1990)) on body mass suggests that territory size may reflect metabolic requirements (Steingrimsson & Grant, 1999). Therefore dominant fish (with a higher metabolic rate) may require larger territories to meet their metabolic requirements. So the reduced probability of settlement of dominant fish compared to fish of a lower rank could be due to the low abundance of suitable territories for high SMR fish. When coupled with early emergence, and hence prior residence, a high SMR is an advantage, but this may become a disadvantage if uncoupled, due to a reduction in suitable territories.

It should be noted that although some fish lost weight in this experiment, in nature competition for resources may lead to some of the fish dispersing downstream. This downstream migration will tend to be by subordinate fish in poor physical condition, who will frequently die (Elliott, 1994). Fast early growth will lead to fish establishing and maintaining a size advantage. This in turn will increase the likelihood of smolting in the first year (Thorpe *et al.*, 1992). Thus early growth rate is instrumental in determining salmon life history strategies.

Chapter 6

Analysis of the strength and causes
of the prior residence effect in territorial
contests between juvenile salmon.

Abstract

One of the central dogmas surrounding territoriality is that territory owners tend to win any conflicts with intruders. This 'prior residence effect' is particularly relevant to situations where dispersing or migrating animals attempt to settle in a habitat in numbers that exceed the carrying capacity, since early arriving individuals would then have a clear advantage in subsequent competition for space. By manipulating the amount of time that Atlantic salmon (*Salmo salar*) fry spent alone in an experimental tank before a conspecific was induced to invade, I examined the strength of the prior residence effect relative to asymmetries in size and metabolic rate (both of which have previously been shown to influence dominance interactions in salmonids). This also allowed me to determine if the resident's advantage was due to a payoff asymmetry and, if so, how long a fish needed to be resident in order to gain this advantage. The results indicate that duration of residency determined the outcome of contests rather than asymmetries in size or metabolic rate, with resident fish tending to win contests with an intruder. The vigour with which a resident defended its territory, and the probability of it winning a contest with an intruder, increased with its duration of residency, suggesting that the resident's advantage was due to a payoff asymmetry. After 1 day residency there was a trend for the resident fish to defeat an intruder, and after 2 days the resident fish was significantly more likely to win a contest than an intruding fish. Early dispersing salmon fry will therefore have an advantage in gaining territories than later arrivals.

Introduction

One of the central dogmas surrounding territoriality is that territory owners tend to win any conflicts with intruders in their territory (Rohwer, 1982; Huntingford & Turner, 1987; Kreb & Davies, 1987; Archer, 1988; Alcock, 1993). Three hypotheses have been put forward to explain this phenomenon. Firstly, the 'Resource Holding Potential' hypothesis (Parker, 1974) states that residents tend to win encounters since they have intrinsic attributes that make them superior to a non-territory holder and so are more likely to have obtained a territory in the first place. An example of this asymmetry in resource holding potential is seen in male black winged damselflies (*Calopteryx maculata*), where the deciding factor in contests over territories is the energy stores of the individuals: damselflies with a higher fat content usually win such contests and so obtain the territories (Marsden & Waage, 1990).

Secondly, residents and intruders may follow an arbitrary rule such as 'if the opponents are otherwise equally matched, the owner of a territory wins, the intruder retreats' (Davies, 1978). An example which apparently supports this hypothesis is seen in the funnel web spider (*Agelenopsis aperta*). Here if the size difference between the owner and the intruder is less than 10% the owner wins, although if the intruder is more than 10% larger than the resident then it will displace the resident and become the new territory owner (Maynard Smith & Riechert, 1984).

Thirdly, the 'Payoff Asymmetry' hypothesis (Maynard Smith & Parker, 1976) suggests that the payoff from holding a territory increases over time. Thus residents will gain more by retaining a territory than an intruder would gain by acquiring it. This hypothesis is supported by an experiment in which resident European robins (*Erthacus rubecula*) were removed from their territories and newcomers allowed to establish themselves in the territories (Tobias, 1997). When the original owners were released after variable amounts of time it was noted that dominance gradually shifted from removed owners to newcomers with increasing duration of the residence time of the newcomers. Removal of the newcomers, and replacement by another newcomer showed that dominance was determined by the duration of residence by the newcomers rather than the time that the original owners were absent.

The reasons why residents tend to win encounters with intruders may therefore vary between species and contexts, but it is noticeable that the last two of the above hypotheses indicate that simply being the prior owner of the territory influences the outcome (the 'prior residence' effect). This has great implications for those territorial species which exhibit a synchronised period of migration or dispersal, which can result in large numbers of conspecifics arriving in a previously empty habitat. The first individuals to arrive will then have a free choice of potential territories, whereas those arriving later will be at a disadvantage and may be excluded from favoured habitats. The selection pressure for early arrival will then depend on both the strength and cause of the prior

residence effect (i.e. if it is due to a payoff asymmetry, how long does the period of territorial residence need to be to produce the asymmetry?), and the extent to which this may be offset by asymmetries in resource-holding potential.

In this paper I investigate these effects in the context of juvenile salmon seeking feeding territories when undergoing dispersal in the first year of life. Salmonid eggs are typically laid in numbers that far exceed the carrying capacity of the habitat into which the fry emerge, so leading to intense competition for territories and high mortality (Elliott, 1994). While the greatest competition occurs during the period of initial fry dispersal from the nest, further territorial competition arises during their first summer and autumn as the fish move to accommodate the change in preferred microhabitat with increasing body size (Beall *et al.*, 1994). It has been observed that late dispersing fish may be forced downstream by the aggressive behaviour of those individuals that have already settled on the available territories (Chapman, 1962; Mason & Chapman, 1965; Backiel & Le Cren, 1978; Elliott, 1986). In the absence of predators, early-dispersing salmonid fry generally survive and/or grow better than late-dispersing fry (Chapman, 1962; Mason & Chapman, 1965; Fausch & White, 1986; Chandler & Bjornn, 1988; Bränäs, 1995).

However, this apparent advantage of early dispersal could in fact be the result of an intrinsic difference between early and late emerging salmon. There are two factors (body size and metabolic rate) which potentially differ between early and late fish and may affect dominance status. The earliest fish to disperse onto territories and begin feeding will be slightly larger than later arrivals, although body size *per se* is generally a poor predictor of dominance in salmon fry (Huntingford *et al.*, 1990, Metcalfe *et al.* 1992). Secondly, early emerging salmon fry have higher average Standard Metabolic Rates (SMR) than do later fry from the same nest, presumably because they exhaust their endogenous food source (the yolk sac) sooner (Metcalfe & Thorpe, 1992b; Metcalfe *et al.*, 1995; Cutts *et al.*, 1999a), and fish with a higher SMR are known to be more aggressive and become dominant (Metcalfe *et al.*, 1995; Yamamoto *et al.*, 1998; Cutts *et al.*, 1999a). It can therefore be difficult to tease apart the relative roles of differences in resource-holding potential and prior residence when interpreting much of the earlier work.

Moreover, while previous experimental studies have demonstrated a real effect of prior residence on dominance and/or territory acquisition in Atlantic salmon (Huntingford & De Leaniz, 1997; Cutts *et al.*, 1999a, b), they have not shown whether the effect is due to an arbitrary decision rule (owner wins) or to a payoff asymmetry, nor how it occurs. In this paper I examine these issues by quantifying the nature and outcome of experimentally-induced territorial intrusions in juvenile Atlantic salmon *Salmo salar*. By measuring the two candidate asymmetries in resource-holding potential (body size and standard metabolic rate) and manipulating the period of prior residence, I test (a) how strong the prior resident effect is in comparison with other asymmetries, (b) whether it is due to a payoff asymmetry, and (c) if so, what period of territorial residence is required to produce an effect.

Methods

A batch of full-sibling eggs from sea run salmon caught in the River Almond, Perthshire were incubated at the Scottish Office Agriculture Environment and Fisheries Department Almondbank salmon rearing unit. The eggs were moved to the University Field Station at Rowardennan, Loch Lomond on 8th November 1996. Once hatched, the fish were kept under ambient photoperiod and temperature conditions in 1m diameter round tanks. These tanks received a continual turnover of water pumped from Loch Lomond and therefore rich in zooplankton. Once the fish's yolk sacs were completely absorbed the diet was supplemented with commercial salmon food (Fulmar feeds, BOCM Pauls Ltd.), which they received *ad libitum* from automatic feeders.

On September 30th 1997 100 lower modal group fish (i.e. those that would delay seaward migration for at least a further 18 months, Thorpe, 1977) were transferred to Glasgow University where they were kept in 1m wide square tanks. The fish were kept at 15°C under ambient photoperiod and hand fed bloodworm (chironomid larvae species) *ad libitum*. At this stage the fish had a mean length of 60.66mm \pm 0.74 (s.e.) (N=82) and weighed an average of 2.34g \pm 0.09 (N=82). To aid further identification, each fish was given a unique combination of marks with alcian blue dye on its pectoral, pelvic, dorsal, anal and/or caudal fins. This marking technique has no effect on the behaviour or growth of juvenile salmon (Metcalfe *et al.*, 1992).

The experiments were carried out between 28th October and 9th December 1997 (i.e. 7-9 months after first feeding) and took place in an aquarium maintained at 12.7°C, with a 12L: 12D photoperiod.

Measurement of Standard Metabolic Rate

Flow-through respirometry was used to calculate the oxygen consumption (and hence metabolic) rate of the fish. The principal of this technique is to calculate the rate of oxygen consumption by a stationary fish using the reduction in oxygen concentration of water flowing past it (Steffenson, 1989).

On day one of the experiment, ten fish were randomly chosen from the stock tank. Their fork lengths and weights were measured (to the nearest mm and 0.01g, respectively) and the fish were placed into individual Perspex chambers of a flow-through respirometer in the experimental laboratory. The fish were then left unfed in the chambers for 16-24 hours prior to measurement of oxygen consumption. This period allowed full gut evacuation to occur and hence avoided any influence of Specific Dynamic Action (SDA) (Priede, 1985) on the rates of oxygen consumption measured.

The next day the respirometer was calibrated and the fish's oxygen consumption rates measured according to the method outlined by Metcalfe *et al.* (1995) and Cutts *et al.* (1998).

Three measurements were made of the oxygen consumption of each fish, 1-2

hours apart, between 1000 and 1300 hours. This was a sufficient time interval to ensure that conditions within the respirometer had again reached a steady state (Steffensen, 1989).

A black sheet was placed over the respirometry chambers to ensure that the fish were kept in semi-darkness. By periodically lifting the corner of the black sheeting to observe the fish, it was ascertained that the fish remained predominately quiescent. Thus the oxygen consumption measured under these conditions approximates to the Standard Metabolic Rate (SMR; Brett & Groves, 1979).

Invasion Experiment

At 1300hrs on day 2 the ten fish were assigned into size matched pairs (mean percentage weight difference between members of a pair = $8.68 \pm 7.66\%$, length = $1.3 \pm 1.84\%$), and one fish was placed in each half of one of the five replicate observation tanks. These tanks were divided into two square halves (10x10cm) by an opaque partition, and had a water depth of 8cm. At the centre of the dividing partition was a circular door (3 cm radius) which was initially kept shut. Three of the glass sides of the tank were coated externally in white paper leaving one side through which observations could be made. The substratum of each tank consisted of small marble chips (0.5cm diameter, Esmo, Roweb) which produced a topographically natural but light coloured substratum against which the fish could easily be seen. Juvenile salmon in the wild will naturally come across patches of substratum of similar colour to the marble chips used in this experiment. The fish placed in the left side of the tank was referred to as the 'resident', and the fish in the right side the 'intruder'. Both sides of the tank were identical in every respect, except that the side of the door facing the intruder was marked with a red cross so that the intruder would be able to distinguish between its own familiar side of the tank and the side into which it was subsequently induced to invade.

At 1400hrs on either day 2, 3, 4 or 5 (depending on the treatment), the door between the two sides of the testing tank was opened and the intruder induced to move into the resident's half of the tank using a transparent Perspex rod. Once both fish were in the resident's half the door was closed. The behaviour of the two fish was then recorded continuously for two hours. The different behaviours of the fish were classified according to a modification of the scheme outlined by Keenleyside and Yamamoto (1962). In order to assign dominance within the pairs of fish, the classified behaviours that they exhibited were assigned point values and the fish that totalled the most points was classified as the winner of the contest. Points were assigned to behaviours as follows:

1 point for lateral display, where the fish expanded all its fins maximally, tensed its body and arched its tail upwards. The fish then began to beat its tail slowly, irregularly and with large amplitude.

2 points for charging, which involved one fish swimming directly and quickly towards its opponent (but without making contact)

3 points for nipping, which involved the fish swimming up to and biting its opponent.

At the end of the observation period the fish were fed and left overnight in the observation tank. Next morning they were removed and returned to the stock tank. The entire experiment was repeated nine times (with 10 new, previously untested, fish each time). Nine of the territorial invasion experiments had to be abandoned due to premature invasion of the resident's side of the tank by the intruder. This meant that a total of 41 invasions were performed, 10 in which the resident had a residency duration of 0, 1 and 2 days, and 11 where the resident had been present for 3 days.

Ethical note: The experiment was carried out under licence from the UK Home Office. The procedure was such that the fish were continuously under observation during the period when the dominance status of the fish was established, so that it was possible to intervene and remove either fish immediately if contests ever escalated to a point where it was thought that injury might occur. Injury could occur. However, this was never necessary, and interaction rates in salmon are low and rarely involve overt aggression once dominance hierarchies are established (Metcalfe *et al.*, 1989). None of the fish sustained physical damage during the contests.

Results

In order to correct SMR for body size, the rate of oxygen consumption (ml/h) was first regressed against fish weight (W, in g) on a double natural logarithmic scale (linear regression: $\ln(\text{oxygen consumption}) = 0.62\ln(W) - 2.83$, $r^2=0.22$, $F_{1,81}=24.14$, $P<0.001$, Figure 1). The relative Standard Metabolic Rate (rSMR, Metcalfe *et al.*, 1995) was then calculated as the residual from this regression; fish with a positive rSMR therefore had higher than expected oxygen consumption rates for their weight, while a negative value indicated a lower than expected oxygen consumption rate.

There was no significant difference in the metabolic rates of residents and intruders (t-test, $t = -0.37$, $df=80$, $P=0.71$), the average difference between the rSMR values of residents and intruders being -0.03 ± 0.03 ($N=41$). Body size was also expressed in relative terms, the relative weights and length difference of the fish within each pair being calculated as:

$$\text{Relative size} = 100(\text{Size}_I - \text{Size}_R)/\text{Size}_R$$

where Size_I is the size of the intruder and Size_R the size of the resident.

