Metabolic Rate, Territoriality and Life-History Strategies of Juvenile Atlantic Salmon (*Salmo salar* L.)

by

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This thesis is dedicated to my parents.

Abstract

The relationships between relative standard metabolic rate, aggression, territoriality, growth and subsequent life-history strategies were studied in juvenile Atlantic salmon. In order to do this a method of calculating mass-independent relative standard metabolic rates is presented. This procedure involved using individual deviations from allometric predictions of standard metabolic rate based on body size (termed residual standard metabolic rate).

As in a previous study, it was found that salmon with higher relative standard metabolic rates were more likely to acquire dominance, in both pairs and groups. However, fish with higher standard metabolic rates appeared to have smaller metabolic scopes within which they had to carry out dominance-acquiring costly activities such as aggression, although fish with higher standard metabolic rates did indeed acquire dominance through greater aggression. Fish with higher standard metabolic rates, although having a higher cost of maintenance, were found to have a lower feeding motivation, possibly because they had a smaller metabolic scope and movements associated with foraging are themselves energetically costly. Therefore it appears that juvenile salmon with high standard metabolic rates and a limited metabolic scope opt to be more aggressive and thus acquire dominance and a feeding territory at the expense of higher foraging rates, since both behavioural strategies are energetically costly. It was also found that in an environment with little food, fish with high standard metabolic rates grew less well than predicted given their position in an artificial stream than conspecifics with lower costs of maintenance. This indicates a potential cost of a high standard metabolic rate.

There is a temporal component to acquisition of territories since juvenile salmon emerge from gravel redds over several days. Through this 'prior residence' effect, fish introduced into a new environment first were more likely to acquire territories than later-arriving conspecifics. First-arriving fish, as a consequence of acquiring a feeding territory, grew faster and were more likely to smolt a year earlier than late-arriving juveniles. However, they did not appear to choose the most profitable territories, implying a time constraint to searching for the best sites. If a salmon takes too long to choose a territory, it risks the territories filling up with later-arriving fish and not acquiring one at all. Prior residence appears to be a powerful asymmetry when tested in both pairs and groups, intruders having to be relatively much larger to overcome it and acquire dominance. Relative standard metabolic rate did not predict dominance when prior residence was included as a competitive asymmetry. However, fish with higher standard metabolic rates were more likely to emerge first since they absorbed their yolk-sacs faster and so needed exogenous food sooner. Therefore, a high standard metabolic rate conferred an indirect benefit since it increased the likelihood of a fish being a prior resident.

Differences in aggression arising from differences in relative standard metabolic rate were also apparent in a hatchery situation. A group consisting entirely of salmon with high standard metabolic rates showed more aggression than a group of salmon with low standard metabolic rates. However, mean growth did not improve as a consequence of lower aggression rates, although the distribution of individual growth rates was more even in the group of fish with low standard metabolic rates. This may be a consequence of fewer fish in that group behaving despotically and monopolizing available food.

As reported in earlier studies, differences in standard metabolic rate between the Upper and Lower Modal Groups of juvenile salmon became apparent during their first winter and spring. However, Upper Modal Group fish had higher weight-specific standard metabolic rates in December, earlier than previously documented, and higher mass-independent metabolic rates in May, prior to smoltification. This is suggested to be a pre-adaptation to the high metabolic demands the smolts will face when they migrate to sea. Individual residual standard metabolic rates varied more in the Upper Modal Group than the Lower Modal Group over winter and spring, possibly because respiratory enzymes in the Upper Modal Group were more seasonally adapted to the changing water temperatures of the period. They may have therefore worked inefficiently at the temperature at which metabolic rate was measured (since it remained constant while the ambient water temperature changed over time), being most inefficient when the difference between sampling and ambient water temperatures was greatest. However, individual residual standard metabolic rates remained broadly invariant throughout the period, demonstrating that individual standard metabolic rate is a relatively stable minimum to aerobic metabolic activity.

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Chapter 1: General Introduction

1.1 General salmon biology

The Atlantic salmon is an anadromous fish that, as with other salmonids, exhibits great flexibility in life-history strategies (Thorpe, 1989). In October-November Atlantic salmon lay relatively few large, yolky eggs (*ca.* 3000-10000 per female) in gravel nests (redds) on stream beds in the cool, temperate waters of America and Europe (Thorpe *et al.*, 1992). Each batch of eggs is simultaneously fertilised by the male and then covered with gravel (Jones, 1959). Juvenile salmon hatch within the redd in the following spring and remain there until their yolk-sacs are almost completely absorbed (Brännäs, 1988). The juveniles emerge from the redds prior to complete yolk-sac absorption, after which they defend feeding territories from one localised station (Kalleberg, 1958; Keenleyside & Yamamoto, 1962). The territoriality of juvenile salmonids has been extensively studied (Symons, 1968; Jenkins, 1969; Li & Brocksen, 1977; Dill, 1978; Fausch, 1984; Grant, 1990), and is mediated through intraspecific aggression (Kalleberg, 1958). A social hierarchy is formed where dominant juveniles are thought to assume the energetically most profitable stream positions (the optimal focal point of a territory is in a low-velocity current to minimise energy expenditure, and is adjacent to a swift current where prey drift rate is high; Fausch, 1984). Subordinate juveniles assume poorer feeding positions, although other juveniles are forced downstream to die as the territories are filled up (Elliott, 1984; 1990). There is therefore strong evidence for a critical period with high mortality in the first few weeks after juvenile emergence. Variation in salmonid territory size is primarily explained by

differences in body size (Grant *et al.*, 1989; Grant & Kramer, 1990; Keeley & Grant, 1995). Therefore a consequence of territoriality is population regulation: population density should decrease with increasing body size. Juvenile salmonids, therefore, may self-thin in a manner similar to plants as body and territory size increase (Grant & Kramer, 1990; Elliott, 1993*a*). Moreover, very large individuals may be selected against, since they spend so much time in territorial defence that they are unable to obtain an adequate energy intake (Elliott, 1993*b*).

1.2 Life-history strategies in juvenile salmon

1.2.1 Bimodality in juvenile salmon

Juvenile salmon, or parr, spend one to seven years in freshwater before entering the sea as smolts, and then return to their natal river to spawn after a further one or more years (Metcalfe & Thorpe, 1990). Alternatively, some fish may remain in freshwater and become sexually mature without having gone to sea (Dalley *et al.*, 1983; Bagliniere & Maisse, 1985). Much of the variation in seaward migration and the onset of sexual maturity is under environmental control (Thorpe, 1989; Metcalfe & Thorpe, 1990), and these two physiological decisions made by juveniles cause much of the flexibility in life-histories.

Whether juveniles migrate to sea after one year depends on individual growth trajectories in mid- to late summer, a few months after first feeding. Juvenile salmon that have maintained relatively high growth rates will migrate the following May, whereas fish with reduced growth rates will remain in freshwater for at least one more

year (Thorpe, 1977; Higgins 1985; Nicieza *et al.*, 1991). The proportion of fish maintaining high growth rates and smolting within one year is therefore under environmental control; more fish will turn into smolts in their second spring (1+ smolts) under conditions of high food availability and high temperature (Bagliniere & Champigneulle, 1986; Metcalfe & Thorpe, 1990). Whether or not a fish smolts becomes evident the previous autumn: the initially unimodal length-frequency distribution of a population of juvenile salmon becomes bimodal, with the faster growing Upper Modal Group (UMG) consisting of fish that will migrate to sea as 1+ smolts and the slower developing Lower Modal Group (LMG) deferring migration for a further year. Fish in the LMG subsequently lose appetite and enter a period of anorexia over the winter (Metcalfe *et al.*, 1988; Metcalfe & Thorpe, 1992*a*; Bull *et al.*, 1996), whereas the UMG maintain relatively high growth rates (Metcalfe *et al.*, 1986; 1988). The phenomenon of bimodality occurs in both wild and hatchery populations (Thorpe, 1977; Bagliniere & Maisse, 1985; Bagliniere & Champigneulle, 1986; Heggenes & Metcalfe, 1991; Nicieza *et al.*, 1991).

Therefore it appears that individual salmon adopt a developmental strategy dependent on reaching a threshold growth rate very early on in their life. This strategy remains fixed over winter. The physiological decision of which strategy to adopt appears to be reached during July and August: the correlation between monthly growth opportunity and proportion of fish subsequently entering the UMG is greatest in July (Thorpe *et al.*, 1989). Also, until this point ratios of otolith to somatic growth are similar in fish destined for either modal group but deviate markedly thereafter; fish in the UMG maintain otolith and somatic growth whereas salmon in the LMG virtually cease somatic growth yet continue otolith growth (Wright *et al.*, 1990). Moreover, the

appetite of UMG and LMG fish is strongly divergent after August, indicating fixed strategies (Metcalfe *et al.*, 1988). However, individual salmon adopt a life-history trajectory based on environmental cues. This must offer greater flexibility than a life-history under genetic control, so will often therefore have a selective advantage (Metcalfe, 1993).

1.2.2 Social status and life-history strategies

Since early growth rates determine the ability of an individual fish to achieve a threshold growth rate and migrate early, social as well as environmental factors must influence the decision of which life-history stategy to adopt. The social status and competitive ability of juvenile salmon should influence the age at which they migrate, through their impact on individuals' ability to acquire food. As noted already, juvenile salmon defend feeding territories against competitors (Kalleberg, 1958; Keenleyside & Yamamoto, 1962). By comparing pairs of fish in narrow raceways, Metcalfe *et al.* (1989) were able to identify the dominant juvenile salmon as the one which was consistently furthest upstream, and which obtained most food. However, larger fish were dominant in only 56% of pairs in June-July (two to three months after first feeding), and among LMG fish in the following April, larger fish were dominant in only 48% of pairwise interactions (Huntingford *et al.*, 1990). This suggests that early social status depends on factors other than relative size; since dominant fish obtain preferential access to food, they are likely to grow faster (Fausch, 1984; Metcalfe, 1986), so larger size is a consequence rather than a cause of dominance in juvenile

salmon (Huntingford *et al.*, 1990). Furthermore, fish of high status are more likely to join the UMG and smolt early, by both acquiring a disproportionate amount of food and suppressing the growth of fish lower in the hierarchy (Metcalfe *et al.*, 1989; Metcalfe *et al.*, 1990; Metcalfe, 1991; Thorpe *et al.*, 1992). In addition, fish of low status that are deferring migration are less able to feed in the presence of a competitor, suggesting they are subordinate in behaviour (Metcalfe, 1989).

Therefore it is clear that the fitness consequences of differing social status are considerable. However, the factors determining initial status are poorly understood, since larger size in juvenile salmon appears to be a consequence of dominance rather than a cause (Huntingford *et al.*, 1990). As mentioned earlier, juvenile salmon emerge over several days from their redds prior to complete yolk-sac absorption. Several studies have shown that those juveniles emerging first and colonising the stream bed have an advantage in subsequent competition for feeding sites over those emerging later (Mason & Chapman, 1965; Chandler & Bjornn, 1988; Brännäs, 1988). This is due to either a 'prior residence' advantage and/or because they are intrinsically more dominant. Metcalfe & Thorpe (1992*b*) disassociated the two effects, discovering that early emerging fish were dominant over late emerging fish after controlling for prior residence. This suggested that there was something intrinsically different between early and late fish - a factor that promoted both earlier yolk-sac absorption and more dominant behaviour.

The conclusions of several studies have indirectly suggested that differences in metabolic rate may play a part in determining dominance; dominance and probability of establishing a territory in salmonids are correlated with the relative sizes of otoliths at emergence (Mosegaard, 1990; Titus & Mosegaard 1991; Metcalfe *et al.*, 1992). Since

rate of otolith deposition is more closely related to metabolic rate than somatic growth (Wright *et al.*, 1990; Wright, 1991), this implies that differences in metabolic rate may cause differences in dominance. Given this line of reasoning, Metcalfe *et al.* (1995) demonstrated that variation in standard metabolic rate (SMR; measured as oxygen consumption, see Chapter 2 for definitions) was directly responsible for governing relative dominance among pairs of post-emergence juvenile salmon tested in white plastic raceways. In this way, variation in metabolic rate is thought to be linked to life-history strategy through the medium of social status.

1.3 Metabolic rate and behaviour

By investigating how relative metabolic rate may determine relative social status in juvenile salmon, Metcalfe *et al.* (1995) contributed to a number of studies on the relationship between physiology and behaviour in animals. To date, most studies have concentrated on instances where differences in behaviour have caused differences in physiology, rather than variation in physiology causing differences in social status, as is the case in the above study. For example, dominant birds have elevated metabolic rates as a consequence of their high social rank (Röskaft *et al.*, 1986; Hogstad, 1987; Bryant & Newton, 1994). In contrast to the situation with juvenile salmon, this elevated metabolic rate was interpreted as a disadvantage, since more energy would be needed to maintain a higher level of metabolism. It is unlikely that a similar causal relationship in juvenile salmon was observed by Metcalfe *et al.* (1995); variation in metabolic rate was thought to govern social status, rather than *vice versa*, since salmon subsequently

shown to be dominant already had larger otoliths at first-feeding (indicating a higher metabolic rate; Wright, 1991; Metcalfe *et al.*, 1992), several days before the onset of aggressive behaviour (Dill, 1977).

In addition to the above studies on birds, behaviour-dependent differences in physiology have also been noted in several fish species. In Nile Tilapia, both the dominant and subordinate fish showed elevated metabolic rates due to social stress in the subordinate and the expression of an agonistic profile in the dominant, some agonistic actions being more costly than others (Fernandes & Volpato, 1993; Alvarenga & Volpato, 1995). Using physiological parameters other than metabolic rate, studies on Siamese fighting fish showed that losers in pairwise interactions oxidised mainly amino acids for energy (a stress-like response to losing), whereas winners degraded carbohydrates more quickly, and could produce more energy per unit time than losers (Haller & Wittenberger, 1988; Haller, 1994; Haller, 1995). Moreover, similar relationships are found in mammals; rats exposed visually (but not physically) to opponents responded by increases in plasma free fatty acids (Koolhaas & van Oortmerssen, 1988). In coyotes, Golightly (1981) found that the metabolic rates of both dominants and subordinates were elevated: when dominants were regularly challenged, their metabolic rates increased, while if the subordinates were continually harassed, their oxygen consumption also increased.

However, there are rather few reports that discuss how differences in physiology can influence variation in behaviour. In arthropods, endothermically elevated thoracic temperature has been shown to be advantageous in the scramble competition of bumblebees for nectar (Heinrich, 1976; Heinrich, 1996) and of dung beetles for dung (Heinrich & Bartholomew, 1979; Ybarrondo & Heinrich, 1996; Heinrich, 1996). In the

latter case, high thoracic temperature is an important determinant of contest outcome: thoracic temperature is often actively regulated by using the flight muscles to shiver (Bartholomew & Heinrich, 1978), so beetles immediately arriving at dung piles usually win contests since their thoracic temperature is at high post-flight levels, compared to conspecifics that have been there for some time. Elevated thoracic temperature speeds up activity, so increasing a beetle's effectiveness at fighting.

A study on spinyhead and roughhead blennies reported similar findings on oxygen consumption and dominance as Metcalfe *et al.* (1995) found with salmon. Spinyheads, with a significantly greater standard metabolic rate than roughheads, outcompeted roughheads for feeding sites, gaining superior feeding sites on coral reefs. This led to roughheads having to occupy microhabitats with lower food availability where spinyheads, with their higher cost of maintenance, would receive inadequate food; only rougheads, with a lower cost of maintenance, could survive there (Clarke, 1992). Similarly, differences in the cost of maintenance have been suggested as potential causes of intraspecific differences in growth as environmental conditions change. Under conditions of low prey abundance a high metabolic rate, which may ordinarily confer dominance in salmonids, would become a disadvantage since they have higher energy demands for survival and growth, and cannot meet them due to lack of food (Titus, 1990).

Therefore physiological processes such as metabolic rate, measured either as oxygen consumption or thoracic temperature, would seem to influence subsequent behaviour. Moreover, juvenile salmon are ideal study animals to further investigate this process due to the relative ease of measuring the metabolic rates of fish and the amount already known about salmonid social systems. The marked territoriality and differing life-

history strategies within a population of juvenile salmon lend themselves well to a study on the behavioural consequences of individual physiology.

1.4 Outline of thesis

Chapter 2 describes the method of estimating oxygen consumption used throughout the thesis, presents a rationale of why that method was used, and defines basic metabolic terms such as standard metabolic rate. It also discusses an experiment on metabolic scope in juvenile salmon and how it may relate to the relationship between standard metabolic rate and dominance: metabolic scope (the difference between upper and lower levels of oxygen consumption) is thought to increase with increasing standard metabolic rate and so is an important factor in the study by Metcalfe *et al.* (1995). The relationship between individual variation in standard metabolic rate and metabolic scope is tested here.