Again there was no consistent difference between residents and intruders, the average relative weight being $8.68\text{mg} \pm 7.66$ (t-test, $t = -0.38$, $df=80$, $P=0.71$) and length being $1.3\text{mm} \pm 1.84$ (t-test $t = -0.36$, $df=80$, $P=0.72$).

The longer the duration of residency (i.e. the longer the resident had been in its side of the tank before the intruder entered), the more likely it was to engage in an aggressive act (i.e. a threat display, charge or nip) during the two hour observation period following the moment of intrusion (logistic regression: Model Chi-Square = 8.37, $df=1$, $P<0.01$: Figure 2). Hence the longer a fish had been in a territory, the more likely it was to attempt to defend that area.

However, the duration of residency had no effect on the time of the first overtly aggressive behaviour by either fish relative to the time at which the intruder entered the resident's side of the tank (Spearman rank correlation: $r_s=0.23$, $N= 41$, $P=0.14$), where overt aggression is taken to be a behaviour that scores 2 or more points (charge or nip). When the data were split into those trials when the first aggressive attack (charge or nip) was made by the resident and those when the intruder made the first move, analysis revealed that the duration of residency had no effect on when the resident made the first aggressive move (Spearman rank correlation: $r_s=-0.14$, $N= 20$, $P=0.55$). However, intruders tended to take longer to make the first aggressive move as the duration of residency increased (Spearman rank correlation: $r_s=0.81$, $N= 7$, $P=0.03$). Although the resident was significantly more likely than the intruder to make the first overtly aggressive behaviour (residents being first in 74.1 % of the 27 trials where overt aggression occurred, Chi-square = 6.26, $df=1$, $P<0.05$), the duration of residency had no effect on the probability that the resident fish would initiate the first aggressive behaviour (logistic regression: Model Chi-Square = 3.33, $df=1$, $P=0.07$: Figure 3).

During six of the trials, neither of the fish exhibited any aggression, and in one trial both fish obtained the same aggression score and so the outcome was unclear. All seven of these trials were excluded from the following statistical analyses. The mean difference in points between the winner and loser in the remaining trials was 66.27 (\pm 15.52 SE, N=34), indicating that in most cases there was a clear outcome, with the winner engaging in many more displays and/or attacks than the loser. I examined which factors contributed most to the outcome of these territorial contests by means of a multiple stepwise logistic regression. The difference in relative length, weight and SMR of the fish in each pair, and the duration of residency, were used as independent factors, while the dependent variable was the probability of the resident winning the territorial contest. Neither relative size (weight or length) or metabolic rate had any effect on the outcome of contests, but there was a significant effect of residency: the longer the duration of residency, the more likely it was that the resident would win the contest (logistic regression: Model Chi-Square = 4.46, df=1, P<0.05; Table 1, Figure 4).

The likelihood that the resident would win a contest with an intruder was therefore significantly influenced by the duration of prior residency. Residents were no more likely to win contest than intruders when they had no prior residence (i.e. duration of prior residence=0 days) (Chi-Square = 0.67, df=1, P=0.41). After 1 day's prior residence there was a trend for residents to win contests (Chi-Square = 3.2, df=1, P=0.07), which was significant after 2 days (Chi-Square = 12.8, df=1, P<0.001). In contests where the resident had a prior residency of 3 days there was still a trend for residents to win (Chi-Square = 3.2, df=1, P=0.07).

Table 1.

Results of multiple stepwise logistic regression showing the effect of relative size (weight and length), metabolic rate and duration of residency on the probability that the resident fish will win. Based on an analysis of 33 contests between a resident and an intruding salmon fry.

Variable	df	P	R
Duration of residency	1	<0.05	0.23
Relative length	1	0.12	0.01
Relative weight	1	0.19	0
Relative SMR	1	0.81	0

Figure 1.

Double-logarithmic relationship between oxygen consumption (ml/h) and fish bodyweight (grams), used in the determination of relative Standard Metabolic Rate (defined as the residual from this regression line).

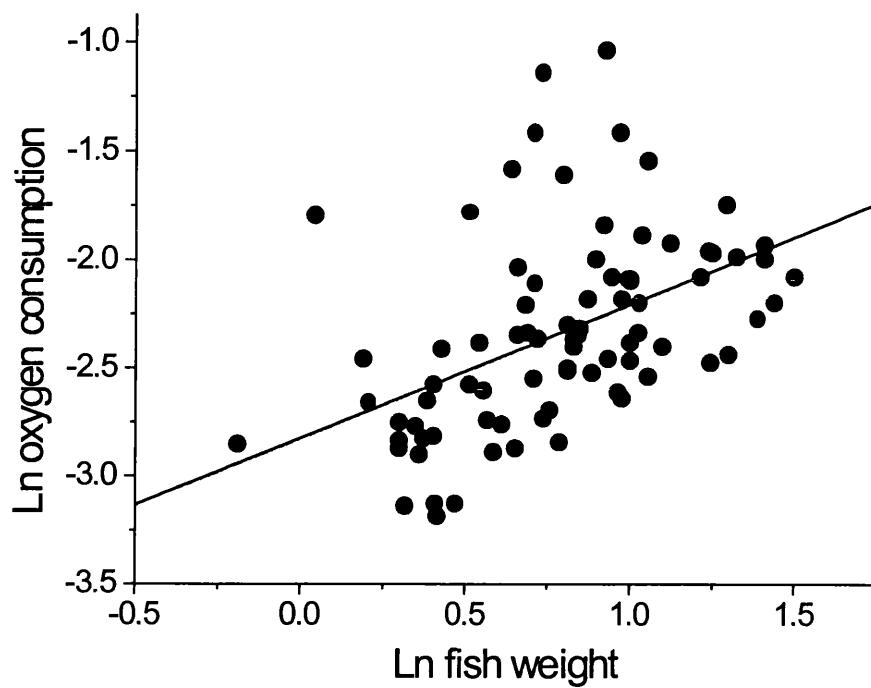


Figure 2.

Relationship between the duration of prior residency and the likelihood of the resident engaging in an aggressive interaction with (i.e. scoring points against) an intruder. Each point on the graph represents either 10 or 11 independent resident fish. Equation of the logistic regression line is given by: Probability of resident winning = $a/(a+1)$, where $a = e^{(1.0294x - 0.2839)}$ ($N = 41$ resident-intruder pairs; see text for statistical analysis).

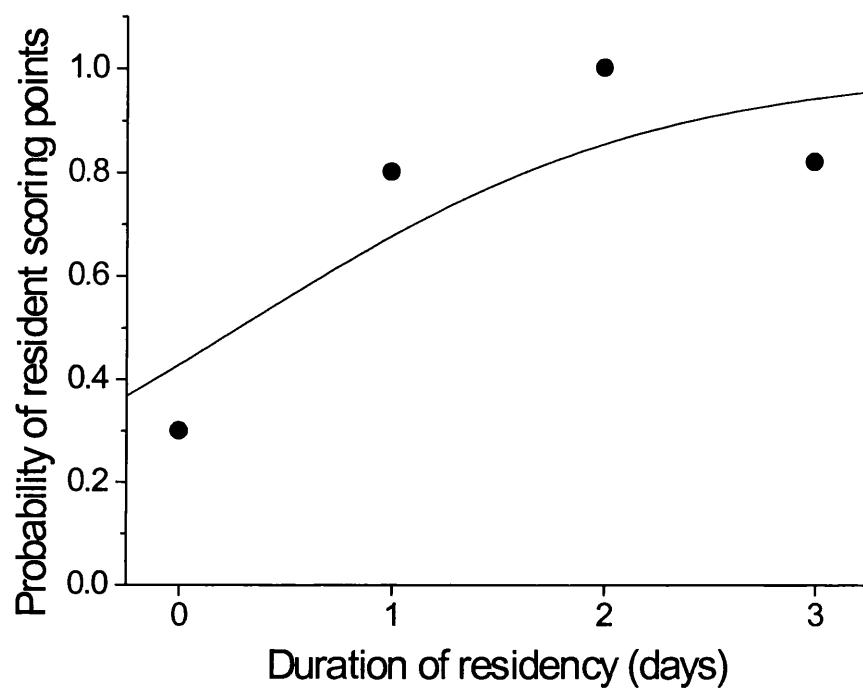


Figure 3.

The relative frequency with which resident (black) and intruding fish (hatched) made the first aggressive move, in relation to the period of time that the resident had been present on the territory. Note that in some trials, especially when the period of prior residence was minimal, neither fish initiated any aggressive interactions.

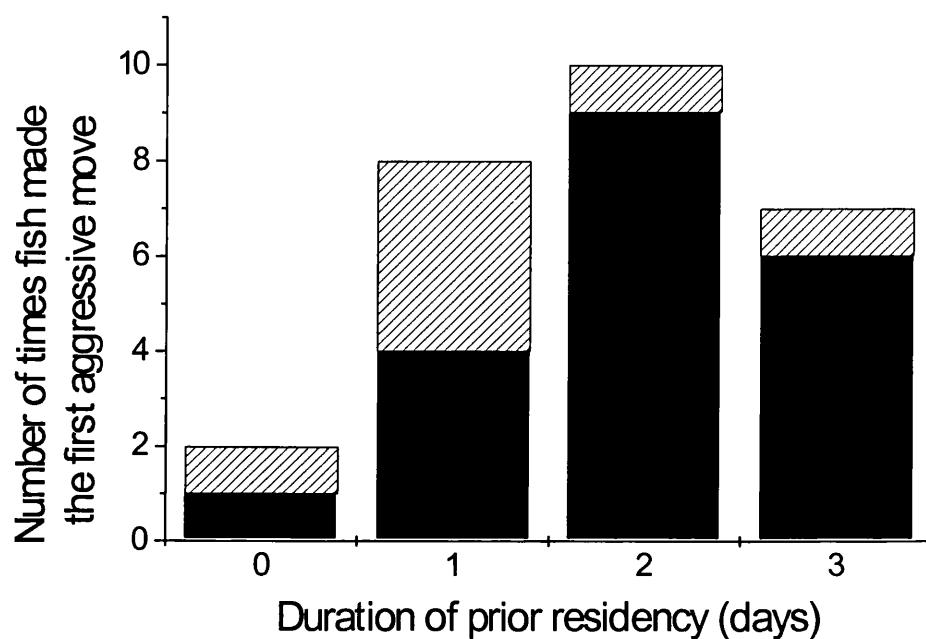
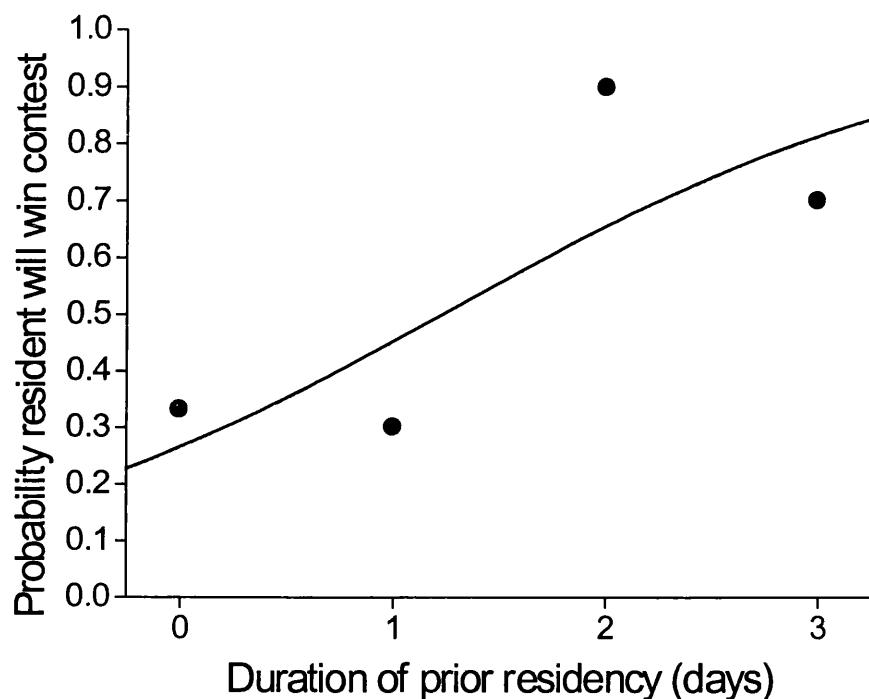


Figure 4.

Relationship between the duration of prior residency and the likelihood of the resident fish winning the contest with the intruder. The datum point for day 0 represents 3 resident-intruder contests and the data points for days 1, 2 and 3 represents 10 separate such contests. Equation of the logistic regression line is given by: Probability of resident winning = $a/(a+1)$, where $a = e^{(0.8276x-1.0158)}$ (see text for statistical analysis).



Discussion

The first aim of this experiment was to test how strong the prior residence effect is in comparison with other asymmetries. The results of the experiment clearly show that the duration of prior residence by a territory owner is a stronger determinant of the outcome of territorial interactions between juvenile salmon than asymmetries in the weight, length or metabolic rate of the contestants. This is in agreement with a previous study, which found that when a prior residence advantage exists, relative size has no effect on the outcome of contests between Atlantic salmon when opponents are of similar size (Cutts *et al.*, 1999a).

However, Cutts *et al.* (1999a) found that a size difference greater than 12% was sufficient to offset the advantage mediated by prior residence. Similarly, Johnsson *et al.* (1999) found that residents won 85% of contests between dyads of wild brown trout, but a 30% size advantage offset this advantage. Although I attempted to size-match pairs of fish as far as was possible, there was still considerable variation, with a relative weight difference of up to 215.49% and maximum length difference of 46.92%. Despite these large disparities, the relative size of the combatants had no effect on the outcome of the contests. This supports the theory that size is a consequence of dominance and not a cause (Huntingford *et al.*, 1990) and suggests that the correlation between dominance status and size reported in older salmonids (Wankowski & Thorpe, 1979; Abbott *et al.*, 1985) might be due to the influence of status rather than size *per se* (Metcalfe *et al.*, 1989). Likewise, analysis revealed that rSMR also had no effect on the outcome of fights regardless of duration of residency. Cutts *et al.* (1999a) and Metcalfe *et al.* (1995) both reported that, in the absence of prior residence asymmetries, rSMR would predict the outcome of fights in juvenile Atlantic salmon. Thus if the strength of the prior residence advantage is related to the duration of residency I would have expected a relationship to exist between rSMR and duration of residency such that the longer a resident is alone the less influence rSMR has on the outcome of fights. However, the results suggest that rSMR is unimportant in determining the outcome of contests regardless of the resident's duration of residency, although it should be noted that there were only 3 contests when the resident had been resident for 0 days and points were scored by either fish and so the power of this result is very low.