Chapter 3 discusses feeding motivation and competitive asymmetries in juvenile salmon. Dominance status increases with increasing energy demand through the medium of greater feeding motivation (Johnsson & Björnsson, 1994). Therefore the hypothesis that feeding motivation increases with increasing standard metabolic rate and its associated energy demand is tested here. In addition, the experiment carried out by Metcalfe *et al.* (1995) is repeated here in a semi-natural setting, with an additional asymmetry of prior residence. It is compared here with the asymmetries of relative standard metabolic rate and relative size in determining the outcome of pairwise contests.

Chapter 4 is divided into two distinct experiments, both carried out in an artificial stream. Both experiments further investigate the relationship between metabolic rate and specific behaviours, and its subsequent effect on social status and life-history strategy. However, the first experiment attempts to elucidate the costs and benefits of a high standard metabolic rate, by investigating the effect of variation in food supply on the behaviour and growth of fish with known metabolic rates. The experiment tests the hypothesis (first suggested by Titus, 1990) that high metabolic rate may be a penalty during periods of low food abundance. The second experiment attempts to mimic the timing of emergence in a population of juvenile salmon, so in effect studies the effects of prior residence on subsequent behaviour and life-history strategy. It also investigates the relationship between the quality of individual salmon (measureable as social status) and their territories, given the assumption that the best territories will go to the most dominant individuals (Maynard Smith, 1974).

Chapter 5 investigates the effect of metabolic rate on aggression and subsequent growth depensation in an aquacultural situation. If high metabolic rate fish are more dominant, it may be as a result of aggression. Aggressive salmonids usually consume disproportionate amounts of food in hatchery tanks; this increases variance and skew of the size distribution of fish (McCarthy *et al.*, 1992; Ryer & Olla, 1996). This chapter tests the hypothesis that aggression and subsequent growth depensation can be moderated in groups of juvenile salmon by varying the proportion of fish with high standard metabolic rates which may potentially exhibit dominance and depress the feeding of others.

Chapter 6 investigates how individual standard metabolic rates may change as a population of juvenile salmon diverge into the two modal groups in their first winter. It

builds on previous studies which demonstrated that smolts have higher metabolic rates than salmon deferring migration. However, the timing of this physiological divergence is unclear. This chapter presents data on how the individual standard metabolic rates of a group of juvenile salmon vary through the winter and spring after bimodality has become apparent.

Chapter 7 contains a general synthesis of all the results and their implications for salmon ecology, and discusses how each set of results complements the other.

Chapter 2: General methods and metabolic scope in juvenile Atlantic salmon

2.1 Introduction

Methods of estimating metabolic rate, measured as oxygen consumption, in juvenile salmon are used throughout this thesis, so are given once in detail here. This chapter also presents data on metabolic scope in juvenile salmon; Metcalfe *et al.* (1995) claimed that those fish with higher relative standard metabolic rates (definitions are presented below) are more dominant in pairwise contests, and hypothesised that the greater standard metabolic rate allowed for a greater metabolic scope (Priede, 1985) within which behaviour attributable to dominance (e.g. aggression) could be performed at a greater intensity. However, the relationship between standard metabolic rate and metabolic scope was untested in that study. Therefore the influence of standard metabolic rate on variation in metabolic scope is investigated here.

Standard metabolic rate (SMR) is the minimal maintenance or resting metabolic rate of unfed fish, below which physiological function is impaired (Brett & Groves, 1979; Priede, 1985). It can be measured either directly with unfed, inactive fish (e.g. Edwards, 1970; Soofiani & Hawkins, 1982) or by extrapolating measurements in active fish back to zero activity (e.g. Brett, 1964; Lucas & Priede, 1992). Ordinarily, fish live above this resting level due to activities such as feeding and locomotion, and the typical rate of metabolism that they experience is termed routine metabolic rate. However, there is an upper limit on aerobic metabolic rate termed the active metabolic rate (AMR). The difference between active and standard metabolic rate is termed the metabolic scope (Fry, 1947) and the animal must function within its confines.

Metabolic scope can either be expressed as the absolute difference between the two limits (in $mlO_2.g^{-1}.h^{-1}$; e.g. Wieser, 1985; Wieser & Medgyesy, 1990), or as a metabolic expansivity coefficient (AMR/SMR; e.g. Lucas & Priede, 1992), also known as factorial metabolic scope (Wieser & Forstner, 1986; Armstrong *et al.*, 1992). Both the standard and active metabolic rates are mandatory and it has been assumed that individual animals cannot regulate their magnitude (Priede, 1985). However, other components of respiratory metabolism can be adjusted; metabolism due to the cost of tissue maintenance, locomotor activity and feeding metabolism must be carried out within the two limits (Brett & Groves, 1979). Feeding metabolism is associated with gut motility, digestive processes and post-feeding activity, and was described by Beamish (1974) as apparent specific dynamic action (SDA); metabolic rate is usually elevated (due to SDA) for some hours following feeding (Kleiber 1961; Beamish, 1974; Elliott, 1976; Vahl & Davenport, 1979). Locomotor metabolism accounts for a large proportion of the metabolic scope, so in fish there is a continual conflict between locomotion and feeding. For example, in largemouth bass (Tandler & Beamish, 1981) and juvenile cod (Soofiani & Priede, 1985), feeding metabolism can occupy all the metabolic scope, theoretically allowing none for locomotion within the confines of aerobic metabolism. Therefore fish may have a potential power budgeting problem, especially when foraging (Brett & Groves, 1979; Priede, 1985).

Much attention has been given to the allometric scaling of standard and active metabolic rate with mass; standard metabolic rate generally scales with size with a mass exponent of less than unity (<1), implying that heavier fish respire less on a per-gram basis, whereas active metabolic rate usually scales with size with a mass exponent of greater than unity (>1), implying that heavier fish have greater active metabolic rates

on a per-gram basis. Consequently, on average the metabolic scope usually increases with fish size (Brett, 1965; Priede, 1985; Wieser, 1985; Goolish, 1991; Armstrong *et al.*, 1992). However, little is known about how individual deviations from allometric predictions of standard metabolic rate affect deviations from predictions of active metabolic rate, after controlling for size. Deviations from predicted metabolic rate are measured as residuals (after subtracting the metabolic rate predicted on the basis of body mass from the actual metabolic rate). This method of investigating intraspecific variation in metabolic rate has been advocated across a wide range of taxa: mammals (McNab, 1988), birds (Daan *et al.*, 1990) and, more recently, fish (Metcalfe *et al.*, 1995).

Therefore, this chapter outlines methods of measuring juvenile salmon oxygen consumption and presents data justifying the protocol used throughout the thesis, and also presents data on the effects of variation in standard metabolic rate on active metabolic rate and consequently metabolic scope.

2.2 Methods

2.2.1 Source and maintenance of fish

All fish used in this thesis were offspring of sea run adults from the River Almond, Perthshire, and were reared at the SOAFD Almondbank hatchery prior to removal to the University Field Station, Rowardennan, Loch Lomond. Prior to experiments, all fish were kept in tangential flow hatchery tanks at ambient temperature and photoperiod and fed *ad lib.* with commercial pelleted food.

2.2.2 General respirometry methods

Oxygen consumption rates of juvenile salmon were measured by placing individual fish in perspex respirometry chambers through which water continually flowed, allowing the screening of large numbers of fish in a relatively short time. The size of chamber and water flow rate depended on the size of fish within them (Table 2.1). For this open method of respirometry the difference in oxygen content between water entering and leaving the chambers was measured, as was the flow rate of water. Water temperature was also noted in order to estimate the capacitance of oxygen in the water (βWO_2, $mlO_2\ .l^{-1}$) (Mackereth *et al.*, 1978; Table 2.2) during a series of oxygen consumption measurements. Water temperature was kept constant throughout by using a recirculating water supply and housing all equpment in a constant temperature cabinet. Water was pumped into a header tank through an ultra-violet steriliser to reduce bacterial respiration (Fig. 2.1). It was kept fully oxygen-saturated by means of an airstone, and then flowed by gravity through the respirometry chambers. A sample of header tank water was injected into a thermostatted Strathkelvin 1302 Oxygen electrode in order to calibrate a Strathkelvin Oxygen meter (Model 781) at 100% oxygen saturation, and a small amount of sodium sulphite in 0.01M *di*-sodium tetraborate solution was used to calibrate it at 0% oxygen saturation.

A rack of 20 chambers was set up, allowing the oxygen consumption rates of 20 salmon to be measured on the same day. The fish were placed in the chambers overnight, and measurements commenced 20 hours later, as by this time they would have settled and evacuated their guts (Higgins & Talbot, 1985; also evidenced by faeces being washed out of the tubes by the water flow). The fish were kept in semi-

Table 2.1: Respirometry chamber dimensions and water flow rates for examples of different size classes of juvenile salmon

Fork length ± S.E.(mm) (range)	Weight ± S.E.(g) (range)	Flow rate ± S.E. ($l.h^{-1}$) (range)	Respirometry chamber dimensions (length x breadth) (mm)
30.2±2.4 (26.8-33.5)	0.24±0.03 (0.14-0.34)	0.152±0.021 (0.086-0.271)	50 x 10
74.4±4.0 (64.5-84.3)	4.79±1.15 (2.65-6.92)	0.769±0.269 (0.276-1.428)	100 x 20
116.3±4.2 (97.0-131.0)	16.74±1.68 (9.19-22.80)	1.264±0.010 (1.209-1.303)	150 x 35

Table 2.2: Solubility of oxygen from moist air at one atmosphere total pressure in $ml.l^{-1}$ for different temperatures in freshwater

Temperature (°C)	Oxygen concentration ($ml.l^{-1}$)
8.0	8.280
8.5	8.183
9.0	8.086
9.5	7.988
10.0	7.891
10.5	7.802
11.0	7.713
11.5	7.623
12.0	7.534
12.5	7.452

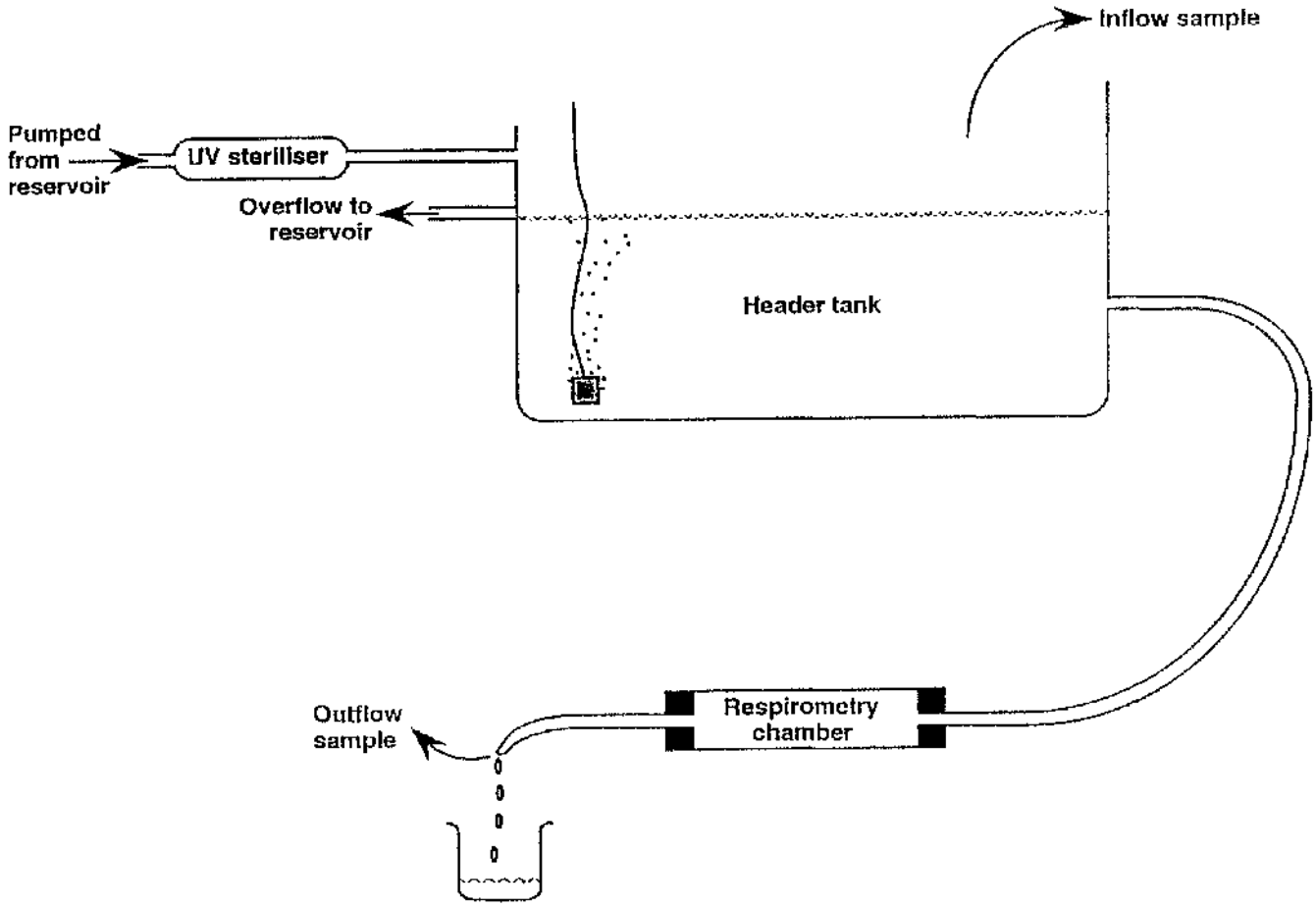


Fig. 2.1: Diagram of the respirometer with one of 20 respirometry chambers illustrated. The water in the header tank is saturated with oxygen using an air stone, and has been sterilised with an ultra-violet steriliser. Each chamber contains one fish, and the outflow from each chamber is injected into an oxygen electrode (not illustrated) calibrated with an inflow sample. Flow rate is measured by weighing the outflow collected in a beaker during a set period of time.

darkness, since they are very inactive at low light levels. Flow rate ($l.h^{-1}$) was measured by catching the water outflow from each tube in a beaker over a measured time period (a minimum of two minutes) and weighing it. Oxygen consumption ($\dot{V}O_2$, $mlO_2.h^{-1}$) was measured by first injecting 5ml of 100% oxygen saturated water from the header tank (representative of the water flowing into each chamber) into the oxygen electrode, and then injecting a 5ml sample of water flowing out of an occupied chamber and noting the percentage reduction in oxygen saturation from 100% (using a Belmont Instruments pen recorder connected to the oxygen meter). The percentage reduction in oxygen concentration was converted to an individual fish's oxygen consumption ($\dot{V}O_2$, $mlO_2.h^{-1}$) with the equation:

$$\dot{V}O_2 = V_W.\Delta C_WO_2 \qquad \text{(Eq. 2.1)}$$

where V_W is the flow rate ($l.h^{-1}$) of water through the respirometry chamber and ΔC_WO_2 is the difference in the oxygen concentration between the inflow and outflow water ((% reduction/100).$\beta\dot{W}O_2$, $mlO_2.l^{-1}$; where $\beta\dot{W}O_2$ is the capacitance of oxygen in the water).

This procedure was repeated twice for each fish (with a minimum interval of 30 min. between measurements), and a third reading was taken if the initial two values were not in close agreement. 'Close agreement' was defined as the second value falling within the first value$\pm$ 20%. The flow rate through each chamber was greater for larger fish (see Table 2.1), ensuring that the percentage reduction in oxygen concentration never dropped further than 25%. A greater reduction would result in undue stress for the fish. The entire procedure was identical for each fish, allowing a measure of relative standard metabolic rate for individual fish. All fish were anaesthetised, weighed (to 0.01g) and measured (fork length, to 0.1mm) after measurements of respiration rate

were completed. This technique allowed a non-invasive mass screening of fish for experiments, and was thought to be an accurate measure of individual rates of oxygen consumption since only fish with very similar rates of oxygen consumption from their two or three readings were used in subsequent experiments.

2.2.3 Changes in metabolic rate during the settling period

To ensure that metabolic rate values measured during experiments were indeed those of resting fish, the rate of oxygen consumption of 8 fish (mean weight = 2.21±0.25(S.E.)g) was measured at intervals over a 24 hour period from when they were first placed in respirometry chambers. The experiment was carried out in October 1994, at a water temperature of 9°C.