These results are likely to be relevant to natural conditions, since a strong effect of prior residence on dominance was also found in two recent trials in an artificial stream, where experimentally induced differences in time of arrival in a habitat were found to have a clear effect on a fish's ability to secure a territory (Huntingford & Leaniz, 1997; Cutts *et al.*, 1999b).

The second aim of this experiment was to test whether the prior residence advantage was due to a Payoff Asymmetry. Since territory ownership was not associated with fighting ability (as I allocated territories randomly), the Resource-holding Potential

hypothesis cannot be used to explain the outcome of these contests. The longer a fish spent in its territory the more likely it was to be dominant over an intruder, hence I cannot exclusively accept the hypothesis that the 'owner always wins', as this does not predict an increase in fighting success with duration of residency. Instead my results fit the Payoff Asymmetry model, where the value of the territory to the resident increases with time. Thus as the duration of residency increased, not only did the probability of the resident defending the area increase, but there was an increased likelihood that it would win any contests with an intruder. It has been suggested that individuals introduced into a novel situation may lack the ability to cope simultaneously with aggressive conspecifics and assessing the potential values and risks associated with the area (Johnsson *et al.*, 1999), however, this explanation does not account for the increased probability of resident success with increased duration of residency.

The duration of residency had no effect on when the resident made the first overtly aggressive move towards the intruding fish. However, as the resident's duration of residency increased, the intruder tended to take longer to initiate a contest. One explanation for this result might be that during the period immediately following invasion there may be visual assessment by the resident, which takes a set period of time and the resident does not initiate an attack before this behaviour is completed. However, something in its behaviour or appearance may signal its period of residency or willingness to defend the site to the intruding fish, which would therefore become less willing to initiate an attack against a resident as the period of residency increases.

The final aim of this experiment was to ascertain how long a resident would need to be resident in order to gain the prior residence advantage. The results indicate that after 1 day alone in a territory there was a trend for residents to win contests with an intruder, which was highly significant after 2 days. Thus 1 or 2 days are needed to gain the prior residence advantage.

Fish with a relatively high standard metabolic rate will tend to emerge earlier from the redd (Metcalfe *et al.*, 1995; Cutts *et al.*, 1999a). They will then establish feeding stations, and the advantages associated with a high rSMR (Metcalfe *et al.* 1995) and prior residence means that these fish will tend to become dominant (Cutts *et al.*, 1999a) and quickly establish a size advantage. As their size increases these fish will have to move away from the natal site (since habitat requirements of young salmonids change with body size (Heggenes *et al.*, 1999)), and hence they may be among the first fish to disperse downstream. In doing so they again receive the prior residence advantage. In this way the advantages of a high rSMR may be coupled with those of prior residence so that fish with high rSMR will gain and secure the most profitable territories. Brännäs (1995) showed that in stream channels early emerging fry have a better chance of establishing a feeding territory than their late arriving siblings, and the results of my experiment suggest that selection should favour early dispersing fish that can maximise the amount of time spent on a territory before later migrants arrive. However there are selection pressures working

against the evolution of increasingly early dispersing fish. For example, Brännäs (1995) highlighted that early emergence is not without its costs, as the first fry to emerge from a redd potentially experience a greater predation from predators such as trout (*Salmo trutta*) than do later arrivals, which benefit from the reduced individual risk of predation afforded by predator satiation (Begon & Mortimer, 1986). The size advantage resulting from dominance mediated by high rSMR and prior residence will lead to an increased probability of the salmon smolting at one year, hence the factors which affect dominance may ultimately determine the life history strategy a fish will adopt (Metcalfe & Thorpe, 1992b).

Finally, an interesting application of this study is the movement of fish between stock tanks in aquaculture. To minimise the competitive asymmetries that may result from this process, this study suggests that fish should be introduced as synchronously as possible to new habitats. A time interval of as little as 24 hours may be sufficient to seriously disadvantage the second batch of fish to arrive and lead to escalated fighting.

Chapter 7

**The stability of Standard Metabolic Rate
during a period of food deprivation in
juvenile Atlantic salmon**

Abstract

Previous work has shown that individual variation in Standard Metabolic Rate (SMR) may be related to variation in social behaviour and performance. In salmonid fish, individuals with a relatively high SMR have been found to be more aggressive and so dominant. However, such studies have not considered the influence of the relative stability of SMR during a period of low food abundance. As juvenile salmonids will tend to live in an heterogeneous environment where food availability is unpredictable and fluctuates widely, the stability of SMR and hence the physiological constraints it implies, will be instrumental in determining individual fitness. This experiment had two aims: firstly to examine the stability of SMR in juvenile Atlantic salmon (*Salmo salar*) in times of food deprivation, and secondly to test whether the relative ranking of SMR within a group of fish remains stable over time despite variation in food abundance.

Repeated measurements of SMR were made at monthly intervals on the same fish, which had either been fed *ad libitum* throughout the three-month experiment or had been subjected to a one month period of food deprivation in the middle month. Food deprivation led to a decrease in SMR, which increased again once food was again supplied *ad libitum*. However, while the rank order of SMR among fish fed throughout remained relatively stable, that within the group subjected to the varying food availability was inconsistent, suggesting that individual fish vary in their ability to reduce metabolic costs when food availability is low.

Introduction

During the course of an animal's life its metabolic rate will tend to fluctuate between two extremes. The upper limit of maximum aerobic metabolic rate is termed the Active Metabolic Rate (AMR) (Priede, 1985; Jobling, 1994). The lower limit is the animal's minimum maintenance metabolic rate, typically referred to as its Standard Metabolic Rate (SMR). SMR is defined as the metabolic rate of a completely quiescent animal, in a post-absorptive nutritional state (Beck & Groppe, 1995). A high SMR has been associated with a high level of aerobic capacity (Lewin, 1982), since it may be coupled with a disproportionately large AMR; this produces a large Metabolic Scope (AMR – SMR) leading to a greater potential for growth (Priede, 1985). The growth benefits associated with a high SMR have been suggested as reasons for the evolution of animals with increasingly high SMRs (McNab, 1980).

In salmonids a high SMR has also been linked to high aggression levels and hence dominance (Metcalfe *et al.*, 1992, 1995; Cutts *et al.*; 1998; Yamamoto *et al.*, 1998). If metabolic scope is positively correlated with SMR, then fish with a high SMR have a greater capacity for energetically costly activities such as aggression. The dominant status achieved by high SMR fish may confer indirect as well as direct benefits, since high SMR individuals may gain the best territories and preferential access to resources such as food (Huntingford & Turner, 1987). In species with a plastic life history, such as Atlantic salmon (*Salmo salar*), the life history strategy that an individual adopts is influenced by its relative dominance status (Metcalfe, 1989, 1991, 1998; Metcalfe *et al.*, 1989, 1990, 1992, 1995) and, since a direct link has been established in Atlantic salmon between metabolism and dominance, the exact value of an individuals' SMR may be pivotal in determining its life history (Metcalfe *et al.*, 1995; see also Forseth *et al.*, 1999).

However, a high SMR is not without its costs. Fish with a high SMR will have a high "cost of living" (Metcalfe, 1998), which may mean that in times of low food abundance they will utilise reserves faster than a low SMR fish and consequently suffer a greater risk of food deprivation. In addition, the greater aggression of high SMR fish will mean a high metabolic expenditure (Li & Brocksen, 1977) which may put further strain on a fish already struggling to meet its energetic requirements. Consequently, if SMR was inflexible, the advantages of a high SMR would diminish under conditions of food shortage when fish with low SMRs would be favoured since their cost of existence would be less (Metcalfe, 1986). High metabolic costs may also force fish to migrate sooner to more productive environments (Forseth *et al.*, 1999).

Studies of the effects of food deprivation on fish metabolism have largely focused on the reduced metabolism as a result of decreased activity or Specific Dynamic Action (SDA), and not the effect on SMR (Beamish, 1964; Glass, 1968; Jobling, 1980; Boggs & Kitchell, 1991; Lucas & Priede, 1992; Weiser *et al.*, 1992). The aims of this experiment were therefore twofold: firstly to investigate the effect of food deprivation on SMR and

hence its relative stability within an individual; and secondly to examine the stability of an individual's SMR in relation to conspecifics, to see whether food availability altered the rank ordering of SMR values within a social group of fish.

Materials and Methods

A batch of full-sibling eggs from sea run Atlantic salmon caught by the Loch Lomond Angling Improvement Association were incubated at the University Field Station at Rowardennan, Loch Lomond. Upon hatching the fish were transferred to 1m diameter tanks where they were kept under ambient photoperiod and temperature conditions. The tanks received a continual turnover of water from Loch Lomond, which supplied the fish with a rich source of zooplankton. Once the young fish had completely absorbed their yolk sacs their diet was supplemented with commercial salmon food (Fulmar feeds, BOCM Pauls Ltd.), which they received *ad libitum* at a trickle rate from automatic feeders operating 24h per day.

On December 2nd 1996, when the fish were approximately 7 months old, the experimental subjects were randomly selected from the lower modal group of the bimodal size distribution of the population. These lower modal group fish would delay seaward migration for at least a further 18 months (Thorpe, 1977). To allow individual identification each experimental fish was given a unique combination of marks with alcian blue dye on its pectoral, pelvic, dorsal, anal and/or caudal fins. This marking technique has no effect on the behaviour or growth of young salmon (Metcalfe *et al.*, 1992). The fish were then placed in a 1m diameter stock tank in the experimental laboratory and maintained at a constant temperature of 10°C, a photoperiod of 15.8D:8.2L and supplied with food *ad libitum*.

Measurement of oxygen consumption

On 12th December the first 19 of the marked fish were randomly selected from the stock tank. Their fork lengths and weights were measured (to the nearest mm and 0.01g, respectively) and the fish were placed into individual Perspex chambers (100mm length, 20mm diameter) of a flow-through respirometer in the experimental laboratory. The fish were then left un-fed in the chambers for 16-24 hours prior to measurement of oxygen consumption. This period allowed full gut evacuation to occur and hence avoided incorporating the influence of SDA into the measurements. Using identical protocols and equipment Cutts (1997) has shown that oxygen consumption is stable after this period of acclimatisation.

Each chamber containing a single fish was supplied in parallel with water from a fully aerated header tank. The water contained in this tank was circulated through an UV steriliser which reduced bacterial growth to a minimum, and hence ensured that the measured rates of oxygen consumption were unaffected by microbial respiration. As an extra precaution to ensure that microbial respiration was reduced to a minimum, an empty chamber was used as a blank in each trial, but the reduction in oxygen saturation of the water passing through this chamber was found to be negligible.

A small tap fitted to each chamber inflow tube facilitated flow rate adjustment throughout the experiment. The water flow rate was calculated by collecting and weighing (to 0.01g) the water leaving each chamber over a period of three minutes. 1 ml samples of the inflow (taken from the header tank) and outflow (taken from the tube leaving the chamber) water were collected using a hypodermic needle and syringe, and injected into a thermostatted cell (MC 100 Strathkelvin Instruments, Glasgow) containing a microcathode oxygen electrode connected to an oxygen meter. Prior to any measurements being carried out, the electrode was calibrated using water saturated with air from the header tank (100% oxygen saturated) and a solution having an oxygen saturation level of zero (sodium sulphite in 0.01M sodium tetraborate).

Rates of oxygen depletion were calculated as the difference in percentage oxygen saturation of the water flowing into the respirometer and that collected from the outflow tubes. The absolute amount of oxygen consumed was then calculated using values for the oxygen capacitance of water at specific water temperatures (Mackereth *et al.*, 1978). The mean water temperature during the experiment was 9.48 ± 0.07 °C.

Rates of oxygen consumption (VO_2 , mlO₂.h⁻¹) were calculated using the formula:

$$VO_2(\text{ml/h}) = V_w \cdot \Delta C_w O_2$$

where V_w is the flow rate (l/h) of water through the respirometer and $\Delta C_w O_2$ is the difference in the oxygen concentration between the inflow and out flow water (ml/l) (Metcalfe *et al.*, 1995).

A black sheet was placed over the respirometry chambers to ensure that the fish were kept in semi-darkness. By periodically lifting the corner of the black sheeting to observe the fish, it was ascertained that the fish remained predominately quiescent. Thus the oxygen consumption measured under these conditions approximates to the Standard Metabolic Rate (SMR; Brett & Groves, 1979).

Three measurements were made of the oxygen consumption of each fish, 1-2 hours apart, between 1000 and 1400 h. This was a sufficient time interval to ensure that measurements were independent (since flushing times were less than 1h) and that conditions within the respirometer had again reached a steady state (Steffenson, 1989).

Once three measurements had been made on each fish they were removed and placed in a new holding tank. A fresh group of 19 fish were placed into the flow-through respirometer chambers, and the procedure was repeated. In total 47 fish were tested for SMR.

Food deprivation

Once initial measurements of SMR had been completed on all fish, the stock tank was split into 2 equal sized areas (each 0.5 x 1 m) using an opaque Perspex sheet. The

sheet had two fine (0.25mm width) meshed sections, 10cm in diameter, which allowed the circulation of water through it without letting fish or food particles move between the two sides of the tank.

On December 16th, after the SMR measurements were completed, the experimental fish were randomly split into 2 groups, one of 23 and one of 24. These two groups were then placed on either side of the tank. An automatic feeder was placed above one half of the tank and fish in that side of the tank received food *ad libitum* dispensed at a trickle rate 24h per day, whereas fish in the other half of the tank were deprived of food. The fish were then left for 22 days during which time the temperature and photoperiod were identical to the conditions under which they had been kept whilst in the stock tank.

Between the 7th-10th January 1997 the fish were removed from the tank and identified from their fin marks. The fish were then placed into the flow-through respirometer and their rates of oxygen consumption measured for a second time, to test whether food deprivation caused any change in either absolute levels of SMR or the relative ranking of SMR among fish. The fishes' weight and fork length were then recorded and they were re-marked as the alcian blue dye-spots had faded appreciably. The Perspex divider was removed from the tank and the amount of food delivered by the automatic feeder increased so that excess food was delivered for all the fish in the tank. The fish were replaced in the tank and left for a further 24 days. During this second experimental period all the fish therefore received food *ad libitum*.

Between February 4th-7th the fish were again removed from the tank, their rates of oxygen consumption measured for a third time using the flow-through respirometer, and their fork length and weights recorded. This third measurement allowed me to check whether any changes in metabolic rate seen in food-deprived fish were reversible once food was again available. The experiment was then terminated and the fish were returned to the original tank population.

Ethical note: Prolonged spells of food deprivation are not unusual for Atlantic salmon, who naturally undergo periods of anorexia in the wild (Metcalfe & Thorpe, 1992a). None of the fish involved in the experiment suffered undue loss of condition and there were no deaths due to starvation.

Results

A standard relationship between oxygen consumption and body size was calculated by regressing the natural log of the initial oxygen consumption of the fish, measured in December, against the natural log of their body weight at the time (Linear regression: $r^2 = 0.19$ N=57 P<0.001, Figure 1). This equation was then used to calculate the expected oxygen consumption levels for a fish of a given weight. By then subtracting the expected oxygen consumption values from the observed values, the residual or relative SMR (rSMR) of each fish was calculated (Metcalfe *et al.*, 1995). Fish with oxygen consumption rates greater than would be expected for a fish of that size had positive values of rSMR and were said to have high rSMR's, and those with negative rSMR values had low rSMR's. All subsequent analyses of metabolic rates are based on these rSMR values.

I analysed the effect of both time and treatment on rSMR using repeated measures ANOVA, with time (December, January and February measurements) as the within-subject effect and treatment (controls = fed *ad libitum* throughout, deprived = deprived of food prior to January measurement) as the between-subject effect. Combining both treatments, there was no overall change in rSMR over the three months ($F_{2, 90} = 1.11$, P=0.33). However, there was a significant interaction between treatment and time ($F_{2, 90} = 3.93$, P<0.05). This effect arose because the relative standard metabolic rates of fish in the two treatment groups, while similar at the beginning and end of the experiment, were different at the time of the middle measurement (Figure 2). Thus fish that had been deprived of food for the preceding 23 days had lower rSMR values than those that had been receiving food *ad libitum* (t test: $t_{45} = 2.89$, P<0.01, Figure 2). Furthermore, if only the deprived group are considered, there was a significant difference in rSMR values over the three month experimental period (Repeated Measures ANOVA: $F_{2, 46} = 3.73$, P<0.05), due to the fish reducing their metabolic rates after a period of food deprivation (repeated measures ANOVA comparing measurements on the same fish in December and January: $F_{1, 23} = 6.41$, P<0.05). However, this effect was reversible, since the final measurements of oxygen consumption, taken after the fish had again been given an *ad libitum* food supply, were not significantly different to the initial values (Repeated Measures ANOVA comparing December and January: $F_{1, 23} = 0.52$, P=0.48). In contrast, the rSMR values of the control fish, fed continuously during the study, did not vary over the three month period (Repeated Measures ANOVA: $F_{2, 44} = 1.34$, P=0.27).

In order to test whether fish with relatively high standard metabolic rates showed a greater metabolic response to food shortage, I examined the extent of the change in rSMR during the period of food deprivation (i.e. January rSMR – December rSMR). There was a negative relationship between initial (December) rSMR and subsequent change in rSMR in the deprived group (Figure 3), which superficially suggest that fish with initially

high metabolic rates showed a greater response to deprivation. However, this relationship was of similar gradient in both treatment groups (ANCOVA: $F_{1, 44}=0.91$, $P=0.34$). Since there was no overall change in rSMR in the control group, this suggests that the negative slope was simply a statistical artefact, being a consequence of extreme initial measurements having a greater likelihood of being less extreme when measured on subsequent occasions. However, the treatment group to which the fish belonged had a significant effect on the elevation of the regression line ($F_{1, 44}=8.11$, $P<0.01$). This result further indicates that food deprivation causes a reduction in standard metabolic rate.

When the fish in the deprived treatment group were ranked according to the magnitude of their rSMR, the order of the fish varied significantly between the three months (Kendal's coefficient of concordance: $W=0.10$, $df=2$, $P=0.09$). In order to identify the influence of each of the three months on this significant result, Spearman's Rank correlations were calculated analysing the months in pairs. The rank ordering of the fish was similar in December and February ($r_s=0.40$, $N=24$), but changed during the period of food deprivation, as indicated by weak correlations between rSMR values in January and those in either December or February ($r_s=-0.11$, $N=24$ and $r_s= -0.29$, $N=24$, respectively). In contrast, the rank order of Standard Metabolic Rates remained relatively constant in the group of fish fed throughout the study (Kendal's coefficient of concordance: $W=0.16$, $df=2$, $P<0.05$). Therefore differences in rSMR among fish were relatively stable in conditions of high food availability, but became unpredictable when food was unavailable.

Figure 1

Double-logarithmic plot of oxygen consumption against fish weight for juvenile Atlantic salmon, based on initial measurements of 47 underyearling fish in December. The regression equation ($\ln(\text{oxygen consumption, ml/h}) = 0.53\ln(\text{fish weight, g}) - 2.14$) was used to calculate expected standard metabolic rates for fish of a given weight, and hence relative SMR (see text).

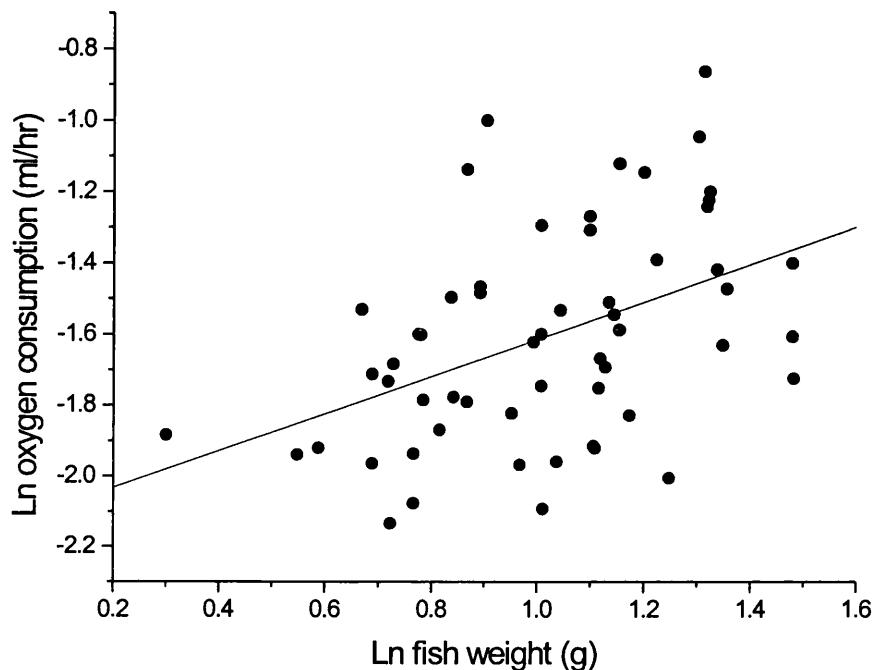


Figure 2

Change in rSMR values of the two treatment groups over the three month study period. The deprived group, represented by filled circles, were deprived of food in the period leading up to the January measurement. The control group, represented by open circles, were fed *ad libitum* throughout the study. Data presented as means \pm S.E.; see text for statistical analysis.

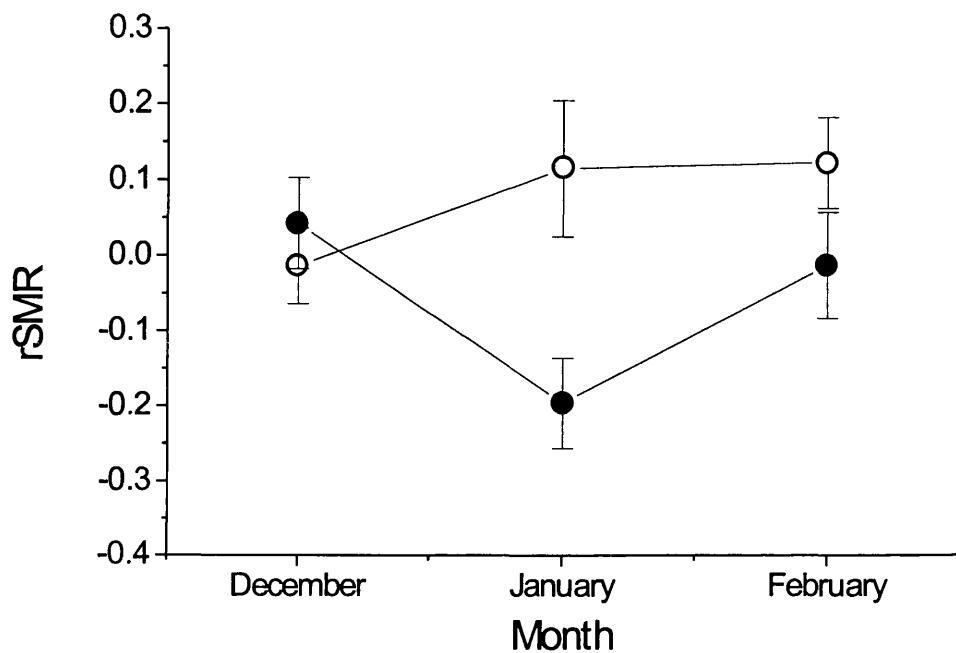
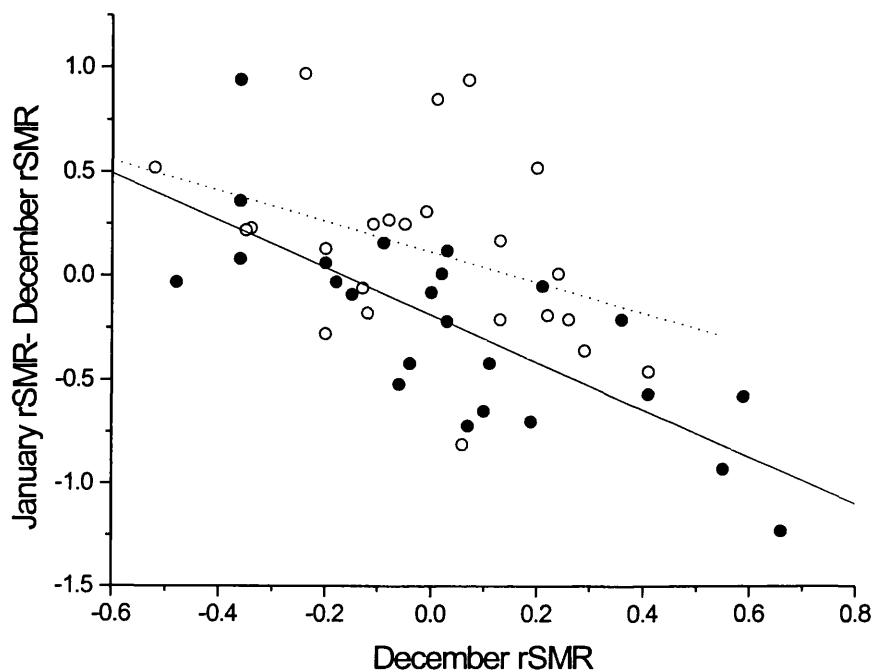


Figure 3

Change in rSMR values of juvenile salmon between the December and January measurements relative to the initial (December) rSMR values. The filled circles and solid line represent fish deprived of food between the December and January measurement, while the open circles and dotted line represent fish fed *ad libitum* throughout the study. See text for statistical analysis.



Discussion

The most striking result to emerge from this experiment is the decrease in the Standard Metabolic Rate (SMR) of juvenile Atlantic salmon when the fish were starved, and the increase once they were re-fed. A decrease in metabolic rate during a period of food restriction has been observed in several fish species (Hickman, 1959; Beamish, 1964; Love, 1970; Du Preez, 1987; Weiser *et al.*, 1992). There is considerable evidence that fish 'down-regulate' their metabolic rates during a period of food deprivation and this may act as an adaptation to the lower food levels, so that weight loss is minimised (Hickman, 1959; Brett, 1965; Muir *et al.*, 1965; Hepher *et al.*, 1983). Jobling (1994) suggested that differences in fasting metabolic rate (the definition of which is synonymous with SMR) resulting from food deprivation may be due to the effects of food deprivation on the biochemical composition of the body tissues, changes in the relative sizes of different organ systems and influences on the rate of synthesis and turnover of various tissue components. The energy expended as SMR meets two basic requirements; those of service functions (such as expenditures of the respiratory and circulatory systems in meeting the costs associated with supplying body tissues with nutrients) and those of cellular maintenance functions (which includes the cost of ion transport and synthesis and turnover of biochemical cellular constituents). It has been suggested that of these functions a substantial portion of SMR is related to the costs of protein synthesis and turnover (Houlihan *et al.*, 1988). Food deprivation has been linked to a reduction in protein synthesis in several fish species (for example; cod *Gadus morhua* Lied *et al.*, 1982; rainbow trout *Oncorhynchus mykiss* Beck & Groppe, 1995; Lauff & Wood, 1996; Payan *et al.*, 1998; golden perch *Macquaria ambigua* Collins & Anderson, 1995; short spine thornyhead *Sebastolobus alascanus* and spotted scorpion fish *Scorpaena guttata* Yang & Somero, 1993). This proven link between protein synthesis and nutritional state suggest that the fall in SMR observed in this experiment when the fish are starved could be partly due to a decrease in protein synthesis.

As in previous studies of fish (Weiser *et al.*, 1992), re-feeding resulted in an increase in SMR values. Studies of the effect of re-feeding in previously starved fish have shown that resumption of feeding is linked to an increase in ribosomal numbers and capacity for protein synthesis (Lied *et al.*, 1983). This suggests that the increase in SMR observed in this experiment could be due partly to an increase in tissue RNA concentration, restoration of protein synthetic capacity and thus rate of protein turnover. In order to confirm this, further experiments examining the exact composition of the tissues of starved and re-fed fish would be necessary.

The implications of reductions in SMR during a period of food deprivation are considerable. If fish lower their SMR they are in fact lowering their "living costs" (Metcalfe 1998). This means that they can survive periods of food deprivation and not suffer the costs associated with a high SMR (Metcalfe *et al.*, 1995). In food rich environments a high

SMR appears to be advantageous in salmonids, since this not only enables efficient use of the available resources (Priede, 1985), but also allows the fish to gain access to the food through its effect on dominance status. However, if SMR's were inflexible a high SMR may be selected against in a heterogeneous environment where food was not always available and thus high SMR fish would struggle to reach their metabolic requirements (Metcalfe *et al.*, 1995). However, if high SMR individuals are able to lower their SMR during times of food deprivation then they avoid the costs while taking advantage of the resources available when food is in rich supply.

It would be interesting to examine the effect of food deprivation on metabolic scope (maximum metabolic rate - SMR). If a fish reduces its SMR, does metabolic scope decrease correspondingly, or does the maximum metabolic rate remain constant, in which case a decrease in SMR would mean an increase in metabolic scope? A change in metabolic scope would have serious implications on the behaviour of the fish in terms of affordable aggressive behaviours i.e. whether a fish is energetically capable of prolonged aggression due to a reduced maximum metabolic rate and hence metabolic scope.