2.2.4 Calculating residual standard metabolic rate

To calculate whether a fish had a relatively high or low respiration rate for its size, the regression line of oxygen consumption ($mlO_2.h^{-1}$) versus weight (g) on a double natural logarithmic scale was used to calculate the expected metabolic rate of a fish of a particular weight. This was then compared with its observed metabolic rate ($mlO_2.h^{-1}$). Absolute rather than proportionate (per gram) values were used, as proportionate values usually decrease with increasing body size, larger fish respiring less on a per gram basis than smaller fish. The difference between a fish's observed and

expected standard metabolic rate was termed the residual standard metabolic rate (rSMR, measured in $mlO_2.h^{-1}$); a positive value therefore indicated that a fish had a higher than expected oxygen consumption rate for its size while a negative value indicated a relatively low consumption rate.

The standard metabolic rates of 106 juvenile salmon (range: 0.17 - 0.95g; mean weight = 0.36±0.05g) were measured during June and July 1993 at 9°C to give an example of the inter-individual variation in standard metabolic rate for a small size range of fish.

2.2.5 Measuring metabolic scope

Metabolic scope (MS) was estimated for 63 juvenile salmon across a weight range of 1.04-8.99g (mean weight = 3.86±0.21(S.E.)g) kept at an ambient temperature of 9°C. However, for logistical reasons, the standard metabolic rates of the fish were measured at a constant temperature of 13°C in April 1994. Standard metabolic rate was measured as above, and residual standard metabolic rate (rSMR) calculated with the regression equation derived from the measurements of oxygen consumption for the 63 fish. However, active metabolic rate (AMR) was measured in the same fish 20 hours prior to the standard metabolic rate measurements. Fish were transferred from a holding tank where they had been fed *ad lib.* and put in a bucket. Their routine metabolic rates will have already been elevated by the specific dynamic action (SDA) resulting from feeding (Beamish, 1974; Brett & Groves, 1979; Priede, 1985). The fish were agitated into burst swimming performance while in the bucket by being chased

with a hand-net, immediately before being placed in the respirometry chambers. This is thought to induce active metabolic rate, as moving from a stationary position to a burst swimming speed is energetically very inefficient (Dickson & Kramer, 1971). Moreover, chasing protocols have been thought to be biochemically and physiologically analogous to exhaustive exercise (Wieser *et al.*, 1985; Pearson *et al.*, 1990; Reidy *et al.*, 1995). The first metabolic measurement of each fish was taken *ca.* 20 minutes after they were placed in the chambers, since a change in measured oxygen concentration in the outflowing water lags behind a change in activity due to a wash-out effect of the chamber, which in turn is due to a dilution factor (= ratio of water flow to volume of water in the respirometry chamber; Spoor, 1946; Frappell *et al.*, 1989; Steffensen, 1989). This first metabolic measurement was therefore assumed to be a measure of active metabolic rate. Factorial metabolic scope was calculated as the ratio of active to standard metabolic rate (FMS = AMR/SMR).

2.3 Results

2.3.1 Changes in metabolic rate during the settling period

A steady decrease in metabolic rate to an asymptote was evident over time (Fig. 2.2), with the basal level being reached after approximately 17 hours. Therefore the protocol of leaving fish for 20+ hours in other experiments is clearly sufficient to allow them to evacuate their guts and to become acclimatised to conditions within the tubes, so allowing a measurement of standard metabolic rate.

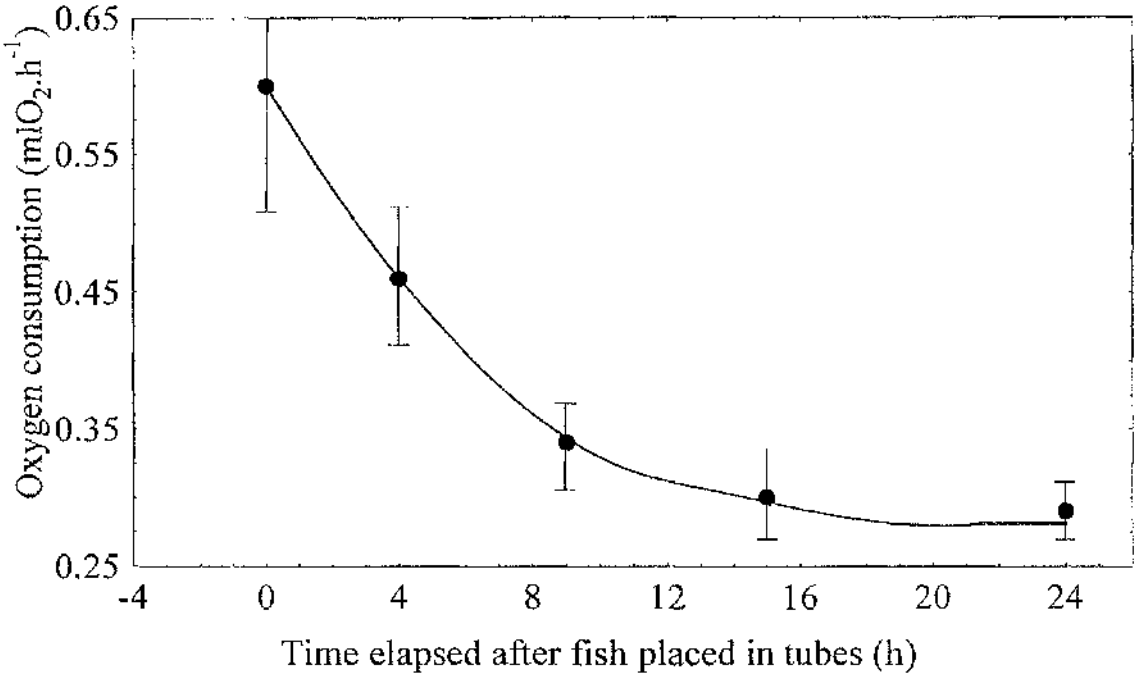


Fig. 2.2: Change in metabolic rate ($mlO_2.h^{-1}$) of 8 salmon measured 5 times over 24 hours at 9°C; 0 hours being the time the fish were put into the respirometry chambers. Error bars denote standard error.

2.3.2. Variation in residual standard metabolic rate

The relationship between standard metabolic rate (SMR, $mlO_2.h^{-1}$) and fish weight (W, g) for the 106 juvenile salmon tested during June and July 1993 is described in equation 2.2 and Fig. 2.3. It provides an example of the variability in standard metabolic rate between fish. Both axes were transformed to natural logarithms to linearise the relationship.

$$\ln SMR = 1.16.\ln(W) - 2.43 \qquad \text{(Eq. 2.2)}$$

($r^2 = 0.233$, $n = 106$, $p<0.005$)

The mean standard metabolic rate (SMR) was 0.033 ± 0.002 $mlO_2.h^{-1}$. However, it is clear that there was much inter-individual variability in metabolic rate (mass exponent S.E. = 0.204); the mean residual standard metabolic rate (rSMR) was -0.011 ± 0.005 $mlO_2.h^{-1}$, while the minimum and maximum values were -0.292 and 0.057 $mlO_2.h^{-1}$ respectively.

2.3.3 Metabolic scope

Regression equations relating standard and active metabolic rate ($mlO_2.h^{-1}$) to juvenile salmon weight (W, g) were:

$$\ln.SMR = 0.85.\ln(W) - 1.91 \qquad \text{(Eq. 2.3)}$$

($r^2 = 0.575$, $n = 63$, $p<0.0001$), and

$$\ln.AMR = 0.83.\ln(W) - 1.30 \qquad \text{(Eq. 2.4)}$$

($r^2 = 0.643$, $n = 57$, $p<0.0001$).

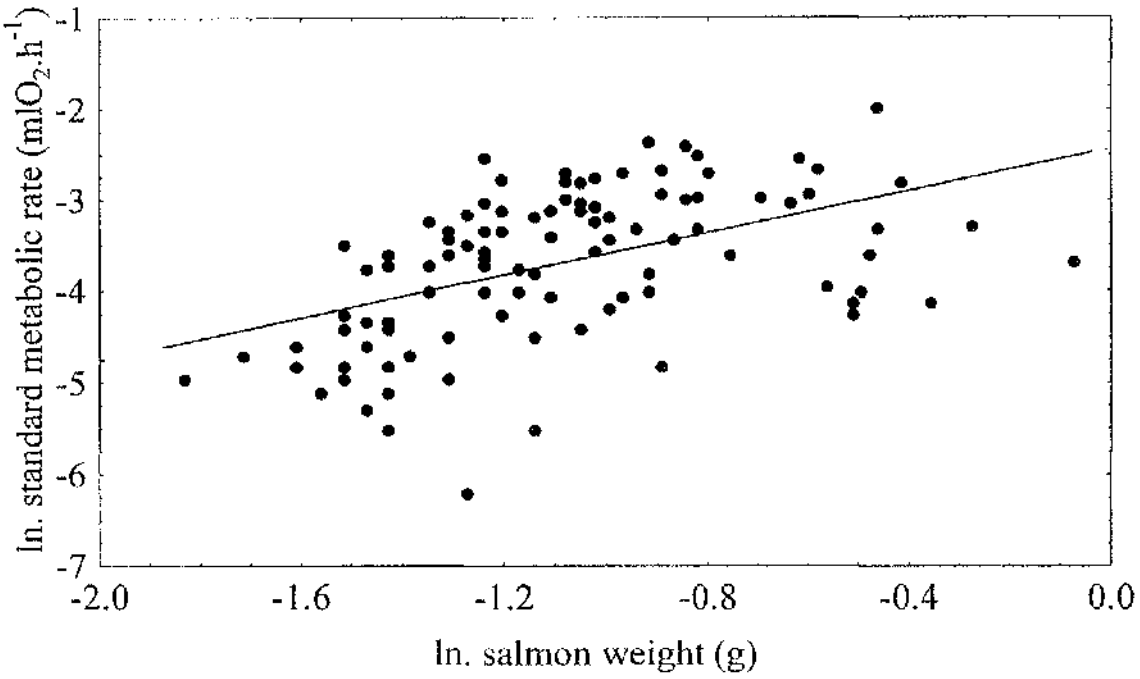


Fig. 2.3: The relationship between body weight (g) and standard metabolic rate ($mlO_2.h^{-1}$) for juvenile salmon (both axes are on a natural logarithmic scale).

The standard errors of the mass exponents for Eqs. 2.3 and 2.4 were 0.301 and 0.271 respectively.

Analysis of covariance indicated that the slopes of the two lines were not significantly different from each other ($F_{(1,118)} = 0.22$, $p = 0.638$). However, there was a significant difference in the elevations of the two lines ($F_{(1,118)} = 100.89$, $p<0.0001$, Fig. 2.4), active metabolic rate being (not surprisingly) significantly greater than standard metabolic rate. Both standard and active metabolic rates were measured in 43 of the fish; factorial metabolic scope (FMS = AMR/SMR) did not vary significantly with fish mass ($r^2 = -0.024$, $n = 43$, $p = 0.950$). On a per-gram, mass-dependent basis, active metabolic rate ($AMR.g^{-1}$) varied significantly with standard metabolic rate ($SMR.g^{-1}$, $mlO_2.h^{-1}.g^{-1}$):

$$AMR.g^{-1} = 0.62.(SMR.g^{-1}) + 0.15 \qquad \text{(Eq. 2.5)}$$

($r^2 = 0.136$, $n = 43$, $p<0.01$, Fig. 2.5). The mass exponent (0.62) was less than unity. There was a similar positive relationship linking the mass-independent measures of standard and active metabolism, residual standard metabolic rate and the analagous residual active metabolic rate ($r^2 = 0.133$, $n = 43$, $p<0.01$, Fig. 2.6). Again, the exponent (0.34) was less than unity. Furthermore, plotting the factorial metabolic scope of individual fish (FMS = AMR/SMR) against their residual standard metabolic rates (rSMR) showed a significant negative relationship ($r^2 = 0.359$, $n = 43$, $p<0.0001$, Fig. 2.7). Therefore, fish with relatively high rates of resting metabolism for their size had low metabolic scopes, so that they had a smaller range from their lowest to their highest rates of metabolism. The mean factorial metabolic scope was 1.93 ± 0.08 (S.E.).

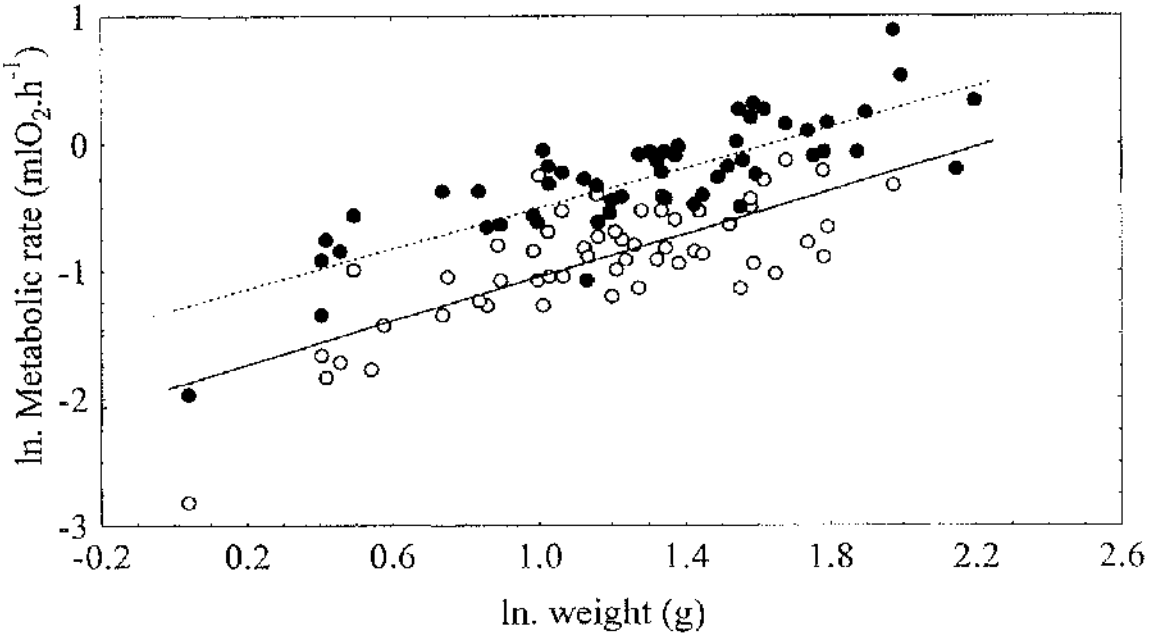


Fig. 2.4: The relationship between body weight (g) and standard (open circles) and active (closed circles) metabolic rates for juvenile salmon. Both axes are on a natural logarithmic scale.

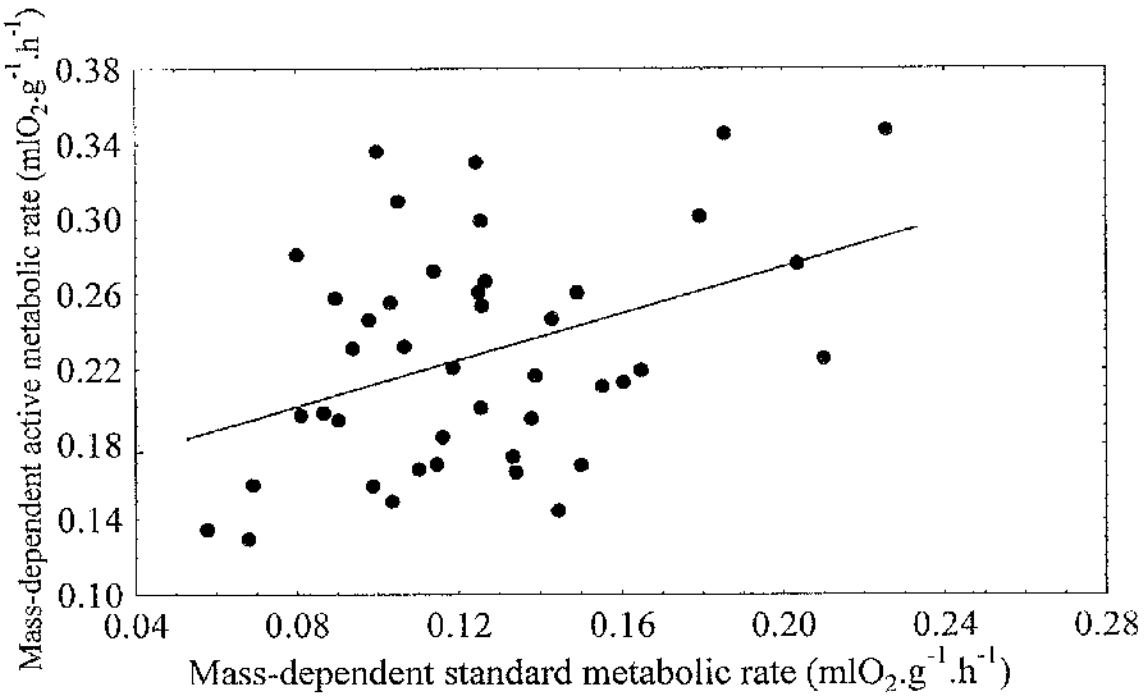


Fig. 2.5: The relationship between mass-dependent standard metabolic rate and mass-dependent active metabolic rate for juvenile salmon.