Another interesting result to emerge from this experiment is the change in order of rSMR within each group over time. Since rSMR is correlated with aggression (Cutts *et al.*, 1998) and dominance (Metcalfe *et al.*, 1995), a change in the order of rSMR may reflect a change in the dominance hierarchy within a group. As the rank order of rSMR within the control group remained relatively consistent throughout the study I can hypothesise that the dominance hierarchy within this group was relatively stable. This is in agreement with previous studies, which have highlighted the stability of dominance hierarchies over time (Abbott *et al.*, 1985). Although high rSMR fish within this group may have been dominant and thus suppressed the feeding behaviour of subordinate low rSMR fish (Metcalfe, 1989), food was supplied to excess so none of the fish should have been under nutritional stress.

The rank order of rSMR within the deprived fish was less stable. In times of food abundance fish had similar rankings of rSMR; however when deprived of food the order broke down. This would seem to suggest a disparity among the fish in the amount that rSMR was reduced. This is particularly interesting as SMR down-regulation (Hickman, 1959; Brett, 1965; Muir *et al.*, 1965; Hepher *et al.*, 1983) is critical in determining weight loss during starvation (Broekhuizen *et al.*, 1994) and hence any differences in the ability to alter SMR will have direct repercussions on a fish's fitness. Only fish that can lower their living costs (Metcalfe, 1998) sufficiently will survive prolonged periods of food deprivation. Hence differential lowering of rSMR between fish may mean that some fish are better able to cope with food deprivation than others. In a heterogeneous environment selection will thus favour the fish with flexible SMRs.

Wild populations of young parr may be geographically isolated and hence experience different food availabilities. If these populations then merge (for example where stream tributaries join) selection may be such that the low rSMR fish will be

favoured within the population coming from the food poor location because of their non-confrontational feeding style. In contrast, the high rSMR fish in poor condition, who tend to be aggressive in order to secure food, will suffer as they cannot compete with high rSMR fish in good condition. Groups of high rSMR salmon therefore tend to show more variation in growth than groups of low rSMR fish (Cutts *et al.*, 1998). In addition there may be differences in the feeding strategies of the two populations of fish. Work on the behaviour of coho salmon has shown that they take greater risks in order to secure food in a period following starvation (Damsgård & Dill, 1998), although risk taking is moderated by size and life history stage (Reinhardt & Healey, 1999). Although studies have shown that there is less variation in growth rate within a group when the ration level is high (juvenile chum salmon, *Oncorhynchus keta*: Davis & Olla, 1987), this does not allow for varying nutritional histories which may have direct bearing on the capability of an individual to secure food. When fish have been in a low food environment and arrive in a high food situation, where they encounter other fish which have not suffered similar food shortage, the most energetically profitable strategy (Fausch, 1984) may be to adopt a subordinate position and not to attempt to secure a territory or defend a food supply. This is the strategy typically adopted by low rSMR fish. These results reinforce the view that energetic efficiency alone does not determine Darwinian fitness (Priede, 1985). Instead it must be viewed in terms of a holistic approach incorporating animal behaviour (in this case feeding strategy), physiology, ecology and environment. In addition environmental conditions may not always be stable and recent studies have highlighted the need to account for these perturbations when considering dominance hierarchies (K. Sloman pers. comm.).

Chapter 8

The effect of social and physiological asymmetries on growth of juvenile Atlantic salmon

Abstract

The asymmetries that cause one fish to be dominant over another have been well studied in Atlantic salmon. These studies have provided ample evidence for the existence of a "Prior Residence" effect among competing juvenile salmon, whereby the resident will tend to win an encounter with an intruder entering its territory. Another well-studied determinant of the outcome of contests is an asymmetry in Standard Metabolic Rate (SMR); in the absence of a residency asymmetry, fish with high SMRs will tend to win contests with low SMR fish. Although the interaction between these variables has been examined, all experiments to date have been carried out in a stable, relatively high food abundance situation.

The aim of this experiment was to examine the role of SMR and Prior Residence in determining the growth rate of fish under conditions of both high and low food availability. As the stream environment is extremely heterogeneous and food supply unpredictable, it was hoped that by varying the food ration received by groups of fish introduced at different times into a tank, an insight would be gained into the importance of asymmetries in residence and SMR. In addition, to assess the influence of SMR on the growth of fish not experiencing the social pressures associated with group living, fish of known SMR were kept in individual tanks and given either a high or low food ration.

Neither SMR or Prior Residence had any effect on the growth rates of fish kept in groups. Similarly, SMR had no effect on growth rates of fish kept individually. However, ration size directly influences growth rate such that fish which were fed more grew more.

As the results of this experiment directly contradict previous work, possible sources of inaccuracy in the experimental design are explored, and modifications of the experimental design are suggested that would lead to a more accurate representation of the natural stream environment.

Introduction

Over the past few years there have been several studies of the influence of physiological and social asymmetries on the outcome of contests between juvenile Atlantic salmon (*Salmo salar*). In concurrence with the large amount of literature on the "Prior Residence" effect (Maynard Smith & Parker, 1976; Leimar & Enquist, 1984; Huntingford & Turner, 1987; Archer, 1988), studies have shown that the first salmon to arrive on a territory will tend to win a contest with an intruder for possession of that area (Brännäs, 1995; Cutts *et al.*, 1999b). These prior resident fish will tend to establish feeding stations and thus have higher growth rates than later arriving conspecifics (Huntingford & De Leaniz, 1997; O'Connor *et al.* 1999b).

Analogous studies of the effect of asymmetries in Standard Metabolic Rate (SMR) have shown that, in the absence of any advantage mediated through prior residence, fish with a high SMR will tend to be dominant over those with lower SMRs, and subsequently grow faster (Metcalfe *et al.*, 1995; Yamamoto *et al.*, 1998). However, when one individual has the advantage of prior residence it will tend to win contests regardless of asymmetries in SMR (Cutts *et al.*, 1999). In addition, experimental work on older salmon suggests that territory ownership *per se* may be more important than differences in Resource Holding Potential (RHP) between fish. Data from a single trial indicated that intrinsically dominant individuals were unable to displace, and consequently grew slower than, subordinates that already held territories (Huntingford & De Leaniz, 1997).

However, all of these experiments have been carried out in situations where food was abundant, and little attention has been paid to the extremely heterogeneous natural stream environment of these young fish in which food availability varies considerably. Juvenile salmon are "sit and wait" predators that have well defined feeding stations from which they intercept food items that travel in the water column (Stradmeyer & Thorpe, 1987). Competition for these feeding stations is fierce (Keenleyside & Yamamoto, 1962), and any asymmetries that exist between individuals may be crucial in deciding dominance.

The aim of this experiment was to examine the relative influence of SMR and prior residence on the growth of juvenile salmon under conditions of both high and low food abundance. In addition, the effects of SMR on growth when fish were kept individually, as opposed to in a group, was also examined. Previous studies have shown that agonistic interactions are energetically costly (Li & Brocksen, 1977; Metcalfe, 1986) and thus fish would be expected to grow better when kept individually than when in social groups. However, while low SMR fish will tend to have a lower "cost of living" (Metcalfe, 1998) than high SMR fish, and hence may grow better on a given amount of food when alone, this advantage may disappear when in a group situation, since high SMR fish tend to be more intrinsically aggressive (Cutts *et al.*, 1999a) and hence are able to obtain more food. By comparing the growth of high and low SMR fish both when in a group and when kept in

isolation, and under conditions of both high and low food availability, it would be possible to test whether the relative benefits of a given SMR varied with the social context.

Methods

A batch of full-sibling eggs from sea run salmon caught in the River Shin, Perthshire were incubated at the Scottish Office Agriculture Environment and Fisheries Department Almondbank salmon rearing unit. On 5th February 1998 the eggs were moved to the University Field Station at Rowardennan, Loch Lomond. Once hatched, the fish were kept under ambient photoperiod and temperature conditions in 1m diameter round tanks. These tanks received a continual turnover of water pumped from Loch Lomond which was rich in zooplankton. Once the fishes' yolk sacs were completely absorbed the fish diet was supplemented with commercial salmon food (Fulmar feeds, BOCM Pauls Ltd.), which they received *ad libitum* from automatic feeders.

On 23rd April 1998, after the onset of exogenous feeding, 300 fish were transferred to Glasgow University where they were kept in 1m wide square tanks. The fish were kept at 14°C under ambient photoperiod and hand fed a mixture of commercial salmon food and bloodworm (chironomid larvae species) *ad libitum*. The experiments were carried out between May 27th and July 18th 1998 (i.e. 1-3 months after first feeding) when the fish had a mean fork length of 35.9mm \pm 0.26 (SE) (N=143) and weighed an average of 0.41g \pm 0.01 (143).

Measurement of Standard Metabolic Rate

Flow-through respirometry was used to calculate the oxygen consumption (and hence metabolic) rate of the fish. The principle of this technique is to calculate the rate of oxygen consumption by a stationary fish using the reduction in oxygen concentration of water flowing past it (Steffenson, 1989). The respirometry measurements commenced on 27th May 1998, when 20 fish were selected randomly from the stock tank and their fork lengths and weights were measured (to the nearest mm and 0.01g, respectively). The fish were transferred to individual Perspex chambers (10mm x 100mm) of a flow-through respirometer. The fish were then left un-fed in the chambers for 16-24 hours prior to measurement of oxygen consumption. This period allowed full gut evacuation to occur and hence avoided any influence of Specific Dynamic Action (SDA) (Priede, 1985) on the rates of oxygen consumption measured. On the following day the respirometer was calibrated and the fishes' oxygen consumption rates measured according to the method outlined by Metcalfe *et al.* (1995) and Cutts *et al.* (1998) (also see Chapter 6).

Three measurements were made of the oxygen consumption of each fish, 1-2 hours apart. This was a sufficient time interval to ensure that conditions within the respirometer had again reached a steady state (Steffenson, 1989). All measurements were carried out between 0900 and 1300 h to avoid any influence of diel changes in their rates of oxygen consumption.

A black sheet was placed over the respirometry chambers to ensure that the fish were kept in semi-darkness and undisturbed by the experimenter. By periodically lifting

the corner of the black sheeting to observe the fish, it was ascertained that the fish remained predominately quiescent. Thus the oxygen consumption measured under these conditions approximates to the Standard Metabolic Rate (SMR; Brett & Groves, 1979).

After the third measurement had been made, the SMR of each fish was calculated (see Metcalfe *et al.* 1995, Cutts *et al.* 1998, Chapter 5). In order to correct SMR for body size, the rate of oxygen consumption (ml/h) was first regressed against the fresh weight of the fish (W, in g) on a double natural logarithmic scale. The relative Standard Metabolic Rate (rSMR, Metcalfe *et al.*, 1995) was then calculated as the residual from this regression; fish with a positive rSMR had higher than expected oxygen consumption rates for their weight, whereas a negative value indicated a lower than expected oxygen consumption rate.

The six fish with the highest and 6 with the lowest rSMR values were used in the experiment, while the other eight intermediate fish were placed into a second stock tank and were not used again. In this way two experimental groups were created: "low SMR" fish, all of which had "low rSMRs" and "high SMR" fish which had high rSMRs.

Once the twenty fish that had been in the respirometer were removed and separated into these three groups (high rSMR, low rSMR and those discarded from the experiment), twenty more fish were randomly selected from the stock tank and placed into the respirometry chambers. The following day the SMR of these fish was measured and the 6 highest and 6 lowest rSMR fish selected as before. The process was repeated until 144 fish had been measured; measurements were completed on 4th July 1998.

Establishing fish groups

From the 12 selected fish (six high and six low rSMR) four were chosen at random with the proviso that two came from the high rSMR category and two from the low SMR. These four fish were then anaesthetised with 5ml/l of a solution of 10g/l benzocaine (ethyl-p-aminobenzoate) in 95% ethanol and given unique combinations of marks with alcian blue dye on their pectoral, pelvic, dorsal, anal and/or caudal fins. This marking technique has no effect on the behaviour or growth of juvenile salmon (Metcalfe *et al.* 1992). Once marked, the four fish were placed into an L shaped experimental stream tank and were referred to as 'Primaries' since they were the first group of fish to arrive in the experimental tank.

Each arm of the stream tank was 1m long and 30cm wide, with a water depth of 15cm. At each end of the tank was a mesh barrier (2mm mesh), through which food could pass but fish could not. The base of the tank was bare grey plastic attached to which were small strips of dark waterproof tape which resembled the colour heterogeneity of a stream and provided a variety of different areas against which the fish could camouflage themselves (Donnelly and Whoriskey, 1993). At the upstream end there was a transparent Perspex tube running from the top of the tank to 1 cm below the surface of the water; this

tube acted as a food chute. Three times a day an ice-cube containing frozen bloodworm was dropped down the chute. The ice-cube floated on the surface of the water and as it melted the bloodworms dropped through the water down the chute. As the bloodworms left the Perspex chute they entered the water stream and travelled diagonally down towards the floor of the tank. It was hoped that this technique of food presentation would closely mimic the natural stream situation where food items are typically carried in the water column. The number of bloodworms in the ice-cube was controlled such that the daily amount of worms was either equal to 5.5% of the total weight of all the fish in the tank (typically about 10 bloodworms), or so that the fish received far more bloodworms than they would eat (typically about 50 bloodworms). The two categories of food availability were referred to as high and low ration. The figure of 5.5% was selected since it is considered to be sufficient for the fish to maintain body weight or grow slowly (Huntingford *et al.*, 1998).

After two days the four fish were removed from the tank and their fork length and weights measured before they were returned to the experimental tank. Six hours later four more fish were added to the tank. These fish were referred to as 'Secondaries' since they were the second group of fish to arrive in the tank. This second batch of fish was made up of fish whose rates of oxygen consumption had been measured in the respirometer two days after the initial batch of fish. As with the Primaries, two of the Secondary fish were chosen randomly from the six highest rSMR fish in their group of 20 and two from the six lowest rSMR fish. In this way each stream tank contained eight fish: four Primaries consisting of two high rSMR and two low rSMR fish, and four Secondaries consisting of two high rSMR and two low rSMR fish.

Fourteen days after the arrival of the Secondaries all eight fish were removed, identified and their fork lengths and weights measured before they were placed in the stock tank with the fish not used in the experiment. Up to three stream tanks were used synchronously, and the experiment was repeated 10 times (5 for each level of food availability) so that a total of eighty fish were used.

Individual tanks.

Once the four fish had been randomly selected from the six highest and six lowest rSMR fish for use in the group trials, the other eight fish were placed individually into circular tanks (20cm diameter). The fish were fed three times a day so that they received either 5.5% of their initial body weight per day in bloodworms (low ration), or more bloodworms than they would eat (high ration). In both treatments the bloodworms were frozen in an ice-cube so that the method of food delivery was identical to that used in the group experiment. Although all of the bloodworms in the low ration cubes were eaten, some of the bloodworms in the high ration trials were not eaten and remained on the bottom of the tank. Every other day any excess bloodworms on the bottom of the tanks were removed.

After fourteen days the fish were removed from the jars and their fork lengths and weights measured before they were also placed in the stock tank with the fish not used in the experiment. A total of 72 fish were used in this part of the experiment, 36 kept on a high ration and 36 on a low ration. Unfortunately 1 fish on the high ration and 8 fish on the low ration died leaving 28 on a low ration and 35 on a high ration.

Individual Specific Growth Rates (SGR) for weight and length were calculated from the formula:-

$$100(\ln(\text{Final measurement}) - \ln(\text{Initial measurement})) / \text{duration of experiment in days}),$$

following Ricker (1979). To control for the effect of body size on growth rates, the values of SGR for fish on high ration were regressed against the initial weight or length of the fish and the equation of the resulting line used to calculate the expected Specific Growth Rate of weight and length for each fish, given its initial size. The difference between the expected and observed Specific Growth Rate (adjusted Specific Growth Rate) was used in subsequent analyses of growth rates. Using the weight (W) and fork length (L) measurements, an index of each fish's condition (Condition factor, K) was also calculated as $K = 10^5(W/L^a)$, where a is the slope of a regression of $\log_{10}(\text{weight})$ on $\log_{10}(\text{length})$ following Bolger and Connolly (1989).

Results

As the experiment progressed the number of fish which had been measured in the respirometer increased and hence the accuracy of the equations used to calculate the expected oxygen consumption value of fish of a specific weight. Thus fish early on in the experiment were classified using a slightly less accurate regression than those later on. However it should be noted that the middle 8 of the 20 fish measured were discarded and it is highly unlikely that the remained 12 would be misclassified since they were not close to the regression line.

Once 152 fish had been measured the expected oxygen consumption was calculated as: oxygen consumption = $0.91W - 1.93$, where W represents fish weight, in g ($r^2 = 0.42$, $F_{1,253} = 183.38$, $P < 0.001$, Figure 1).

Fish kept in groups of 8

Initial size and condition

As the fish had grown larger by the onset of later trials the fishes' initial weights and lengths varied significantly between trials. However, there was no overall difference in the initial size of Primary (mean weight = 0.43 ± 0.02 g (SE) (n=40), fork length = 36.42 ± 0.54 mm (40)) and Secondary fish (weight = 0.46 ± 0.02 g (40), fork length = 36.57 ± 0.43 mm (40); two-way ANOVA, effect of trial number on initial weight: $F_{9,59} = 27.57$, $P < 0.001$; Primary/Secondary residence: $F_{1,59} = 0.03$ $P = 0.86$; effect of trial number on initial fork length: $F_{1,59} = 37.44$, $P < 0.001$; Primary/Secondary residence: $F_{1,59} = 0.03$, $P = 0.86$). The initial condition factor (K) of the fish varied with neither trial nor resident category (two-way ANOVA: effect of trial: $F_{9,59} = 1.82$, $P = 0.08$; resident category: $F_{1,59} < 0.001$, $P = 0.98$).

Growth rates and change in condition factor.

One secondary fish, with a high SMR and in a trial receiving the high food ration, died the day before it was due to be removed from the tank. Although it was not possible to measure the fork length or weight of the dead fish, the data for the remaining fish in that trial were used in subsequent analyses as the social group would have been stable for all except one day of the experiment.

The analyses revealed that although residence category (i.e. Primary or Secondary) and metabolic rate category (i.e. high or low rSMR) had no effect on the change in condition factor or adjusted SGR (see Methods) of either weight or length, the food treatment to which a fish was subjected did have a strong effect (three-way ANOVA; see Tables 1a, b and c). This suggests that, not surprisingly, the food availability had the strongest effect in determining the growth rate of fish.

To examine the effect of residence and metabolic rate category in more detail, the two food treatments were separated. Within the low ration treatment there was no

difference between trials in either the change in condition factor or the adjusted SGR of weight or length (one-way ANOVA, effect of trial number on change in condition factor: $F_{4,35}=1.53$, $P=0.49$, $P=0.21$; effect of trial number on SGR weight: $F_{4,35}=0.87$, $P=0.49$; effect of trial number on SGR length: $F_{4,35}=1.84$, $P=0.14$). There was no effect of residence category or metabolic rate category on the change in condition factor, SGR of weight or length in low ration fish (two-way ANOVA; see Table 2, Figure 2). Thus, within the fish kept on a low ration, residence category and metabolic rate category seem to have no effect on the growth rates or change in condition factor.

Within the high ration treatment there was no difference between trials in the adjusted SGR of length (one-way ANOVA, effect of trial number on SGR length: $F_{4,34}=0.97$, $P=0.43$). There was no effect of residence category or metabolic rate category on the change in SGR of length in low ration fish (two-way ANOVA; see Table 3a). However, the adjusted SGR of weight and change in condition factor were significantly different between trials (one-way ANOVA, effect of trial number on SGR weight: $F_{4,34}=2.95$, $P<0.05$; effect of trial number on change in condition factor: $F_{4,34}=2.74$, $P<0.05$). To control for the effect of trial number, the mean changes in condition factor and SGR of weight for each trial were determined and the difference between an individual's value of these two variables and the mean for the trial was calculated. These values were referred to as the residual adjusted SGR of weight (the change in condition factor of a fish after correcting for differences between replicate trials) and the residual change in condition factor (the difference in growth rate of a fish after correcting for its body size and differences between replicate trials). There was no effect of residence category or metabolic rate category on the change in SGR of weight or condition factor of these high ration fish (two-way ANOVA; see Tables 3 b & c, Figure 3). Thus, even when the effect of ration size is removed, residence category and metabolic rate category seem to have no effect on the growth rates or change in condition factor of the fish.

Fish kept individually

Initial size

Initial weights and lengths of the fry varied between trials as fish had grown larger by the onset of later trials. The average initial length of a fish was 35.33mm (± 0.36) and initial weight was 0.39g (± 0.01).

Growth rates and change in condition factor.

Although ration size significantly affected the change in condition factor during the experiment, the metabolic rate category (high or low rSMR) did not (two-way ANOVA; see Table 4a). Likewise, ration size affected SGR of weight and length but metabolic rate category had no effect (two-way ANOVA; see Table 4b and c, Figure 4).

Figure 1

Double-logarithmic relationship between oxygen consumption (ml/h) and fish bodyweight (grams), used in the determination of relative Standard Metabolic Rate (rSMR; defined as the residual from this regression line) and classify fish as either high or low rSMR.
($\ln(\text{Oxygen consumption}) = 0.91 \cdot \ln(\text{fish weight}) - 1.93$; $r^2 = 0.42$, $F_{1,253} = 183.38$, $P < 0.001$).

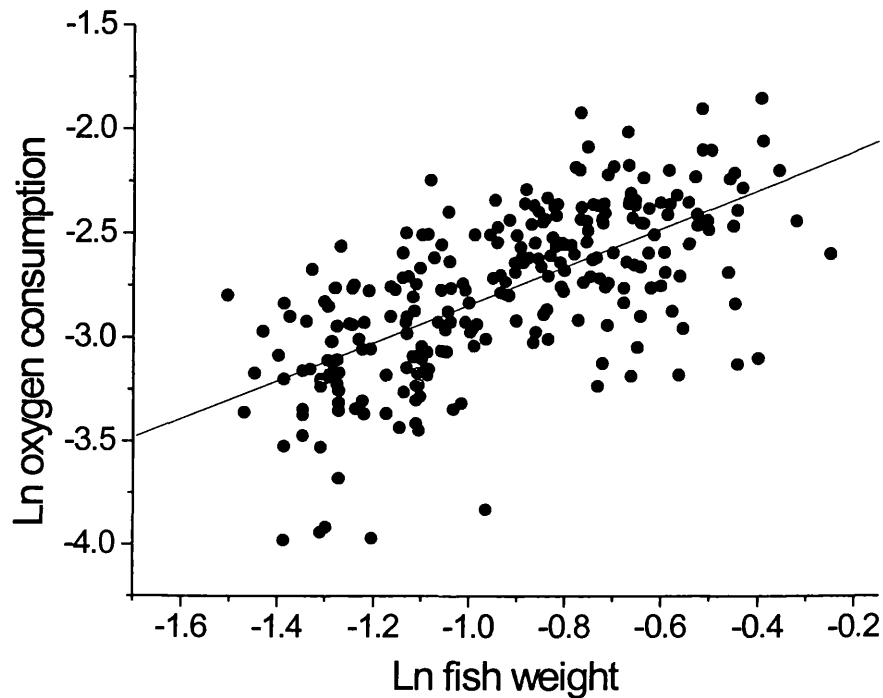


Figure 2

Primary (i.e. prior resident) and Secondary (i.e. later immigrant) Atlantic salmon fry mean (\pm SE) a) change in condition factor, b) adjusted SGR (% increase in weight per day), c) adjusted SGR (% increase in length day), when kept for 2 weeks in groups of 8 and given a low food ration. Hatched bars represent fish with low SMRs and solid black bars represent fish with high SMRs. See table 2 for statistical analysis.

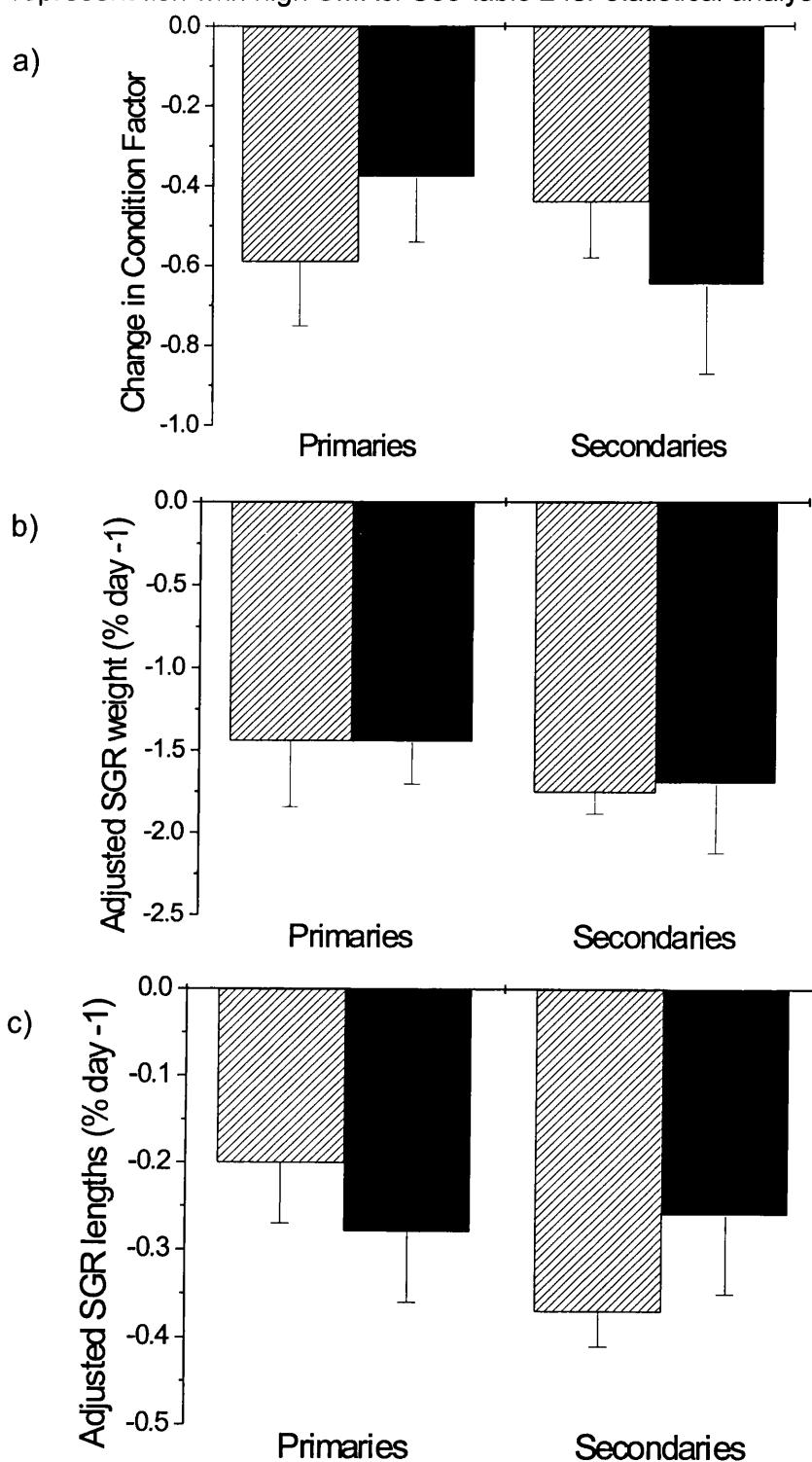


Figure 3

Primary (i.e. prior resident) and Secondary (i.e. later immigrant) Atlantic salmon fry mean (\pm SE) a) adjusted SGR (% increase in length day), b) residual adjusted SGR (% increase in weight per day), c) residual change in condition factor, when kept for 2 weeks in groups of 8 and given a high food ration. Symbols as in figure 2. See table 3 for statistical analysis.