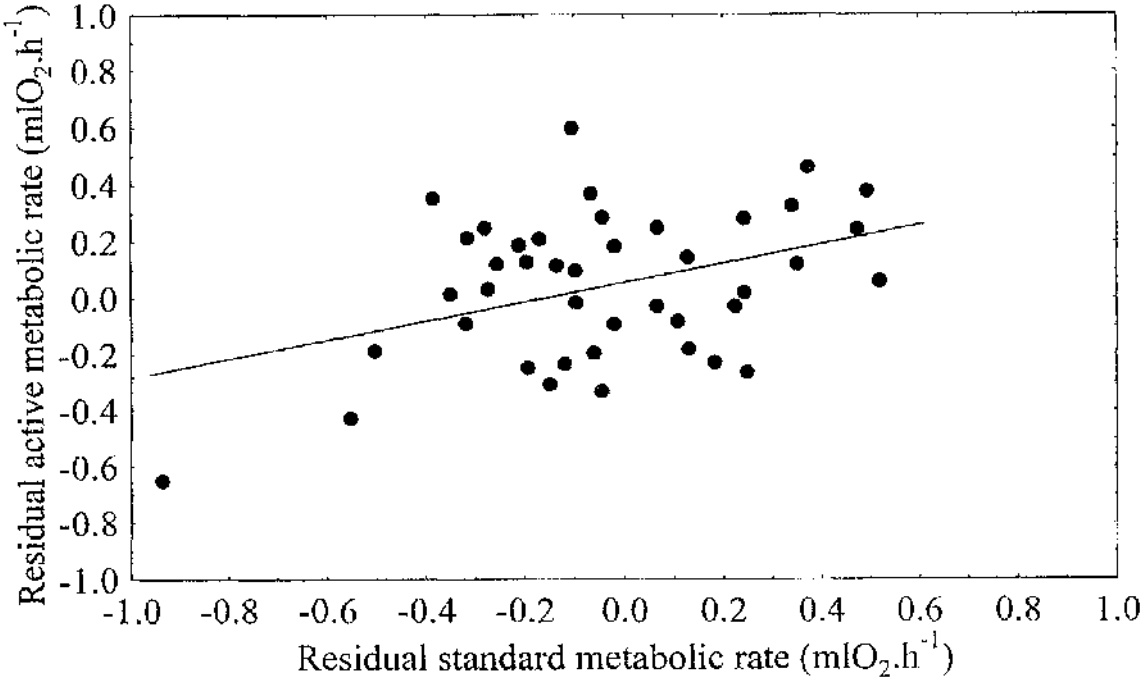


Fig. 2.6: The relationship between residual standard metabolic rate and residual active metabolic rate for juvenile salmon.

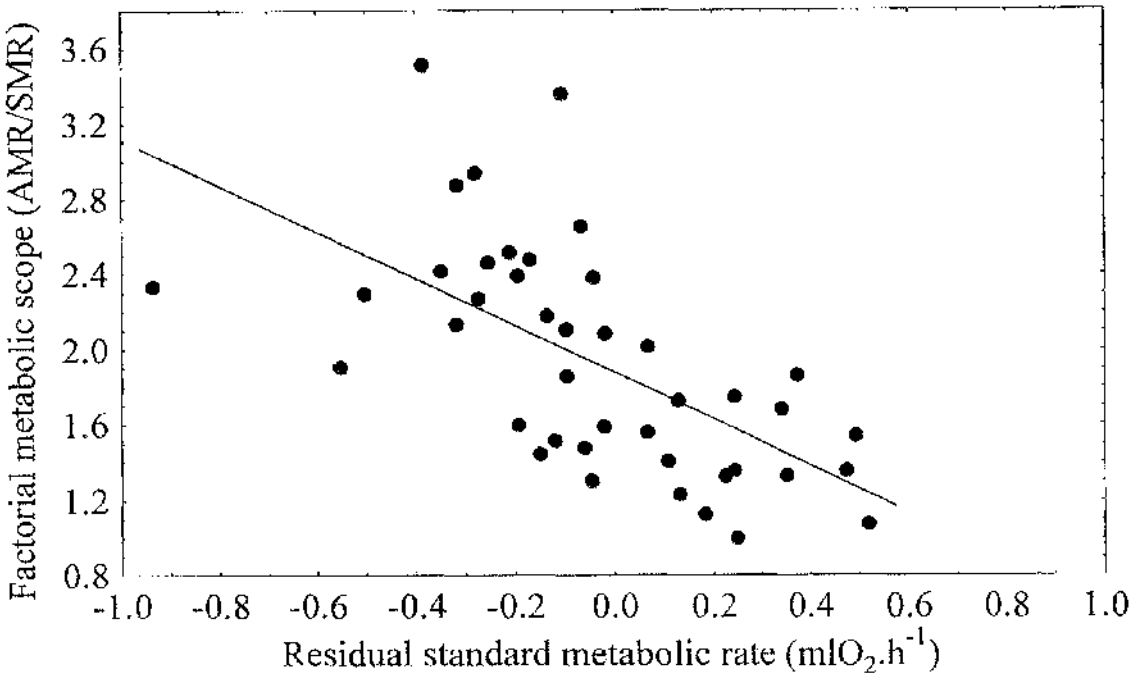


Fig. 2.7: The relationship between residual standard metabolic rate and factorial metabolic scope (active metabolic rate/standard metabolic rate) for juvenile salmon.

2.4. Discussion

It was apparent that the fish quickly became acclimated to the respirometry chambers, so that oxygen consumption gradually declined to a resting asymptote within 17 hours. Similar decreases to standard levels in respirometry chambers have been documented in roach (Wieser & Medgyesy, 1990), northern pike (Armstrong *et al.*, 1992), zebrafish (Lucas & Priede, 1992), and adult Atlantic cod (Reidy *et al.*, 1995). This suggests that oxygen consumption values measured 20 hours after the fish were placed in the respirometry chamber give a reliable measure of standard metabolic rate, and this protocol was used throughout the thesis.

The mass exponent (1.16±0.20 (=S.E)) of the regression equation relating standard metabolic rate to fish weight (Eq. 2.2) was greater than unity. This may be due to the very small size range of fish (0.17 - 0.95g); Wieser (1985) stresses the importance of determining metabolic rate over a wide range of sizes, although this was not possible for a study on first-feeding salmon, since they are quite uniform in size. Moreover, the mass exponent in Eq. 2.3 was less than unity (0.85±0.30), showing the variability in mass exponents from narrow size ranges of fish. There was no overlap in fish sizes between Eqs. 2.2 and 2.3, so the different mass exponents are not necessarily contradictory.

There was also considerable inter-individual variation in standard metabolic rate within each range of fish sizes, despite all fish being measured when unfed and at rest. Using oxygen consumption as a measure of standard metabolic rate in the mass-screening method discussed in this chapter was the only effective way to estimate individual relative metabolic rates for the numbers of fish necessary for the forthcoming

experiments. However, the salmon lived at ambient temperatures prior to being introduced to the testing temperature and so were not acclimated to it, although they were all treated in exactly the same way. This would therefore result in measurements of *absolute* metabolic rates being possibly misleading, but those of individual *relative* standard and active metabolic rates would be valid, and it is these relative measurements that are important in the forthcoming chapters.

The inter-individual variation was reported to govern pairwise relative dominance in juvenile salmon (Metcalfe *et al.*, 1995), fish with high residual standard metabolic rates tending to be more dominant than those with low residuals. This variation was unlikely to be a consequence of agonistic encounters, as dominant juvenile salmon tend also to have larger otoliths (an indicator of higher metabolic rate in salmonids; Mosegaard *et al.*, 1988; Wright, 1991) at first feeding (Metcalfe *et al.*, 1992), which occurs several days before initiation of aggressive behaviour (Dill, 1977).

Regression equations for standard and active metabolic rates both had similar mass exponents (SMR = 0.85, AMR = 0.83), so the regressions did not differ significantly in slope. There was also no relationship between weight and factorial metabolic scope. This implies that factorial metabolic scope did not increase with fish size, and was in fact mass-independent. Moreover, on a mass-dependent basis, the mass exponent for the relationship between standard and active metabolic rate was less than unity (displaying negative allometry), suggesting that active metabolic rate increases at a lower rate than standard metabolic rate with fish size. This contradicts a previous study, in which the mass exponent for the same relationship in rainbow trout was greater than unity (Wieser, 1985). Metabolic scope has previously been reported to increase with fish weight in sockeye salmon (Brett & Glass, 1973), charr (Beamish,

1978), Northern pike (Armstrong *et al.*, 1992), and zebrafish (Lucas & Priede, 1992). This study did not concur with their findings. However, the mean metabolic scope of 1.93 presented here is in close agreement with the metabolic scope expected for salmon of this size at the same temperature (Schmidt-Neilsen, 1984).

Despite evidence from the previously mentioned papers that metabolic scope increases with fish weight, there have also been studies stating that no relationship exists between scope and weight: Ivlev (1960) reported no difference between the mass exponents of standard and active metabolic rate in juvenile salmon, and Wieser & Forstner (1986) also found no relationship in juveniles of three species of cyprinid. This may also be due to the different weight ranges used in the studies, since Weiser (1985) has stressed the importance of determining metabolic rate over a wide range of sizes. The present study only measured metabolic rates of fish from 1.04-8.99g; similarly, Wieser & Forstner (1986) used a small size range of 0.001-0.400g. These studies contradict the accepted model for the development of active metabolism in poikilotherms that suggests that anatomical and physiological characteristics associated with a high active metabolic rate impose costs when at rest, giving a correspondingly high standard metabolic rate. Proposed characteristics for a high active metabolic rate are increased permeability of cell membranes that facilitates movements of metabolic substrates into cells; a concomitant of higher permeability may be 'leakier' cells and an increase in Na^+-K^+ transport that raises standard metabolic rates (Taigen, 1983).

However, Wieser (1984) and Goolish (1991) expressed caution in applying the same mass exponents to all stages of an animal's ontogeny. In small, fast growing fish such as juvenile salmon, metabolism associated with the viscera is higher than metabolism associated with red muscle. The former is metabolism associated with food processing,

and scales with negative allometry (mass exponent <1; Goolish & Adelman, 1988). This may explain the negative allometry in the relationship between mass-dependent standard and active metabolic rates shown here, and the lack of a relationship between size and metabolic scope. Despite the fish in this study being agitated to burst swimming performance (thought to express active metabolic rate; Dickson & Kramer, 1971; Wieser *et al.*, 1985; Pearson *et al.*, 1990; Reidy *et al.*, 1995), most of the measured active metabolic rate may have been due to visceral metabolism. Because different physiological activities are responsible for active metabolic rate (and hence metabolic scope) in different sized fish, it would seem unwise to use one single method of expressing active metabolic rate (e.g. swimming to exhaustion) across a wide range of animal sizes in order to generate a mass exponent (Goolish, 1991).

On a mass-independent basis, factorial metabolic scope was negatively correlated with residual standard metabolic rate, and the regression of residual active metabolic rate on residual standard metabolic rate had an exponent of less than unity. This suggests that active metabolic rate represents a 'ceiling' for metabolic activity on a mass-independent basis: if the basal, standard metabolic rate is higher, less scope for activity remains than if the standard level was lower. This has implications for Metcalfe *et al.*'s (1995) study on relative standard metabolic rate and dominance, which also used residuals to express inter-individual variation in standard metabolic rate, and assumed higher residual values would correspond to a larger metabolic scope (in that metabolic scope increases with mass-dependent standard metabolic rate; Brett, 1965; Priede, 1985). In fact the opposite seems to be the case. Consequently, fish with high residual standard metabolic rates that tend to be more dominant actually have a smaller metabolic scope within which they must carry out dominance-acquiring activities such

as aggression. More importance could therefore be attached to the fact that dominant fish have a relatively large standard metabolic rate, and a higher cost of maintenance. Instead of acquiring dominance through having a larger metabolic scope and being more physiologically able, they may have to be aggressive (and so acquire dominance) in order to monopolise a food source to maintain their higher cost of living.

Chapter 3: Feeding motivation and competitive asymmetries in territorial juvenile Atlantic salmon.

3.1 Introduction

Social dominance is determined by several asymmetries between individuals, such as size, age and sex (Arcese & Smith, 1985; Lemel & Wallin, 1993). However, competitive ability often seems not to conform to such fixed predictors of dominance; instead, the importance of status signals is conditional on the motivational state of contestants (Maynard Smith & Harper, 1988). Therefore, motivational state will also be an asymmetry that may affect the outcome of an interaction; hunger increases aggression and strengthens social hierarchies in birds (Andersson & Ahlund, 1991) and fish (Symons, 1968; Dill *et al.*, 1981), with the *proviso* that higher hunger levels increase competitive ability through higher feeding motivation (Bernstein, 1981; Milinski & Parker, 1991). In rainbow trout, dominance status increased with energy demand and subsequent feeding motivation, by elevating aggression to promote competitive exclusion (Johnsson & Bjornsson, 1994). However, fasted trout with a high energy demand were only dominant for a short time, since their high feeding motivation was eventually offset by declining energy reserves reducing their competitive ability (Johnsson *et al.*, 1996). Conversely, feeding motivation and hence tendency to compete will decrease as a fish nears satiation, for example, the distance moved to intercept prey decreases in coho salmon with decreasing hunger (Dunbrack & Orr, 1983; Dill & Fraser, 1984).

Moreover, in juvenile salmon differences in standard metabolic rate can account for differences in dominance. In pairwise contests, individuals with higher standard

metabolic rates (after controlling for body size) than their opponents are more likely to be dominant (Metcalfe *et al.*, 1995). It was hypothesised that individuals with a higher standard metabolic rate have a greater capacity for costly activities such as aggression, since Priede (1985) suggested that standard metabolic rate would correlate positively with metabolic scope. Consequently, Metcalfe *et al.* (1995) suggested that such fish may acquire dominance through a greater capacity for aggression (but see chapter 2).

Therefore, internal factors such as motivation and standard metabolic rate must be taken into account in dominance contests among fish as well as obvious asymmetries such as size. Furthermore, asymmetries in experience and/or knowledge must also be considered. Prior experience of either a site where contests occur or of the other contestant can contribute to resource holding power (Parker, 1974; Zayan, 1975; Henderson & Chiszar, 1977). The 'prior residence' effect was first described by Braddock (1949); in it the resident possesses knowledge of a territory (including its resource value). The resident is therefore more likely to expend energy in defence than an intruder, who is less likely to fight over a resource of unknown quality (Krebs, 1982). Also, individuals may be fearful in a novel environment, whereas a resident has become habituated to novel stimuli, making it better able to engage in aggression than an intruder (Figler & Einhorn, 1983). Dominance attributable to prior residence has been documented in a wide range of taxa. Site-related dominance was a highly significant asymmetry in predicting outcomes of contests between great tits (Sandell & Smith, 1991), differences in familiarity with an area had a decisive role in conflicts between convict cichlids (Henderson & Chiszar, 1977; Ratnasabapathi *et al.*, 1992) and dart poison frogs (Baugh & Forester, 1994), and dominance due to prior residence is widespread amongst insects (Fitzpatrick & Wellington, 1983; van Buskirk, 1986).

Juvenile salmonids are ideal animals for studying the relative effects of competitive asymmetries. They have often been used in studies of dominance (Metcalfe, 1989, 1991; Metcalfe *et al.*, 1989, 1990, 1992, 1995) and feeding motivation (Metcalfe & Thorpe, 1992*a*; Johnsson & Bjornsson, 1994; Bull *et al.*, 1996; Johnsson *et al.*, 1996). Moreover, there is variation of up to several weeks in the date on which juvenile salmonids emerge from a single redd and begin to search for territories (Gustafson-Marjanen & Dowse, 1983; Brännäs, 1987). Early emerging salmonids may therefore benefit from the asymmetry of prior residence in a natural situation. This chapter aims to study how feeding motivation varies with relative standard metabolic rate in juvenile Atlantic salmon, given that salmon with higher relative standard metabolic rates are more dominant (Metcalfe *et al.*, 1995), and salmonids with higher feeding motivation also tend to have a higher social status (Johnsson & Bjornsson, 1994; Johnsson *et al.*, 1996). I therefore test the hypothesis that juvenile salmon with high standard metabolic rates will have a correspondingly higher feeding motivation to fuel their greater cost of maintenance. Furthermore, the relative effects and interactions of a set of competitive asymmetries (relative size, relative standard metabolic rate, and prior residence) on the outcome of pairwise encounters in juvenile salmon is also investigated, and the standard metabolic rates of early and late emerging salmon are compared, to see whether early emerging fish have the hypothesised benefit of a higher relative standard metabolic rate (Metcalfe *et al.*, 1995) in addition to the potential advantages of prior residence.

3.2 Methods

3.2.1 Feeding motivation trials

The standard metabolic rates of 64 0+ juvenile salmon were measured at a constant temperature of 9°C from 11th June to 27th July 1995 (methods outlined in chapter 2). After measurement of standard metabolic rate, fish were placed singly in sections (25cm x 10cm, water depth of 5cm) of long raceways through which water flowed at a slow rate. Each section contained a small opaque shelter under which fish could hold station (Bull *et al.*, 1996). The fish were unmarked, being identified only by the order they were placed in the sections (salmon in respirometry chamber 1 placed in section 1, respirometry chamber 2 to section 2 *etc.*). The fish were constrained to their individual sections by upstream and downstream meshes, preventing them from moving to other sections and confusing identification.

The fish were allowed to settle for 48 hours and were not fed during this time, giving a total food deprivation time of 68 hours (including the settling time in the respirometry chambers). In this way all fish should have had equally empty stomachs; fish were not fed during the settling period because initial differences in feeding motivation would cause differences in stomach fullness by the start of the appetite trials, potentially affecting any subsequent measurement of feeding motivation. Feeding motivation measurements were carried out between 0900h and 1700h, on the third day after the fish were moved to the raceways. Seven trials were carried out in total; numbers of fish in each trial were 6, 13, 3, 11, 5, 13, 13 respectively. Feeding motivation was assessed as the response of a fish to five commercial food pellets, presented singly *ca.* 10cm upstream of the fish at intervals of 30 min. Responses were

scored as: 0 = no response, 1 = orientates head but does not move, 2 = turns back after initially moving towards food pellet, 3 = attacks food pellet but misses, 4 = ingests and subsequently rejects food pellet, 6 = consumes food pellet (*sensu* Metcalfe *et al.*, 1986; Bull *et al.*, 1996). The advantage of this scoring method is that it should provide a measure of feeding motivation as the scores included movement and intent of the fish, and not just intake rate. The mean of the five responses was used as an index of the feeding motivation of an individual fish. After the trials the fish were removed, weighed (g), measured (fork length, mm) and transferred back to a holding tank where they were fed *ad lib.*. Since fish were not weighed until after scoring for feeding motivation all the data were collected blind with regard to residual standard metabolic rate.

3.2.2 Dominance trials

Juvenile salmon from a single egg batch (0+ age class) were segregated into two groups on the basis of yolk-sac size a few days before the first fish were ready to feed. Fish with mostly absorbed yolk sacs were classified as early first-feeders, while fish with more of their yolk sac remaining were classified as late first-feeders. The standard metabolic rates of the juvenile salmon were measured at a constant temperature of 9°C (methods outlined in chapter 2) after the yolk sacs had been totally absorbed in both groups. After measurement of standard metabolic rate, the fish were anaesthetised, weighed (g) and measured (fork length, mm) for calculation of residual standard metabolic rate (see chapter 2). Measurements of metabolic rate were therefore made before any dominance trials, to control for the effects of winning/ losing encounters on

oxygen consumption. Early first-feeding fish (with faster yolk sac absorption and potentially higher standard metabolic rates) were then paired with late first-feeding fish to test for factors determining dominance. One randomly-chosen fish from each pair was marked with an alcian blue dye spot on the dorsal surface to aid identification.

When investigating the relationship between relative metabolic rate, relative size, and dominance, pairs of fish were introduced into small contest arenas simultaneously, and relative dominance status was assessed after a settling period of 48 hours. If the effects of prior residence on relative dominance were also being assessed, one fish was placed in the contest arena for 48 hours before a competitor was introduced, and relative dominance status assessed after a further 48 hours. In such prior residence trials, I alternated between marking the prior resident and the intruding fish to remove any bias associated with the mark itself. Furthermore, when the intruder was introduced into the contest arena (with a small hand net), the resident was similarly netted and released to control for any stress the intruder might have experienced when being caught and released. The intruder had no prior knowledge of the contest arena.

The contest arenas consisted of a single 24 x 11cm gravelled enclosure within each of twelve 41 x 31cm observation tanks. The enclosures were walled with plastic mesh to allow flow-through of water, and water depth was maintained at 10cm with standpipes. Two water inflow nozzles per enclosure provided a continuous water current through the enclosure. Observations were made through slits in a screen placed in front of the tanks, which allowed the observer to measure relative dominance without disturbing the fish. The gravelled, flat substratum of the arenas provided a more natural environment for the fish, in contrast to previous, similar studies which consisted of white, plastic V-shaped channels which were deliberately designed to

prevent the pairs of fish from swimming side by side (Metcalfe *et al.* 1990, 1992, 1995). Dominance was assessed using repeated feeding and positional trials, following a protocol similar to that adopted by Metcalfe *et al.* (1990, 1992, 1995) and Johnsson & Bjornsson (1994). The preferred feeding position was assumed to be upstream of the other fish and facing into the current, as this would ensure first access to food (Fausch, 1984). Six observations were recorded for each pair; one every 20 minutes. At each observation a commercial fish food pellet was dropped into the water current from a pipette (hidden by the screens). A scoring system was used to determine which fish was dominant: a fish scored one point each time it was furthest upstream and facing into the current, and another point for every food pellet ingested. If the food pellet was contested by both fish, the successful fish scored an extra point. The fish with the highest total score was considered to be the more dominant individual of the pair. Differences in scores within pairs of fish would range from 1: incomplete dominance, to 12: complete dominance.

Differences in residual standard metabolic rate for each pair were calculated after the trials, so again the behavioural data were collected blind with regard to relative standard metabolic rate. The fish were returned to a holding tank after the dominance trials and fed *ad lib.*, and were not used in subsequent dominance trials. This ensured that fish in future dominance trials had no prior knowledge of the contest arenas. Both simultaneous entry and prior residence experiments were carried out between June and August, 1994 and 1995.

3.3 Results

3.3.1 Feeding motivation

The 64 fish scored for feeding motivation had a mean weight of 0.44±0.03 (S.E.)g and fork length of 35.39±0.61mm. The mean residual standard metabolic rate (rSMR) was -0.003±0.003mlO_2.h^{-1} (range: -0.039 to 0.072mlO_2.h^{-1} respectivcly), calculated from Eq. 2.2 (Chapter 2). Since the experiment was carried out over 2 months, any seasonal trends in feeding motivation exhibited by all the fish could potentially obscure any effects of individual residual standard metabolic rate and size on feeding motivation. Therefore I tested the mean feeding motivation scores from each trial for any significant trends over time; there were no significant differences in mean feeding motivation between trials (one-way ANOVA; $F_{(6,57)} = 1.81$, p = 0.113, Fig. 3.1), which justified pooling the results from all the trials for subsequent analysis.

There was no significant relationship between size (fork length, mm) and feeding motivation ($r^2 = 0.001$, n = 64, p = 0.306). However, there was a weak but significant negative relationship between residual standard metabolic rate and feeding motivation ($r^2 = 0.043$, n = 64, p = 0.05, Fig. 3.2), implying that those fish with high residual standard metabolic rates have a lower feeding motivation than those with low residual standard metabolic rates. It might be argued that since fish with a high residual standard metabolic rate may be more dominant (see below), their lower feeding motivation might simply be due to their being in a better nutritional state at the start of the experiment. There was little evidence of this: condition factor (K = W(g)/(FL(mm))^3) was unrelated to feeding motivation ($r^2 = -0.016$, n = 64, p = 0.985). Moreover, there was little variation in condition factor amongst the experimental fish

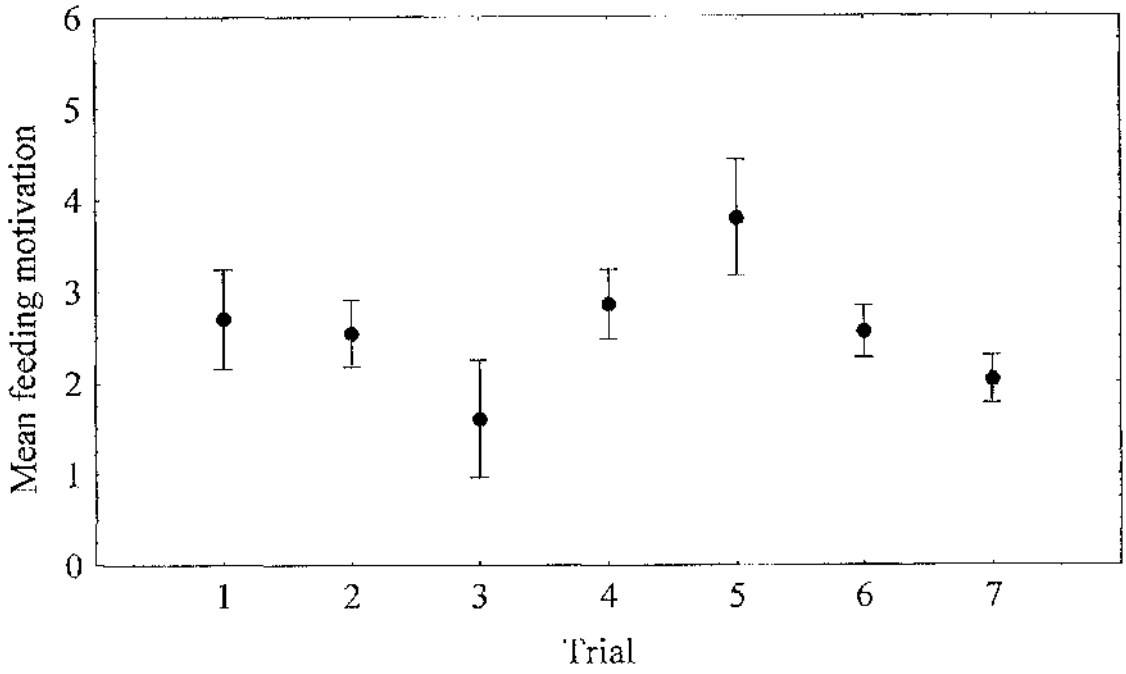


Fig. 3.1: Mean feeding motivations of juvenile salmon across 7 trials (n = 6, 13, 3, 11, 5, 13, 13 fish per trial). There was no significant difference in feeding motivation between trials (see text). Bars denote standard errors.

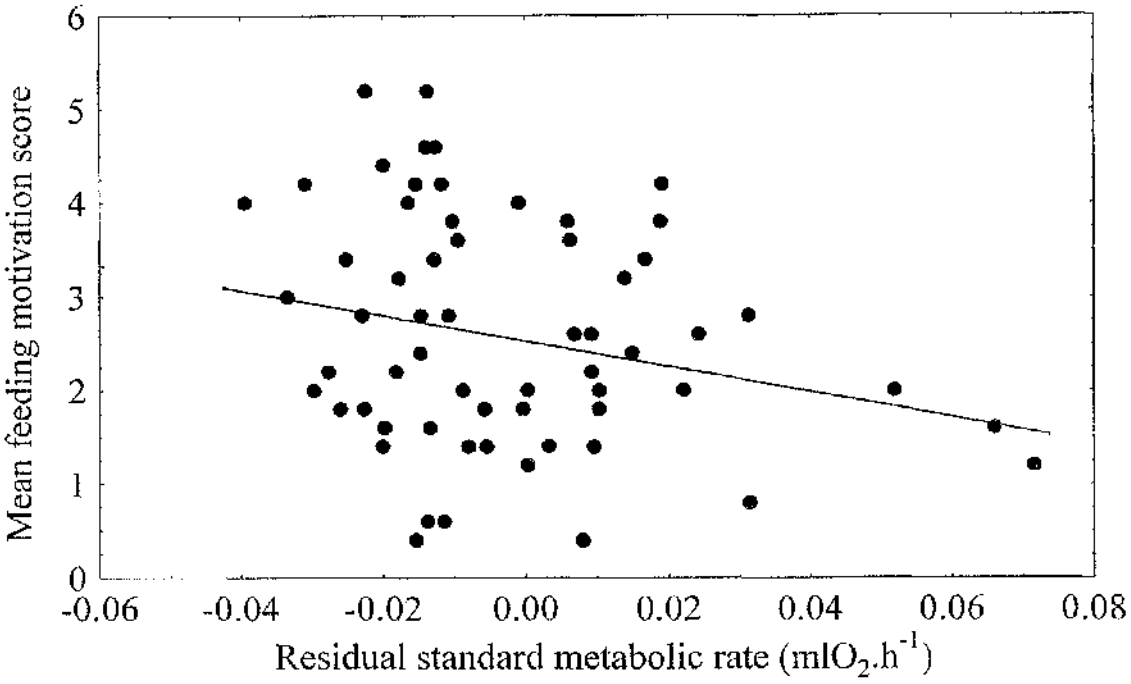


Fig. 3.2: The relationship between residual standard metabolic rate ($mlO_2.h^{-1}$) and individual mean feeding motivation in juvenile salmon.

(mean condition factor = 0.931±0.011), and condition was generally high. Therefore, differences in feeding motivation appear to be related to differences in residual standard metabolic rate between juvenile salmon, independent of nutritional state.

3.3.2 Dominance

In dominance trials where fish were introduced to contest arenas simultaneously, early first-feeding fish were paired with late first-feeding fish in 53 contests. Early fish did not differ significantly in size from late fish ('early' mean weight and fork length: 0.350±0.017 (S.E.)g, 34.1±0.5mm; 'late' mean weight and fork length: 0.368±0.021g, 34.3±0.6mm, n = 53; paired t-test comparing members of a pair, t = 0.368, 51 d.f., p = 0.714). However, early first-feeding fish did have significantly higher residual standard metabolic rates (rSMR) than late first-feeding fish ('early' mean rSMR = 0.003±0.006mlO_2.h^{-1}, 'late' mean rSMR = -0.013±0.006mlO_2.h^{-1}; paired t-test, t = 2.182, 51 d.f., $p<0.05$). The mean difference in percentage size by fork length between fish was 4.12±0.58% (range, 0.00-16.39, n =53), and the mean difference in residual standard metabolic rate between fish was 0.028±0.005mlO^2.h^{-1} (range, 0.001-0.174mlO_2.h^{-1}, n = 53), so there was considerable variation in relative standard metabolic rate between competitors.