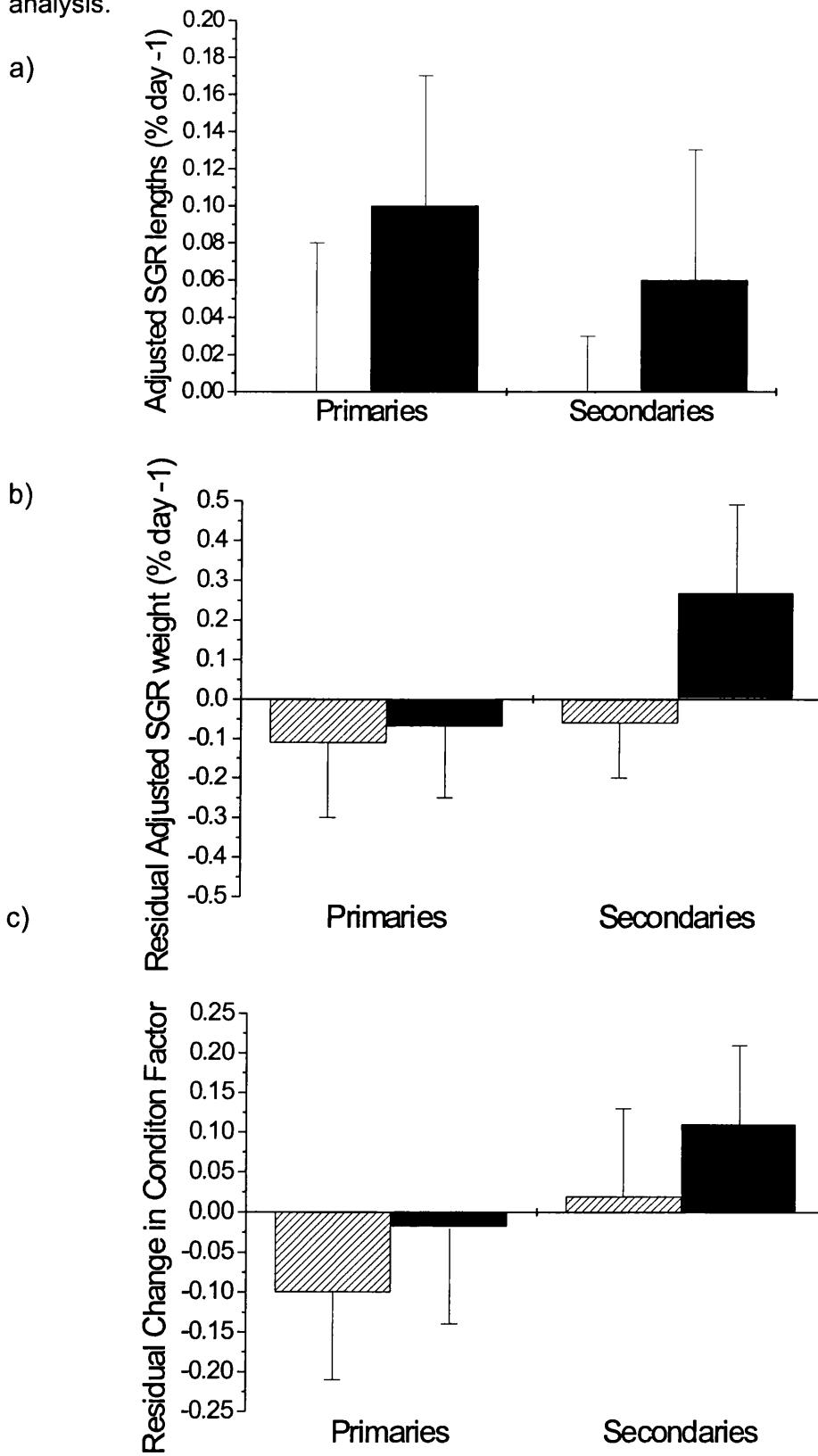
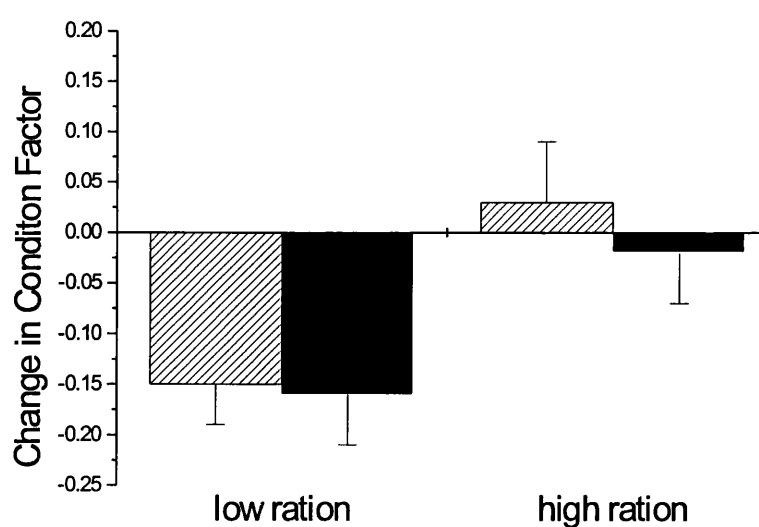


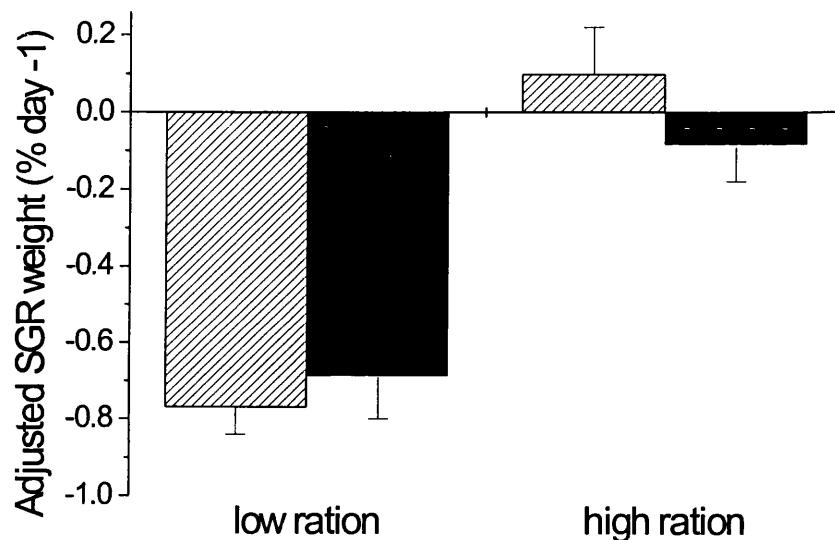
Figure 4

Mean (\pm SE) a) change in condition factor, b) adjusted SGR weight and c) adjusted SGR length of low SMR (hatched bars) and high (black bars) Atlantic salmon fry kept individually for 2 weeks and given either a low or high food ration. See table 4 for statistical analysis.

a)



b)



c)

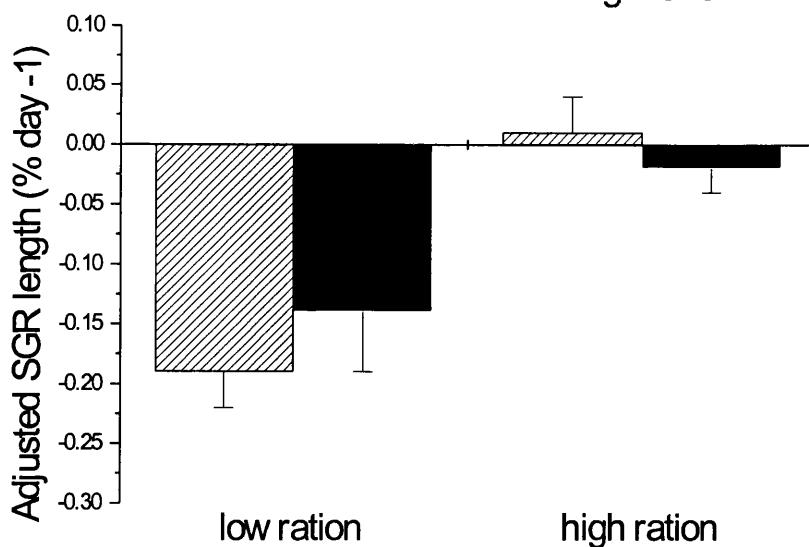


Table 1

Results of a three-way ANOVA investigating the influence of food ration treatment (Food, high or low), residence category (Res., Primary or Secondary) and relative standard metabolic rate category (rSMR, high or low) on

- the change in condition factor
- adjusted Specific Growth Rate (% increase in weight per day)
- adjusted Specific Growth Rate (% increase in length per day)

of fish kept in groups of 8.

a)		df	F	P
Main effects	Food	1	22.25	<0.001
	Res.	1	0.06	0.80
	rSMR	1	0.10	0.75
2-Way Interactions	Food * Res.	1	0.63	0.43
	Food * rSMR	1	0.10	0.75
	Res. * rSMR	1	0.95	0.33
3-Way Interactions	Food * Res. * rSMR	1	0.92	0.34
Residual		71		
b)		df	F	P
Main effects	Food	1	67.24	<0.001
	Res.	1	0.08	0.78
	MR	1	0.22	0.64
2-Way Interactions	Food * Res.	1	1.39	0.24
	Food * MR	1	0.12	0.73
	Res. * MR	1	0.15	0.70
3-Way Interactions	Food * Res. * MR	1	0.05	0.83
Residual		71		
c)		df	F	P
Main effects	Food	1	37.93	<0.001
	Res.	1	0.30	0.59
	MR	1	0.23	0.63
2-Way Interactions	Food * Res.	1	1.18	0.28
	Food * MR	1	0.07	0.79
	Res. * MR	1	1.43	0.24
3-Way Interactions	Food * Res. * MR	1	0.50	0.48
Residual		71		

Food, ration food category (high or low); Res., residence category (Primary or Secondary); MR, metabolic rate category (high or low)

Table 2

Results of a two-way ANOVA investigating the influence of residence category (Res., Primary or Secondary) and metabolic rate category (MR, high or low) on a) the change in condition factor, b) adjusted SGR (% weight change per day) and c) adjusted SGR (% length change per day), of fish kept in groups of 8 on low ration diet.

a)

		df	F	P
Main effects	Res.	1	0.11	0.74
	MR	1	<0.001	1
2-Way Interactions	Res. * MR	1	1.46	0.24
Residual		36		

b)

		df	F	P
Main effects	Res.	1	0.78	0.38
	MR	1	0.01	0.94
2-Way Interactions	Res. * MR	1	0.01	0.92
Residual		36		

c)

		df	F	P
Main effects	Res.	1	1.22	0.28
	MR	1	0.02	0.89
2-Way Interactions	Res. * MR	1	1.64	0.21
Residual		36		

Res., residence category (Primary or Secondary); MR, metabolic rate category (high or low)

Table 3

Results of a two-way ANOVA investigating the influence of residence category (Res., Primary or Secondary) and metabolic rate category (MR, high or low) on a) adjusted SGR (% length change per day) the change in condition factor, b) adjusted SGR (% weight change per day) and c) the change in condition factor adjusted SGR (% length change per day), of fish kept in groups of 8 on high ration diet.

a)

		df	F	P
Main effects	Res.	1	0.16	0.69
	MR	1	0.31	0.58
2-Way Interactions	Res. * MR	1	0.13	0.72
Residual		35		

b)

		df	F	P
Main effects	Res.	1	1.16	0.29
	MR	1	0.98	0.33
2-Way Interactions	Res. * MR	1	0.59	0.45
Residual		35		

c)

		df	F	P
Main effects	Res.	1	1.23	0.28
	MR	1	0.51	0.48
2-Way Interactions	Res. * MR	1	0.01	0.94
Residual		35		

Table 4

Results of a two-way ANOVA investigating the influence of food ration category (Food high or low) and metabolic rate category (MR, high or low) on;

- the change in condition factor
- adjusted Specific Growth Rate (% increase in weight per day)
- adjusted Specific Growth Rate (% increase in length per day)

of fish kept individually.

a)

		df	F	P
Main effects	Food	1	8.47	<0.01
	MR	1	0.34	0.57
2-Way Interactions	Food * MR	1	0.16	0.70
Residual		59		

b)

		df	F	P
Main effects	Food	1	52.17	<0.001
	MR	1	0.30	0.59
2-Way Interactions	Food * MR	1	1.72	0.19
Residual		59		

c)

		df	F	P
Main effects	Food	1	27.41	<0.001
	MR	1	0.09	0.77
2-Way Interactions	Food * MR	1	1.22	0.27
Residual		59		

Food, food ration category (high or low); MR, metabolic rate category (high or low)

Discussion

Despite a large amount of evidence to the contrary (Metcalfe *et al.*, 1995; Cutts *et al.*, 1998, 1999; Huntingford *et al.*, 1998; Yamamoto *et al.*, 1998; Chapter 5) no effect of prior residence or metabolic rate was found in the current experiment on the change in condition factor and growth rates of either fish kept alone or in groups. The only clear effect was that of ration size, with fish receiving more food having higher growth rates and a greater change in condition factor. This would seem to suggest that the growth rate of a fish is dependent purely on the amount of food it receives and is independent of its social or physiological state. In the light of previous experiments outlined in the introduction this result seems questionable, and in order to have confidence in the results the experiment should perhaps be repeated with a few modifications to the methods.

It is possible that certain aspects of the experimental design may have masked the true effect of metabolic rate and prior residence. One example is the method in which food was presented to the fish. Unlike studies of the distribution of convict cichlids (*Cichlasoma nigrofasciatum*; Grand & Grant, 1994) in relation to the spatial predictability of food, this study did not stagger the introduction of food into the tank over time. Although it was hoped that the ice-cubes would release the bloodworms into the water column in a slow and temporarily unpredictable manner they melted far too fast; each ice-cube melted completely in approximately 20 minutes. This meant that the fish received the bloodworms over a short period of time and from an identifiable source (from the end of the chute). Previous studies of coho salmon (*Oncorhynchus kisutch*; Ryer & Olla, 1996) have shown that when food is localised, dominant fish defend positions close to where food enters the tank. It is possible that the dominant fish in the present study also secured the territories nearest the site of food availability, but as the bloodworms arrived in rapid succession they would have been impossible to monopolise. Hence fish which would not otherwise have secured food managed to do so.

Theory predicts that the aggressiveness of animals will increase as the spatial clumping of resources increases (Brown, 1964; Trivers, 1972; Monaghan & Metcalfe, 1985; Grant, 1993) and decrease as the temporal clumping of increases (Trivers, 1972; Wells 1977), and the interdependence of these two variables has been highlighted in a recent study by Robb and Grant (1998) of Japanese medaka (*Oryzias latipes*). If resources become available asynchronously each item can be contested and dominant individuals will tend to secure the greatest proportion of the resource (Bryant & Grant, 1995). However, if resources are temporally clumped, any time that an individual spends attempting to defend the resources will be time that it does not exploit the resource. In this situation the dominance hierarchy will not necessarily determine which animals obtain resources. Temporal clumping of resources may thus lead to less variation in growth within a group (Bryant & Grant, 1995) which is possibly what happened in the present study. Thus although high SMR fish, or prior residents, may have been dominant they did

not grow faster as they were unable to secure a greater proportion of the resources. To improve on this method of presentation so that any effects of dominance are reflected in growth depensation (Magnuson, 1962) a new, less synchronous method of food presentation is needed.