In these 53 pairwise encounters, there was no size difference in 8 pairs, and in the remaining 45 pairs the dominant fish was the larger of the two in 22 (45.9%) of the pairs (mean percentage size difference = 4.71±0.80; Fig. 3.3*a*). However, the likelihood of being dominant did increase with the size difference, fish greater than

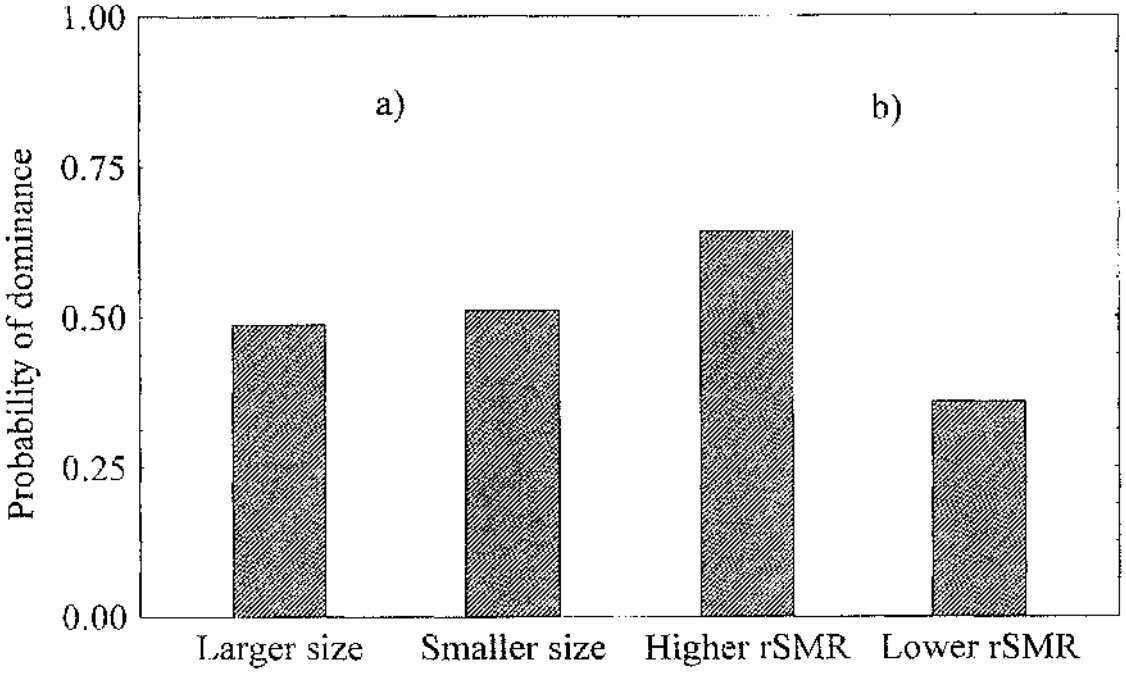


Fig. 3.3 (*a*) The probability of dominance for the earlier feeding member of pairs of juvenile salmon that were larger and smaller than their opponent (n = 22 and 23 respectively) in pairwise contests. Relative size did not significantly predict dominance (see text) and (*b*) the probability of dominance for the earlier feeding member of pairs of juvenile salmon with higher and lower relative standard metabolic rates than their opponents (n = 34 and 19 respectively). Juvenile salmon with higher relative standard metabolic rates were significantly more likely to acquire dominance (see text).

12% larger than their opponent invariably winning (Fig. 3.4). This size advantage was unlikely to be very important, since in 40 of the 53 dyads (75%) the size difference was less than 6% (Fig. 3.4). Furthermore, the size frequency distribution in the pairs is a realistic depiction of size differences for juvenile salmon at first feeding, as pairs of competing fish were picked at random with regard to size.

In contrast, 34 of the dominant fish (64.2%) had higher residual standard metabolic rates than their competitors (Fig. 3.3*b*). Hierarchical log-linear analysis showed that fish with higher relative standard metabolic rates had a significantly greater chance of acquiring dominance (Likelihood-ratio chi-square: $\chi^2_{LR} = 3.524$, 1 d.f., $p = 0.05$), whereas relative size did not significantly predict dominance ($\chi^2_{LR} = 3.066$, 1 d.f., $p = 0.216$). Relative standard metabolic rate was thus more important than relative size in determining dominance when neither competitor had prior knowledge of a potential territory.

A further 53 dyads of juvenile salmon were used to test the effect of prior residence on subsequent dominance. The mean mass and forklength of the fish was 0.464±0.017g and 36.4±0.4mm, and their mean residual standard metabolic rate was 0.000±0.003 $mlO_2.h^{-1}$, ranging from -0.054$mlO_2.h^{-1}$ to 0.101$mlO_2.h^{-1}$. The mean percentage size difference between prior residents and intruding fish was 5.9±0.9%, ranging from 0.0 to 33.7%. The mean difference in residual standard metabolic rate amongst pairs was 0.027±0.003$mlO_2.h^{-1}$, ranging from 0.001 to 0.128$mlO_2.h^{-1}$.

Significantly more resident juvenile salmon won the trials than intruders: 40 out of 53 dyads were won by the resident (75.5%; goodness-of-fit test, $\chi^2 = 29.380$, 1 d.f., $p<0.0001$). The mean dominance score for dominant residents was 9.57±0.53, compared to 7.31±1.25 (n = 13) for dominant intruding fish. I also investigated

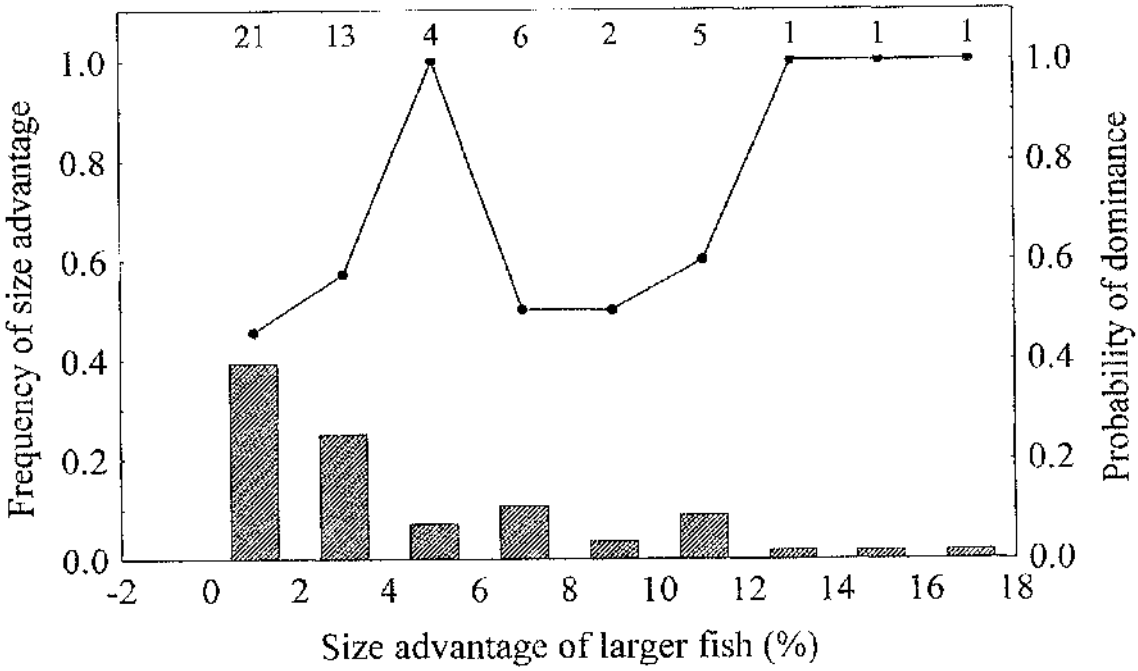


Fig. 3.4: The frequency distribution of the size discrepancy in 53 pairs of juvenile salmon (hatched bars), and the probability of dominance for the larger fish of a pair across the range of size discrepancies (closed circles). There was a general trend of increasing probabilities of dominance with increasing size advantage of the larger fish (Spearman's rank correlation: $R_s = 0.682$, $n = 9$, $p<0.05$), but large size discrepancies were rare (the numbers along the top denote sample sizes for each size group).

whether relative standard metabolic rate and relative size had any effect on the outcome of the trials, despite the asymmetry of prior residence, and whether there was any significant interaction between the three asymmetries. Table 3.1 presents a detailed breakdown of the characteristics of dominant fish, with regard to prior residence, relative standard metabolic rate and relative size. It is apparent that within the powerful asymmetry of prior residence, larger size confers a greater probability of dominance (0.92 for larger versus 0.62 for smaller residents, 0.38 versus 0.08 for intruders), and greater relative standard metabolic rate confers a greater advantage when the resident is smaller than the intruder (probability of dominance for smaller residents with high rSMR: 0.72, smaller residents with low rSMR: 0.45). Furthermore, in larger dominant intruders, a higher relative standard metabolic rate appears to confer a further advantage (probability of dominance = 0.55, compared to 0.28 if the intruder had a lower relative standard metabolic rate). Hierarchical log-linear analysis was used to test interactions between the three asymmetries. Prior residence was a significant predictor of the outcome of dominance trials (χ^2_{LR} = 19.239, 3 d.f., $p<0.0005$), concurring with the ordinary goodness-of-fit test (see above). Second-order, or two-way effects, using prior residence interacting with relative standard metabolic rate and relative size were almost significant (χ^2_{LR} = 7.320, 3 d.f., $p = 0.062$). However, the interaction term between prior residence and relative size did significantly predict dominance (partial chi-square: χ^2 = 6.805, 1 d.f., $p< 0.01$), whereas the interaction between prior residence and relative standard metabolic rate did not (partial chi-square: $\chi^2 = 0.170$, 1 d.f., $p = 0.680$).

Therefore, involving all three variables did not significantly improve the predictive power of the model. The effect of prior residence alone best modelled the outcome of

Table 3.1: Probabilties of dominance for 53 dyads of juvenile salmon with differing asymmetries (prior residence, relative standard metabolic rate and relative size).

Status	Relative size compared to opponent	Mean percentage difference in size ±S.E. compared to opponent	Relative standard metabolic rate compared to opponent	Mean differences in residual standard metabolic rate ±S.E. ($mlO_2.h^{-1}$)	Probability of dominance (dyads won: total dyads)		
Resident	Larger	5.82±1.19	Higher	0.041±0.013	0.75 (40:53)	0.92 (22:24)	0.92 (12:13)
			Lower	-0.012±0.036			0.91 (10:11)
	Smaller	-7.11±1.29	Higher	0.022±0.005		0.62 (18:29)	0.72 (13:18)
			Lower	-0.030±0.011			0.45 (5:11)
Intruder	Larger	6.53±2.83	Higher	0.027±0.005	0.25 (13:53)	0.38 (9:29)	0.55 (6:11)
			Lower	-0.029±0.011			0.28 (5:18)
	Smaller	-1.50	Higher	0.012		0.08 (2:24)	0.09 (1:11)
			Lower	-0.011			0.08 (1:13)

the trials, with relative size the next most important asymmetry, through its interaction with prior residence (larger residents being more likely to win than smaller; Table 3.1). Incorporation of relative standard metabolic rate did not significantly improve the model.

3.4 Discussion

Juvenile salmon with high residual standard metabolic rates had significantly lower feeding motivation than fish with low residual standard metabolic rates. This contradicts the hypothesis that fish with relatively high costs of maintenance and energy demand will have a higher feeding motivation in order to survive. Consequently, fish with greater energy demands must balance their energy budget by alternative methods. Energy expended in intercepting food items is a substantial proportion of overall energetic costs in salmonids. In a study on wild coho salmon, Puckett & Dill (1985) reported that although feeding took up only 13% of the coho's time, it accounted for 26% of their energy costs, so maintaining a basic energy requirement is itself energetically expensive. It has already been stated that salmon with higher relative standard metabolic rates have a greater probability of dominance (Metcalfe *et al.*, 1995), so it would appear that they are not acquiring dominance through the asymmetry of greater feeding motivation, as documented in fasted rainbow trout (Johnsson *et al.*, 1996) and salmonids manipulated with exogenous growth hormone (Markert *et al.*, 1977; Johnsson & Bjornsson, 1994). Instead, fish with higher relative standard metabolic rates probably acquire dominance simply through greater

aggression. It was shown in chapter 2 that such fish have a smaller metabolic scope than fish with low relative standard metabolic rates. If this is so, they may opt for a strategy of elevating aggression at the expense of elevated foraging, as both are costly within a limited metabolic scope: movements associated with aggression and feeding such as acceleration and turning can be six times more energetically expensive than forced swimming (Webb, 1991; Krohn & Boisclair, 1994). Furthermore, within a salmonid social hierarchy aggression will increase the probability of acquiring a feeding territory (Fausch, 1984; Puckett & Dill, 1985; Grant, 1990). Since salmonid social hierarchies can persist for several months (Jenkins, 1969), fish with a high relative standard metabolic rate may be able to guarantee a food source to maintain their greater energy demand for a considerable length of time if they use aggression to secure a territory. The territorial salmonid will have a virtual monopoly on food items passing through its territory (Elliott, 1984, 1990), so even by opting to reduce costly levels of foraging (measured as feeding motivation), it may still be able to maintain its greater cost of maintenance.

Although fish in the feeding motivation trials were not subsequently tested for dominance, the absence of competitors in the raceways should not have altered the feeding motivation of the fish, provided that lower feeding motivation is indeed an adopted strategy. This was the case in a previous study on juvenile salmon, where subordinate Lower Modal Group fish maintained a reduced feeding motivation in the absence of a competitor, as they had adopted a strategy of low appetite and reduced growth (Metcalfe *et al.*, 1988).

During dominance trials when pairs of juvenile salmon where placed into the contest arena simultaneously, relative size did not significantly predict dominance. This

concurs with previous studies on juvenile salmon, where large size was found to be a consequence of dominance and not a cause (Huntingford *et al.*, 1990). However, when there was a large size discrepancy (>12%), larger fish were almost certain to become dominant. This, in turn, agrees with the established tenet that large size is a superior asymmetry in determining dominance; together with weapons and prior experience, size is one of the principal indicators of resource holding power (Maynard Smith, 1982; Turner & Huntingford, 1986). It has been well documented in conferring dominance in birds (Garnet, 1981; Järvi & Bakken, 1984), fish (Francis, 1983; Abbott *et al.*, 1985; Johnsson, 1993), mammals (Booth & Parrot, 1986) and invertebrates (Evans & Shehadi-Moacdieh, 1988; Glass & Huntingford, 1988; Wells, 1988). However, in the case of first-feeding juvenile salmon, where there is relatively little variation in size, size-based dominance will be a rare event, and other asymmetries must account for relative social status.

In agreement with a previous study (Metcalfe *et al.*, 1995), size-controlled differences in relative standard metabolic rate significantly predicted the outcome of dominance trials when neither fish had prior residence. The relationship between relative standard metabolic rate and dominance was not so pronounced as in the previous study, in which there was a significant relationship between the degree of difference in standard metabolic rate and subsequent probability of dominance. However, the study by Metcalfe *et al.* (1995) tested dominance in V-shaped white plastic raceways, and may have made existing differences in dominance more pronounced since pairs of fish could not swim side by side, and the fish furthest upstream was credited as being more dominant. Flat, gravelled substrata were used in this study for a more natural setting. These occasionally resulted in the two fish

swimming side by side, potentially obfuscating the measurement of dominance, especially as the fish with the lower relative standard metabolic rate (and therefore possibly the subordinate) may have had a higher feeding motivation.

However, the semi-natural conditions of the contest arena may allow for a more robust test of the hypothesis, and since the data obtained during the present study agree with those of Metcalfe *et al.* (1995), they only reinforce the hypothesis that differences in standard metabolic rate can predict dominance in pairs of juvenile salmon.

In dominance trials investigating the effects of prior residence, prior residents were indeed far more likely to acquire dominance after as little as 48 hours at a site. This effect concurs with previous studies that state that prior residence determines dominance when the size difference is small (Zayan, 1975; Henderson & Chiszar, 1977; Figler & Einhorn, 1983; Beaugrand & Beaugrand, 1991; Beaugrand *et al.*, 1991; Ratnasabapathi *et al.*, 1992; Beaugrand *et al.*, 1996). After prior residence the next most important asymmetry was relative size, larger residents and intruders having a greater probability of dominance than smaller ones. This means that the two asymmetries influence dominance through an additive process, so that an intruder can potentially offset its disadvantage if it has a large enough size advantage. This is also in agreement with previous studies where asymmetries in size and prior residence or information work together to determine the probability of dominance (Pitcher et al., 1986; Wazlavek & Figler, 1989; Beaugrand *et al.*, 1991; Turner, 1994; Beaugrand *et al.*, 1996).

Relative standard metabolic rate had no real contributory effect in determining dominance when prior residence was included as an asymmetry. This may be due to the

overriding effect of prior residence. In such situations, the only way to dominate and displace a prior resident would be to have a considerable size advantage, which is a potent and obvious status signal (Turner & Huntingford, 1986). This leads to relative size being statistically the second best predictor of dominance. Prior residence or experience may have great importance in salmonid social hierarchies, as their relative long term stability (Jenkins, 1969) is a consequence of using experience as a social cue, as opposed to a greater reliance on continual assessment of status signals in intermittent or short term hierarchies (Abbott *et al.*, 1985; Bégin *et al.*, 1996), such as those in mouthbrooding cichlids (Turner, 1994).

Early first-feeding salmon had significantly higher standard metabolic rates than late first-feeders. This is unsurprising, as early first-feeders use a greater amount of their yolk reserves over a set period of time due to their high standard metabolic rate, and must switch to exogenous food earlier (Metcalfe *et al.*, 1995). Early first-feeders emerge from the gravel redds and establish feeding territories sooner (Mason & Chapman, 1965; Fausch & White, 1986; Chandler & Bjornn, 1988). Therefore fish with higher residual standard metabolic rates may also gain dominance advantages indirectly, since they are more likely to become prior residents.