It is likely that the synchrony of food presentation also affected the fish kept individually. Juvenile Atlantic salmon are naturally "sit and wait predators" that intercept food drifting in the water column and do not tend to feed off the stream bed (Wankowski, 1981). Thus, despite the relative abundance of bloodworms, the only ones that were truly available were those drifting through the water column. The amount of bloodworms in the ice-cube may have had little bearing on the fish's meal size since it would be limited by the amount it could eat in the time it took for the ice-cube to melt. If this was less than the number contained in a low ration ice-cube, and low and high ration cubes melted at the same speed, then the 'available' meal size presented by a low and high food ice-cube would be almost identical. The presence of uneaten bloodworms in the tanks of the fish on a high ration may thus be a direct result of the synchronous food presentation rather than indicative of excess food. The absence of bloodworms left in the low ration tanks could mean that the rate at which they were supplied from the melting ice-cube was the maximum rate at which the fish could eat them. If this were true then any increase in the number of bloodworms per ice-cube would be superfluous since they melted at the same speed. To ascertain whether low ration fish are eating the same number of bloodworms as high ration fish it would be necessary to repeat the experiment with closer observation of the fishes' food consumption. The number of bloodworms eaten by the fish could be recorded by direct observation of the fish as the ice-cubes melt and if the fish are taking the same number of bloodworms the low ration size could be decreased.

Another possible reason for the invariability of growth among fish kept individually could be stress. Juvenile salmon tend not to live alone; rather they live in close proximity to conspecifics (Fausch, 1984). The stress that resulted from being kept alone could have increased the metabolic rates of the fish so that growth was reduced regardless of ration size. Indeed a previous study of Atlantic salmon found that subordinate fish kept alone ate less than those kept in a tank with a transparent partition between them and a dominant conspecific (Huntingford *et al.*, 1993). However, this does not account for the lack of variation in growth within food ration groups. This is in contrast to work on steelhead trout (*Oncorhynchus mykiss*) which found that subordinate individuals (which would presumably be low SMR salmonids) grow less well than their dominant (high SMR) companions even when they were fed on their own on identical rations (Abbott & Dill, 1989). It is likely that the stress of isolation upon high and low SMR fish was similar, and if so, this would not produce similar growth rates due to the differences in metabolic costs of living. However, in order to be certain that the stress of isolation is the same amongst fish it would be necessary to repeat the experiment recording a stress indicator such as cortisol levels in the blood. But in the light of the steelhead trout study it is hypothesised

that the lack of variation in growth between high and low SMR fish kept individually within each ration size is almost entirely due to the food presentation method.

Chapter 9

General Discussion

The two main objectives of this thesis were firstly to examine the fighting behaviour of juvenile Atlantic salmon and to relate it to the natural situation under which these contests will occur, and secondly to elucidate the factors that determine dominance and their consequences. In this general discussion each of these objectives will be addressed in turn and their implications in terms of salmon life history considered. In this way the results of the experiments contained in this thesis will be used to explain various aspects of contests for space in salmon and, where applicable, their interdependence addressed.

Fighting behaviour

The social system of salmonids in streams is very stable: whilst a small proportion of fish are mobile, the majority maintain the same small home range for long periods of time (Kalleberg, 1958; Saunders & Gee, 1964; Armstrong *et al.*, 1994, 1997). Within these small home ranges some fish aggressively defend a territory while others adopt a floating strategy, avoiding conflict by living in the interstices between the sites occupied by more dominant individuals (Kalleberg, 1958; Bachman, 1984; Puckett & Dill, 1985). The close proximity of neighbouring fish will tend to result in a high rate of contact between fry and competition for feeding stations. Although obtaining a feeding station is an important factor in determining early performance in salmonids (Elliott, 1994), the amount of effort invested in attempting to obtain or defend a particular feeding territory must be finely tuned to the value of the contested resource (Enquist & Leimar, 1990). Fry are at an early life history stage and should not engage in potentially fatal contests over a resource since the long-term benefits of survival far outweigh the short-term benefits of contested resources. Hence, selection will tend to favour any mechanism that avoids unnecessary and potentially costly fights. One such mechanism is signalling and Chapter 2 and 3 investigate the role of colour change as a means of communicating submission.

Although a relationship between temporary changes in body colour and dominance has been observed in several fish species (Baerends *et al.*, 1955; Okaichi *et al.*, 1958; Stacey & Chiszar, 1977; De Boer, 1980; Johnsson *et al.*, 1999), this thesis is the first to demonstrate a temporal direct link between darkening of a subordinate fish and a reduction in the aggressive behaviour of the dominant (Chapter 2). The results of the experiments in Chapter 2 and 3 suggest that the onset of darkening of a subordinate fish marks the point at which it becomes subordinate and leads to a reduction in the aggressive behaviour of the dominant. It could thus be hypothesised that darkening acts as a signal of submission to the dominant fish.

Previous studies have shown that darkening subordinate rainbow trout also change their body postures when dominant fish are present (Abbott *et al.*, 1985) and it is entirely possible that factors other than the colour changes observed in this thesis may act in consort to signal motivation and status. In order to prove irrefutably that darkening acts as a signal of submission further experiments are needed. If either the colour of the fish or

their ability to darken could be manipulated it may be possible to assess the impact of colour alone on the dominant's behaviour and in this way tease apart the influence of colour and other variables (for example body posture). In addition, experimental manipulation of body or sclera colour may lend itself to identification of the roles of the two individual areas in signalling submission.

The value of signalling relies heavily upon an individual's ability to recognise familiar opponents and use signalling to avert futile battles with previously dominant individuals. Individual recognition on the basis of familiarity has been demonstrated in several freshwater fish including: bluegill sunfish (Dugatkin & Wilson, 1992), three spined sticklebacks (Van Havre & FitzGerald, 1988), fathead minnows (Brown & Smith, 1994) and guppies (Magurran *et al.*, 1994; Griffiths & Magurran, 1999). Recent work has shown that salmonids also have the capacity for individual recognition and exhibit less aggression towards familiar than towards unfamiliar opponents (Johnsson, 1997). When body darkening was examined in relation to familiarity there appeared to be a tendency for fights between familiar opponents to result in either one fish darkening after relatively little aggression, so averting an escalated fight, or for neither fish to darken so that a high intensity fight ensued (possibly a result of a prior residence asymmetry offsetting any previous dominance relationship). This lends further support for the hypothesis that darkening acts as a signal of submission and is used among familiar opponents to avert costly fights. This differential treatment of neighbours and strangers (the 'Dear Enemy' phenomenon; Fisher, 1954) can reduce the costs of territory defence in terms of the energy expended during fights and the risk of injury (Archer, 1988; Ydenberg *et al.*, 1988). For example, territory holding Augrabies flat lizards (*Platysaurus broadleyi*) are less aggressive to neighbours than non-neighbours and have shorter contests with familiar conspecifics (Whiting, 1999).

Although the effect of kinship was not examined within this thesis it has been suggested that competition between kin should be less intense as there will be fewer advantages in mortal aggression between related individuals (Hamilton, 1979). Thus, individuals may prefer the company of kin to non-kin. Indeed a recent study found that common tern chicks (*Sterna hirundo*) show a significant preference for siblings over familiar non-siblings (Palestis & Burger, 1999). However, in the wild, related fish do not necessarily have adjacent territories (Fontaine & Dodson, 1999) and the ability to recognise familiar opponents shown in this thesis will be more valuable in terms of averting contests than kin recognition. Studies of Trinidadian guppies (*Poecilia reticulata*) have shown that fish are more likely to associate with familiar conspecifics than kin (Griffiths & Magurran, 1999), and have demonstrated the value of knowing a potential opponent's resource holding potential. Similarly, studies of avian flocks have shown that tolerance of familiar individuals increases an animal's direct fitness as repeated escalated fights are avoided through recognition and acknowledgement of dominants (Whitfield, 1987). Whereas kin recognition in fish may rely on water-borne cues or other phenotypic

characteristics (Brown & Brown, 1992, 1996), recognition and status recognition between non-kin conspecifics may rely upon signals such as the darkening observed in this thesis. The behaviour of the fish in terms of their colour during a fight will thus be pivotal in determining its duration and intensity.

The tendency of subordinate fish to darken during intraspecific competition could be used in studies of dominance hierarchies. Whereas previous studies have constructed dominance hierarchies on the basis of stream position (Metcalfe *et al.*, 1992) or food acquisition (Johnsson *et al.*, 1996), it may now be possible to rank dyads according to which fish changes colour. In this way protracted fighting which leads to the establishment of dominance and upstream position or access to food could be avoided, and the duration of time that competing fish need to spend together in order for an observer to allocate dominance would be reduced. If the hypothesis that signalling signals submission is proven then an observer would be able to assign dominance as soon as the fish themselves have assigned dominance.

Factors determining dominance and their consequences

Competition for food and space amongst juvenile Atlantic salmon is fierce (Keenleyside & Yamamoto, 1962; Dill *et al.*, 1981, McNicol *et al.*, 1985; Puckett & Dill, 1985) and populations regularly exceed the carrying capacity of their habitat. The population density of fish within a cohort will decrease over time for a variety of reasons (see Grant 1993 for review), one of which will be intraspecific competition. As individuals become larger they require larger territories and the number of fish that a habitat can support will decrease resulting in the death or emigration of surplus individuals (Chapman, 1962; Mason & Chapman, 1965; Backiel & LeCren, 1978; Elliott 1986; Grant & Kramer, 1990). This 'self-thinning' in the first couple of months will act to favour dominant fish that can obtain and maintain a territory (but see Armstrong 1997 for a critique of the self-thinning hypothesis). During the first few months of life any asymmetries that exist between fry will be crucial in determining which fish succeed in establishing a feeding station and thrive, and which are displaced down stream where they will probably die (Elliott, 1986).

In this thesis, three asymmetries were addressed: date of first feeding, prior residence and standard metabolic rate (SMR). Although a high SMR in salmonids had been previously linked with high aggression levels and dominance (Metcalfe *et al.*, 1992, 1995; Cutts *et al.*, 1998, 1999; Yamamoto *et al.*, 1998) it did not appear to influence dominance in any of the experiments in this thesis (Chapters 6 & 8). An experiment examining the effect of food deprivation on SMR (Chapter 7) suggested that the ranking of SMR within a group, and hence the order of dominance, may alter during times of nutritional stress. This would seem to suggest that the flexibility of an individual's SMR rather than its absolute value may be important in determining individual fitness. However,

while flow-through respirometry allows the experimenter gain an approximate reading for SMR caution should be exercised when interpreting the results. It is a relatively crude method of measuring SMR since it not only relies upon several key assumptions (e.g. that the fish is quiescent when in the respirometry chamber) but involves extremely sensitive apparatus. It would have been possible to get more accurate measurements of SMR for individual fish by increasing the number of samples obtained for each fish. Unfortunately, this would have meant a smaller sample size of fish that could have been screened in one day. This would have led to excessively large time intervals between measurements of fish within the same batch or reduced sample sizes, neither of which was considered acceptable.

The date of first feeding influenced both the stability of a fish's territory and possibly its quality (Chapter 4) but the duration of the experiments was insufficient to detect any long-term effects on growth. A similar correlation between hatching date and access to food is seen in Black guillemots (*Cephus grylle*) (Cook *et al.*, 1999), where in times of food shortage the first bird to have hatched secures the majority of the food supplied by the parent bird.

The prior residence effect, whereby interactions between residents and intruders are more commonly won by the resident (Leimar & Enquist, 1984; Maynard Smith & Parker, 1976), was by far the strongest influence upon the outcome of fights, dominance and subsequent growth (Chapters 5 & 6). It is entirely possible that the effect of prior residence was so strong that it masked the potential influence of any asymmetry in SMR, size, date of first feeding or any other variable. In support of this hypothesis, previous studies of salmon have shown that when a prior residence advantage exists, relative size has no effect on the outcome of contests unless the size disparity is very large (Cutts *et al.*, 1999). Chapter 6 highlighted that a time interval of as little as 24 hours between introducing groups of fish to a new habitat may be sufficient to seriously disadvantage the second batch of fish to arrive and lead to escalated fighting. This has serious welfare implications for the movement of fish between stock tanks in aquaculture. To minimise the competitive asymmetries that may result from this process every effort should be made to move the fish as synchronously as possible.

SMR, date of first feeding and prior residence are so interwoven that to analyse their individual effects masks the extent of their true effect. Fish with a high SMR will tend to exhaust their yolk sacs sooner than those with low SMRs and so emerge from the redd and start to feed exogenously sooner. Thus, their date of first feeding will be earlier and they will gain the prior residence advantage. Although SMR *per se* does not appear to determine dominance when other asymmetries are present, the repercussions of a high metabolic rate (i.e. early emergence and a prior residence advantage) will be pivotal in determining dominance.

This thesis has focused on the relatively short-term consequences of dominance such as territory acquisition and growth. Dominance, mediated through prior residence or early emergence, confers advantages in terms of territory ownership and growth (Chapter 4, 5 & 6). Dominant fish will tend to grow at a higher rate and so a self perpetuating cycle will be set up whereby dominant fish obtain more food and grow more quickly, and larger fish are more dominant (Wankowski & Thorpe, 1979; Abbott *et al.*, 1985). In this way size is a consequence of dominance and not a direct cause (Huntingford *et al.* 1990). Since the habitat preferences of young salmonids change with body size (Heggenes *et al.*, 1999) the most dominant fish within a cohort will be the first to disperse downstream and thus will again acquire the prior residence advantage. In this way the advantages of a high SMR may be coupled with those of prior residence so that a high SMR fish will gain and secure the most profitable feeding territory.

The size advantage established by dominant individuals will be reflected in the probability of them metamorphosing into smolts after just one year in the river (S1 strategy; Metcalfe *et al.*, 1988; Metcalfe & Thorpe, 1992b; Metcalfe, 1998). Hence the competitive ability of juvenile salmon in their first few months of life will ultimately influence their life history strategy through its effect on growth rates (Metcalfe *et al.*, 1989, 1990; Metcalfe, 1991). Subordinate fish that fail to obtain the growth threshold that triggers smolting during the critical period will adopt the S2 strategy and defer smolting for a further year.

It would be interesting to examine whether the dominance hierarchy established in the first few months of a salmon's life is reflected in the fecundity of adults. A recent study of little egrets (*Egretta garzetta*; Thomas *et al.*, 1999) established a correlation between the nestling size rank and subsequent breeding success of the offspring, larger nestlings having greater breeding success as adults, and it is entirely conceivable that a similar relationship may be present in fish. A long-term study of Atlantic salmon may also reveal other consequences of early dominance. For example in addition to smoltification date, early dominance may affect later life history decisions such as the period of time spent in the sea before returning to spawn, or (in the case of males) access to females on the spawning grounds.

Although the experiments described in this thesis have gone some way to explain the causes, resolution and consequences of contests for space in juvenile salmon there is still a lot that remains unknown. Future experiments should focus on the long-term implications of early dominance and further exploration of the role of signalling. Apart from adding to our knowledge of salmon biology, the experiments contained in this thesis have relevance to aquaculture and salmonid research in terms of animal welfare. Issues such as prior residence and colour signalling must be considered when working with salmonids, and wherever possible the results of these experiments used to avoid escalated fighting among captive fish.

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