However, emerging too early can result in heavy mortalities from predation (Brännäs, 1995), as the earliest emergers do not enjoy the 'dilution effects' resulting from the presence of many conspecifics. Newly emerged salmonids are especially vulnerable to predation since they persist in vertical swimming movements until they reach a state of neutural buoyancy (Dill, 1977; Godin, 1982). Conversely, late emergers often suffer from habitat saturation, emerging to find no suitable unoccupied feeding habitats (Brännäs, 1995). Consequently, they must migrate further downstream

to inferior feeding sites (Elliott, 1989). Therefore juvenile salmonids tend to emerge synchronously over an approximately three night period (Gustavson-Marjanen and Dowse, 1983), in order to offset the opposing risks from predation and habitat saturation. Although prior residence can have strong effects after less than three days (48 hours in this study), many juveniles emerging within such a short time could relegate the asymmetry of prior residence to a comparatively minor role in the natural world, and relative standard metabolic rate could play a greater part as an asymmetry in determining dominance.

Chapter 4: The effects of metabolic rate and prior residence on aggression and growth in juvenile Atlantic salmon.

4.1 Introduction

It is well known that differences in competitive ability in territorial species have major short- and long-term consequences. Even in the absence of strict territories, individuals of high status in a dominance hierarchy and good competitive ability may obtain preferential access to resources, such as food or mates, have a higher survival rate (Huntingford & Turner, 1987), and higher growth rates (Metcalfe *et al.*, 1989; 1990). Juvenile Atlantic salmon have been extensively studied in this respect. Together with other salmonids, their life history is highly plastic (Thorpe, 1989). Within a single year class of juvenile salmon wide discrepancies in growth rate soon occur, in as little as four months after emergence. Juvenile salmon exceeding a threshold growth rate by August of their first year will metamorphose into the marine smolt phase the following spring, forming an Upper Modal Group (UMG), whereas slower growing salmon (the Lower Modal Group, LMG) will defer metamorphosis for up to 8 years (Thorpe, 1977; 1989; Metcalfe & Thorpe, 1990).

It has been shown that relative dominance and competitive ability of juvenile salmon in the first few months post-emergence influence subsequent life-history strategies through their effect on growth rates (Metcalfe *et al.*, 1989; 1990; Metcalfe, 1991). Juvenile salmonids in general are territorial, and work on other salmonids such as brown trout has shown that the inability of a young salmonid to acquire a feeding territory will result in a forced emigration downstream, resulting either in taking up

inferior feeding sites or in starvation (Elliott, 1984; 1990). The consequences of differences in competitive ability are therefore well understood, although the differences in physiology and behaviour underpinning individual life-history decisions have been relatively neglected.

Recent studies, however, have established links between the physiology of an individual animal and its subsequent behaviour. Work on brown trout showed that a fish's prospects of establishing a territory and surviving are correlated with the relative size of its otoliths at emergence (Mosegaard, 1990; Titus & Mosegaard, 1991). Further work on Atlantic salmon demonstrated that otolith size was not related to fish size at first feeding, but was correlated with dominance status (Metcalfe *et al.*, 1992). Furthermore, evidence suggested that otolith growth is more closely linked to metabolic rate than to somatic growth rate (Wright *et al.*, 1990; Wright, 1991), implying that dominant fish with larger otoliths at first feeding have higher metabolic rates. This was directly tested in pairwise dominance interactions: juvenile salmon with higher standard metabolic rates (SMR), after controlling for size, were indeed found to be more dominant (Metcalfe *et al.*, 1995). A similar relationship has been found interspecifically in spinyhead and roughhead blennies, spinyheads gaining better feeding grounds through a higher standard metabolic rate which was hypothesised to give them an advantage in agonistic interactions (Clarke, 1992).

It has also been suggested, however, that subordinate salmonids, forced to occupy less profitable feeding stations, may adopt a strategy of minimizing energy expenditure, such as maintaining stations in areas of low current. This reduces metabolic costs to a minimum so that subordinates may still continue to grow, despite the low abundance of drifting food at these sites (Metcalfe, 1986). Therefore it has been suggested that

under conditions of low prey abundance the advantages of a high metabolic rate (conferring dominance) could be negated, the environmental conditions instead favouring individuals with lower metabolic rates and hence lower energy demands for survival and growth (Titus, 1990).

In salmonids, a confounding variable in elucidating any links between individual physiology and subsequent aggressive and foraging behaviour is prior residence of a territory (see chapter 3). Juvenile Atlantic salmon exhibit a normally distributed temporal pattern of emergence from both their natural spawning grounds and from artificial redds (Gustavson-Marjanen & Dowse, 1983; Brännäs, 1987) with a duration of approximately two weeks, although the majority tend to emerge synchronously over a three night period (Gustavson-Marjanen & Dowse, 1983). Early emerging juveniles are competitively superior to their later emerging conspecifics, by being first to acquire the available territorial space, and are also larger by the time other juveniles emerge (Mason & Chapman, 1965; Chandler & Bjornn, 1988; Metcalfe & Thorpe, 1992*b*). Such differences in competitive ability due to relative time of emergence could obscure differences in competitive ability due to physiology.

Many previous studies of salmonid behaviour have taken place in laboratory tanks, and are unrealistic in that fish may not be setting up true territories as would occur under natural conditions. Therefore this chapter aims to investigate further the relationship between metabolic rate and social status, and the behavioural mechanisms conferring dominance, in the semi-natural setting of an artificial stream. The results of two separate experiments are presented. In experiment I, I manipulated food abundance for two groups of fish (one fed *ad lib.*, the other on reduced rations), to investigate the costs and benefits of having a high standard metabolic rate; juvenile

salmon with a high standard metabolic rate might ordinarily become dominant with plentiful food, but may be disadvantaged when food becomes limited.

Because prior residence is such a confounding variable in studying causal links between physiology and behaviour, and how behaviour influences subsequent success (Stamps & Krishnan, 1994), the second experiment (experiment II) tested the relative effects of prior residence and differences in metabolic rate on subsequent behaviour and success, by releasing groups of juvenile salmon into the stream sequentially. It also examined which individuals obtained which territories within each group of introduced fish, given the virtually untested assumption that the best territories will go to individuals of highest rank (Maynard Smith, 1974).

4.2 Methods

4.2.1. Methods for experiment I

In April 1994 the standard metabolic rates of 48 11-month old juvenile salmon were measured at a constant temperature of 9°C, and their residual standard metabolic rates (rSMR) calculated (see chapter 2 for full account of respirometry methods). The fish (mean fork length of 72.0±3.4 (S.E.) mm) were full siblings reared under laboratory conditions at the University Field Station, Rowardennan, and were divided into two groups of 24, designated as a control and an experimental group. To keep size differences, and potential size effects, to a minimum within each group (so increasing the chances of revealing any effects of metabolic rate) the smaller fish were assigned to the control group and the larger fish to the experimental group (mean initial fork

lengths, 63.9±8.8 (S.E.) and 80.1±8.3 mm respectively). Each fish was marked prior to the experiment with combinations of alcian blue dye spots on both sides so that the fish were individually recognisable when viewed laterally.

The two groups of fish were placed in the two separate straight arms of a U-shaped artificial stream. The arms of the artificial stream were both 3m long and 0.55m wide, and were landscaped with gravel (mean diameter of gravel = 0.03±0.02m) and small pebbles (mean diameter of pebbles = 0.10±0.03m) into an identical series of pools and riffles to simulate a stream setting (Fig. 4.1), consisting of three pools separated by two riffles. Fish were kept within each arm by upstream and downstream mesh screens. The depth of each pool was 0.28m, with a mean water velocity of 0.11±0.01ms^{-1}. The two riffles were situated 1m and 2m downstream of the first screen, and were 0.19m deep, with a mean water velocity through them of 0.15±0.01ms^{-1}.

Each arm of the flume was partitioned into thirty 0.1m wide strips using marks on the inner glass-sided wall and the opposite opaque wall. This enabled the observer to read positions of fish in terms of zones individually numbered from the upstream ends of the two arms.

Automatic feeders were hung above the most upstream part of the two sections, to allow food to drift downstream towards the fish. The control group (group 1) was fed *ad lib.* on commercial pelleted slow-sinking food dispensed in small amounts every 30 minutes 24 hours a day. The feeder for the experimental group (group 2) was switched off for the first stage of the experiment (five weeks), although a very small amount of uneaten food from the control group was recirculated into the section of the flume occupied by the experimental fish. The experimental group was placed on an identical food regime to the control group for the second stage of the experiment (three weeks).

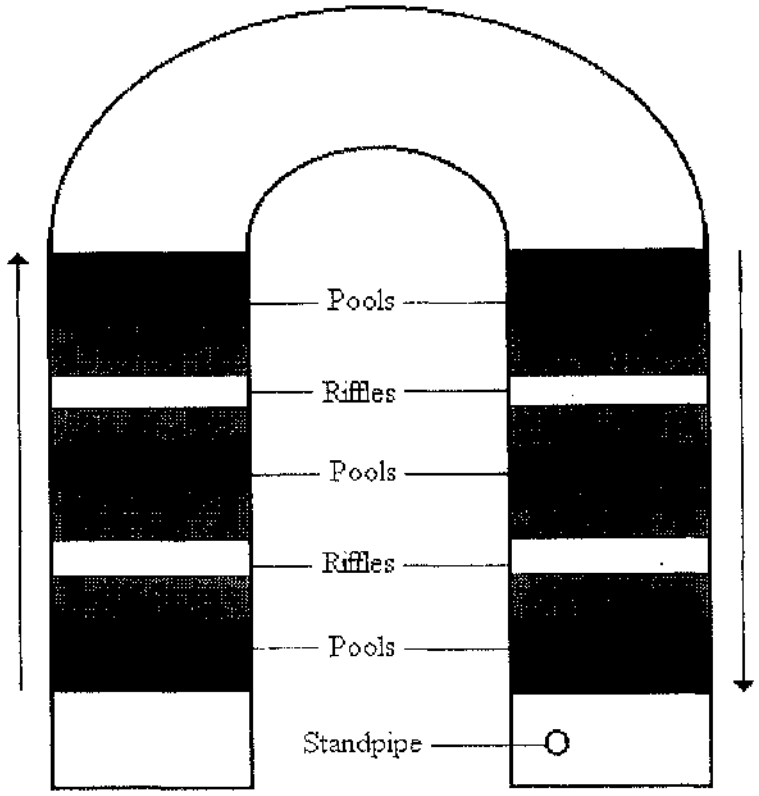


Fig. 4.1: Plan view of the artificial stream. The arrows denote direction of water flow. Water drains from the right hand side and is circulated through a pump. The intermediate hatching denotes slope, the darkest corresponding to pool areas. Each arm is 3m long and 0.55m wide.

Three one hour behavioural observations of the fish were made every day within the time periods 0900-1200, 1400-1700 and 1800-2000h for the duration of the experiment. Observations consisted of recording during scan samples the distance of each fish downstream from the feeder (i.e. the zone occupied) and whether the fish was touching the substratum or swimming in the water column. The rate of aggression was measured by observing each fish in turn for a one minute period and recording the number of interactions and the identities of the attacking and attacked fish. Aggression was defined as charges towards a conspecific; repeated charges were counted as separate incidents. This method was chosen because the fish initiating aggression invariably won, the attacked fish swimming away from the aggressor.

Owing to changes in the total number of fish present during the course of the experiment (due to mortality), the rate of aggressive interactions was standardised by dividing the number of aggressive interactions by the number of fish present, giving aggressive interactions $fish^{-1}$ $minute^{-1}$.

Both groups of fish were removed and anaesthetised once a week to be weighed (to the nearest 0.01g) and fork lengths measured (to the nearest 0.1mm), and were then allowed to settle for 24 hours after replacement before any further behavioural observations were taken. The fish recovered from anaesthesia quickly, resuming feeding and aggressive activity, and resumed their favoured positions almost immediately. Size data were used to calculate weekly specific growth rates (percentage change in weight per day). The observations were carried out from May to July 1994, a total number of 64 observation days and 192 observation sessions, under ambient photoperiod and temperature conditions. The percentage of fish present that were detected in each observation session was high (90.0$\pm$4.0(S.E.)%); there was no

evidence of bias towards fish being seen only when involved in aggression or when in a particular location.

4.2.2 Methods for experiment II

In August 1994 the standard metabolic rates of three successive randomly-chosen groups of 0+ juvenile salmon were measured at a constant temperature of 9°C, and their residual standard metabolic rates (rSMR) were calculated (see Chapter 2 - general respirometry methods). The fish were full siblings, previously reared under hatchery conditions at the University Field Station, Rowardennan. The three groups consisted of 14, 17, and 11 salmon respectively and were introduced into the artificial stream exactly seven days apart in order of group number. As a consequence, the fish in the three groups were of similar size at any one time but differed in average size at the time each was introduced to the stream: mean fork lengths at the time of introduction were 52.2±0.9 (S.E.)mm (group 1), 53.1±0.7mm (group 2), and 57.0±1.2mm (group 3) (ANOVA: $F_{(2,39)}= 7.13$, $p< 0.005$). In this experiment the entire length of the artificial stream was used, the U-bend being a long (1.25m) pool with a depth of 0.28m and a mean water velocity of 0.11±0.01 (S.E.)ms^{-1}, with an identical gravelled substratum to that of the arms. The arms were each landscaped into the same pattern of three pools (0.28m deep) and two riffles (0.19m deep), as in experiment I. Frozen *Daphnia* were thawed out in a reservoir above the most upstream part of the artificial stream. The reservoir received a constant slow inflow of water and overflowed into the artificial stream, maintaining a relatively constant, low influx of

prey items into the water. The reservoir was replenished thrice daily with frozen *Daphnia*, after each observation session.

As in experiment I, fish were marked on both sides with a combination of alcian blue dye spots to aid identification, and aggression, position and growth were measured using the same methods as for that experiment. Individual feeding rates were also measured: each fish was observed for one minute per observation session and the number of movements towards food recorded as feeding attempts (attempts.min^{-1}). Successful prey capture rates (items.min^{-1}) were also recorded within feeding attempts.

Once the favoured feeding positions of the fish were established, defined as the position where each individual fish spent the greatest percentage of its time, the quality of these positions was assessed by catching prey drift in a mesh net (15x20.5cm) suspended in the water column for five minutes. The sampled prey were dried out and the dry weight of food passing each point per minute calculated. Water velocity at the same sampling sites was measured with an OTT flow-meter. The experiment was carried out from August to October 1994, a total of 60 observation days and 180 observations.

4.3.1 Results for experiment I

4.3.1.1 Group effects on growth and aggression

Changes in fish size during the course of the experiment are presented in Table 4.1. As mentioned in the methods, fish in group 2 (experimental group) were larger than group 1 (control group) at the start of the experiment. This was deliberate, so as to

Table 4.1: Mean sizes of group 1 (control) and group 2 (experimental) fish at the end of each week in experiment I (group 2 fish were on reduced rations during weeks 1-5).

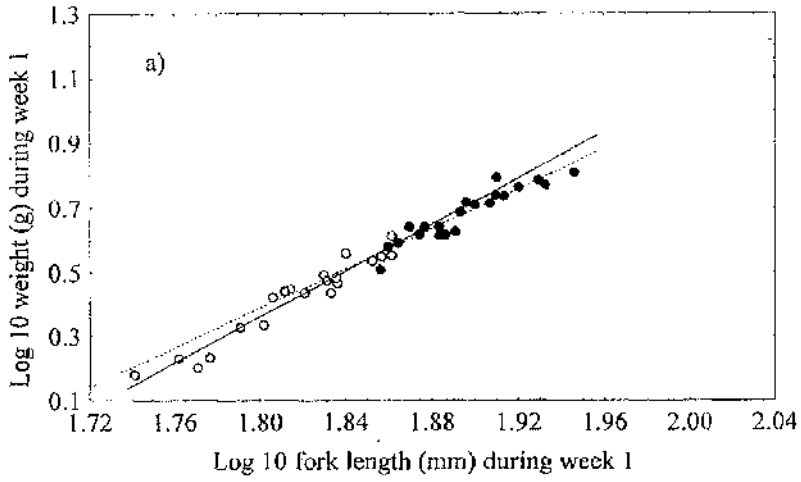
Week	Group 1		Group 2		t-test between groups by weight (g)
	Mean fork length (mm) ± S.E. (n)	Mean weight (g) ± S.E. (n)	Mean fork length (mm) ± S.E. (n)	Mean weight (g) ± S.E. (n)	
1-2	66.87±1.37 (20)	2.86±0.21 (20)	79.79±0.89 (22)	4.86±0.18 (22)	**
3	70.22±1.61 (17)	3.70±0.31 (17)	80.22±0.79 (17)	5.28±0.18 (17)	*
4	74.69±1.70 (17)	4.60±0.38 (17)	81.56±0.99 (13)	5.18±0.21 (13)	NS
5	79.99±2.57 (13)	5.78±0.64 (13)	82.61±1.36 (10)	5.38±0.39 (10)	NS
6	86.32±2.71 (12)	7.48±0.82 (12)	86.95±1.81 (10)	7.21±0.53 (10)	NS
7	89.48±2.39 (12)	8.78±0.98 (12)	92.27±2.45 (9)	8.97±0.80 (9)	NS
8	91.80±2.39 (11)	8.77±0.83 (11)	98.76±2.37 (7)	10.63±1.02 (7)	NS

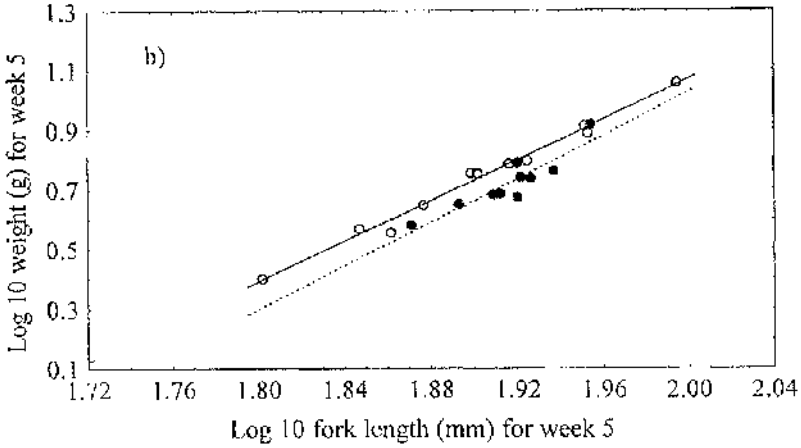
N.b.: "**" denotes significance at $p < 0.0001$, "*" denotes significance at $p < 0.001$.

reduce possible size effects within groups and highlight effects of variation in residual standard metabolic rate. However, both groups were similar in size by the end of the period that group 2 received reduced food (week 5), indicating that the experimental manipulation had affected the growth of group 2. Between-group differences in body condition were analysed for each of the eight weeks of the experiment by comparing the log10 transformed regressions of fish weight (g) against fork length (mm) of each group, using analysis of covariance (Table 4.2). There were no significant differences between the regression slopes of the two groups for the duration of the experiment. However, there were significant differences in elevation from week 3 to week 5 (the last week of reduced food for group 2), group 2 having the lower elevation (i.e. a lower body weight for a given fork length). This implies that group 2 maintained skeletal growth (fork length) at the expense of body weight, which did not increase at the same rate. Regression elevations did not differ significantly between the groups during the period of *ad lib.* feeding for group 2 (weeks 6-8), implying that group 2 fish quickly recovered condition. Fig. 4.2*a* shows the relationship between log10 weight (g) and log10 fork length (mm) for both groups at the start of the experiment (combined $r^2 = 0.967$, $n = 47$, $p<0.0001$), while Fig. 4.2*b* shows the same relationship during week 5; group 2 is similar to group 1 in fork length but the fish are significantly lighter in weight (group 1: $r^2 = 0.986$, $n = 13$, $p<0.0001$, group 2: $r^2 = 0.806$, $n = 10$, $p<0.0005$, see Table 4.2). Fig. 4.2*c* shows the relationship between log10 weight (g) and log10 fork length (mm) at the end of the experiment (week 8). Group 2 has recovered condition and there are no significant differences in slope or elevation between the groups (combined $r^2 = 0.952$, $n = 19$, $p<0.0001$).

Table 4.2: Analyses of covariance comparing the regression lines of log10 weight (g) on log10 fork length (mm) for group 1 (control) and 2 (experimental) at the end of each week in experiment I. Group 2 fish were on reduced rations during weeks 1-5.

	Analyses of covariance			
	Slope		Elevation	
Week	F test (d.f.)	Probability	F test (d.f.)	Probability
1	2.30 (1,43)	0.137	0.27 (1,44)	0.609
2	2.97 (1,37)	0.093	0.41 (1,38)	0.528
3	2.91 (1,30)	0.099	5.35 (1,31)	0.028
4	0.74 (1,28)	0.398	26.02 (1,29)	0.00001
5	0.27 (1,19)	0.610	25.77 (1,20)	0.00006
6	0.02 (1,19)	0.885	2.02 (1,20)	0.170
7	1.00 (1,17)	0.332	0.24 (1,18)	0.628
8	0.12 (1,15)	0.734	1.19 (1,16)	0.291





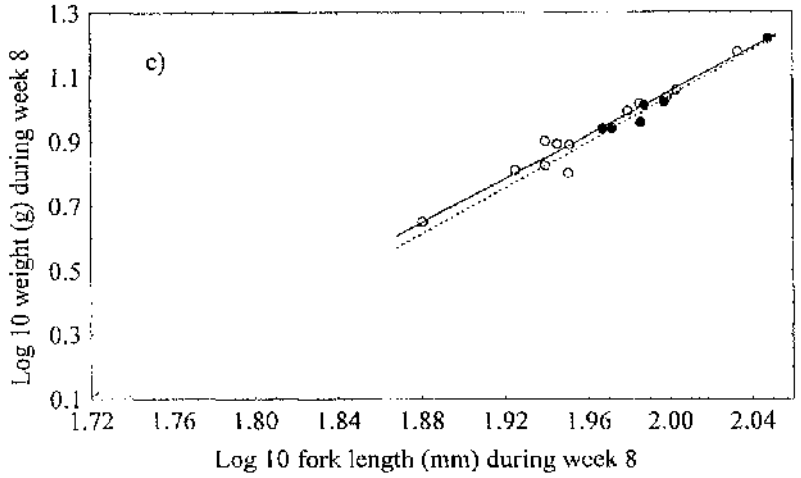


Fig. 4.2: The relationship between log 10 transformed fork length (mm) and log 10 transformed weight (g) for the fed and reduced food groups during (*a*) week 1, (*b*) week 5 and (*c*) week 8 of experiment I. Open circles and solid line denote the control group and closed circles and dashed line the reduced food group. See text for analysis of covariance between the two groups.

Table 4.3 presents information on growth rates in terms of weight. Control fish maintained a high growth rate after the initial weeks of the experiment, while the experimental group unsurprisingly grew at a significantly lower growth rate than the (fed) control group during the period of food restriction. When put onto an identical feeding regime as the control group, they showed a compensatory growth response, growing faster than the control group, but for only one week, showing similar growth rates to the control group for the remainder of the experiment.

Aggression rates in Table 4.4 are presented as the total number of aggressive acts (initiated and received) involving a focal individual during a minute observation, divided by the number of fish in the group at the time. A mean aggression rate was calculated for each individual per week, and the mean of those means is presented in Table 4.4. Aggression was generally low, and surprisingly there were no differences in aggression rate between the groups during the period that the experimental group received reduced rations, with the exception of weeks 4 and 5, the last two weeks of reduced rations. This is the result of a gradual increase in mean aggression rates of the experimental group over the period of reduced food, becoming significantly greater than the control group by week 4. However, mean aggression rate of the experimental group for week 5 was not significantly greater than week 4 (Mann-Whitney U-test: $U = 5.00$, $p = 0.221$). Moreover, the experimental group did not show a significantly higher aggression rate than the control group when they were put onto similar rations at the beginning of week 6.

Table 4.3: Mean specific growth rates in weight of group 1 (control) and group 2 (experimental) salmon in experiment I. Group 2 fish were on reduced rations during weeks 1-5.

Week	Mean growth (%.d^{-1}) ± S.E. (n)		Significance (ANOVA)
	Group 1	Group 2	
1-2	0.24±0.08 (20)	0.03±0.03 (22)	$F_{(1,40)}$=5.75; p<0.05
3	1.16±0.06 (17)	0.52±0.04 (17)	$F_{(1,32)}$=72.15; p<0.0001
4	1.08±0.09 (17)	0.05±0.07 (13)	$F_{(1,28)}$=70.87; p<0.0001
5	1.14±0.08 (13)	0.11±0.17 (10)	$F_{(1,21)}$=36.46; p<0.001
6	1.27±0.07 (12)	1.57±0.07 (10)	$F_{(1,20)}$=11.60; p<0.005
7	0.94±0.13 (12)	1.19±0.18 (9)	$F_{(1,19)}$=1.36; p = 0.258
8	0.88±0.11 (11)	0.72±0.10 (7)	$F_{(1,16)}$=1.01; p = 0.331

Table 4.4: Comparison of aggression rates (acts.fish^{-1}.min^{-1}) between control (group 1) and experimental (group 2) groups in experiment I. Group 2 were on reduced rations during weeks 1-5.

Week	Mean aggression rate ±S.E. (no. fish) (acts fish^{-1} min^{-1})		Significance (Mann-Whitney U test)
	Group 1	Group 2	
1	0.009±0.003 (20)	0.026±0.015 (22)	U = 12.00; p = 0.34
2	0.052±0.034 (17)	0.045±0.035 (17)	U = 8.00; p = 1.00
3	0.076±0.030 (17)	0.047±0.020 (13)	U = 10.80; p = 0.68
4	0.007±0.004 (13)	0.189±0.094 (10)	U = 0.00; p< 0.05
5	0.021±0.010 (12)	0.227±0.025 (10)	U = 0.00; p< 0.01
6	0.022±0.013 (12)	0.063±0.048 (9)	U = 7.00; p = 0.77
7	*	*	*
8	0.073±0.010 (11)	0.060±0.007 (7)	U = 4.00; p = 0.25

N.b.: Asterisks denote no aggression data for both groups during week 7.

4.3.1.2 Individual variation and performance in the control group (group 1)

Net aggression for each fish over the entire eight week period (i.e. the balance between the number of attacks initiated versus the number received) was measured by subtracting the rate of being attacked from the rate of aggressions initiated (both rates being expressed as per fish present at the time per min.). Net aggression (an index of social status) varied greatly between individuals, and increased significantly with an individual's residual standard metabolic rate ($r^2 = 0.165$, $n = 22$; $p < 0.05$, Fig. 4.3).

The percentage of time spent in the water column (i.e. the percentage of scan samples when each fish was recorded as being in the water column) was also found to vary significantly with residual standard metabolic rate (Fig. 4.4). The best fit to the data was obtained by a polynomial regression, since the relationship was apparently U-shaped:

$$\text{Arcsine \%time in column} = -119.2(\text{rSMR}) + 484.8(\text{rSMR}^2) + 45.3 \qquad \text{(Eq. 4.1)}$$

($r^2 = 0.412$, $n = 22$, $p < 0.01$), although any conclusions drawn from this can only be tentative.

Mean individual specific growth rate by weight (%.d^{-1}) over the eight week period also correlated significantly with arcsine transformed percentage time in water column (Fig. 4.5), the relationship being described by the polynomial equation:

$$\%\text{wt(g)d}^{-1} = 0.146(\text{arcsin\%time in column}) - 0.001(\text{arcsin\%time in column})^2 - 2.570 \qquad \text{(Eq. 4.2)}$$

($r^2 = 0.244$, $n = 22$, $p < 0.05$), although again, the relationship is weak and conclusions must be tentative.

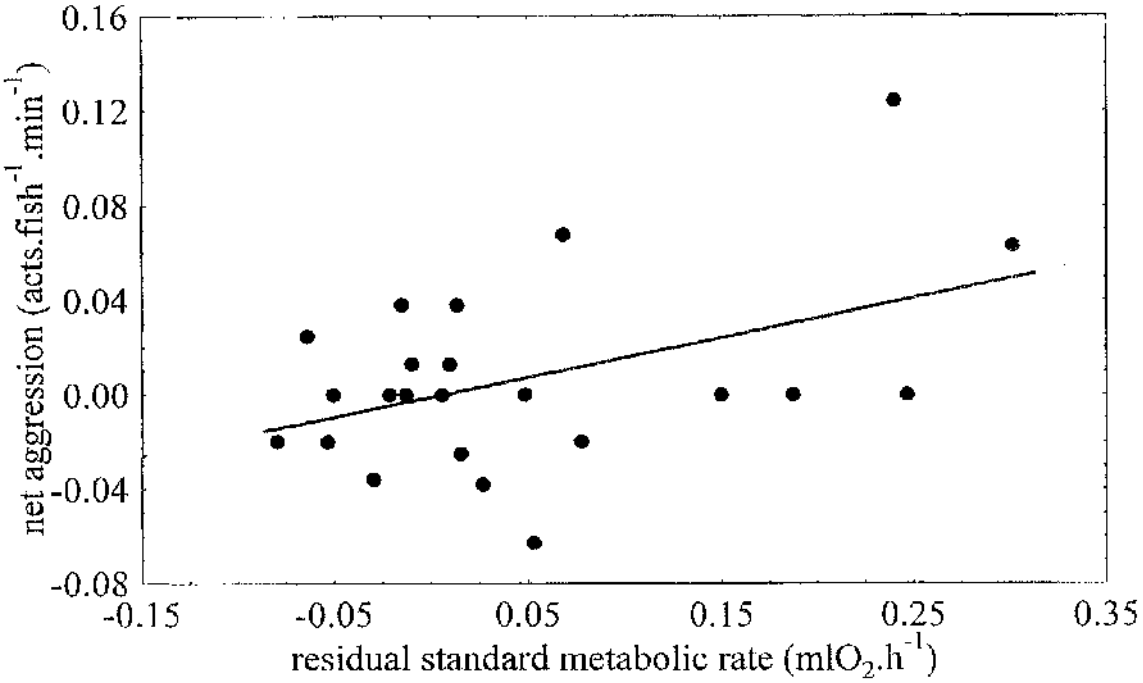


Fig. 4.3: The relationship between residual standard metabolic rate ($mlO_2.h^{-1}$) and net aggression ($act.fish^{-1}.min^{-1}$) for the fed group in experiment I.

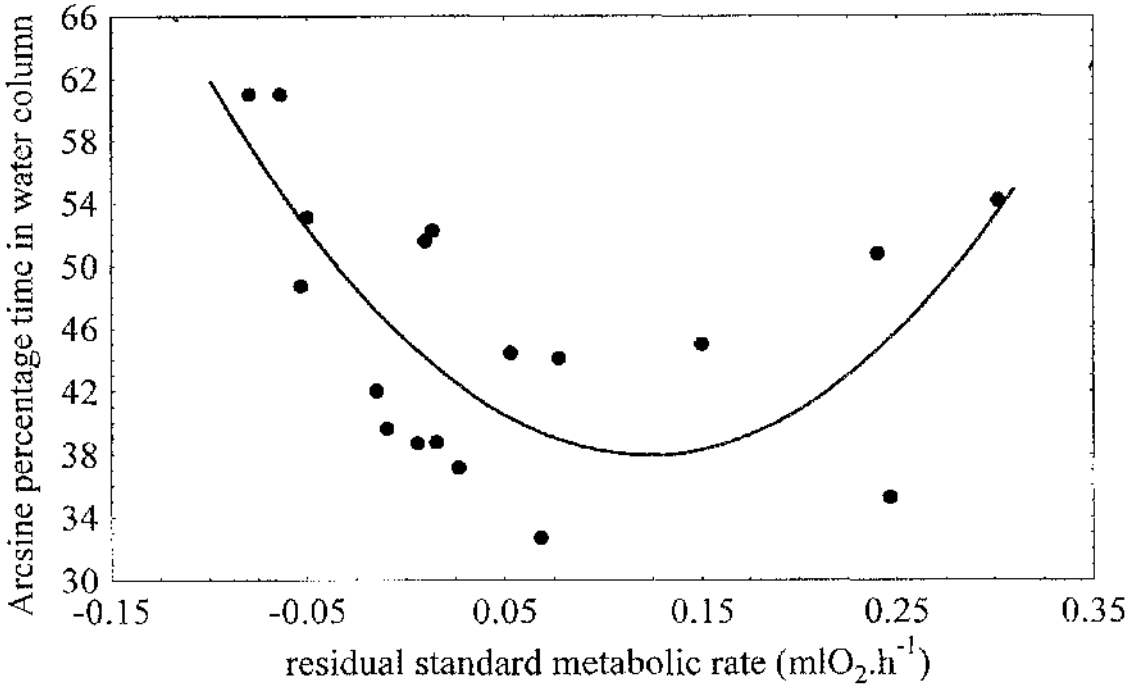


Fig. 4.4: The relationship between residual standard metabolic rate ($mlO_2.h^{-1}$) and arcsine transformed percentage time in water column for the fed group in experiment I. See text for the polynomial regression equation.

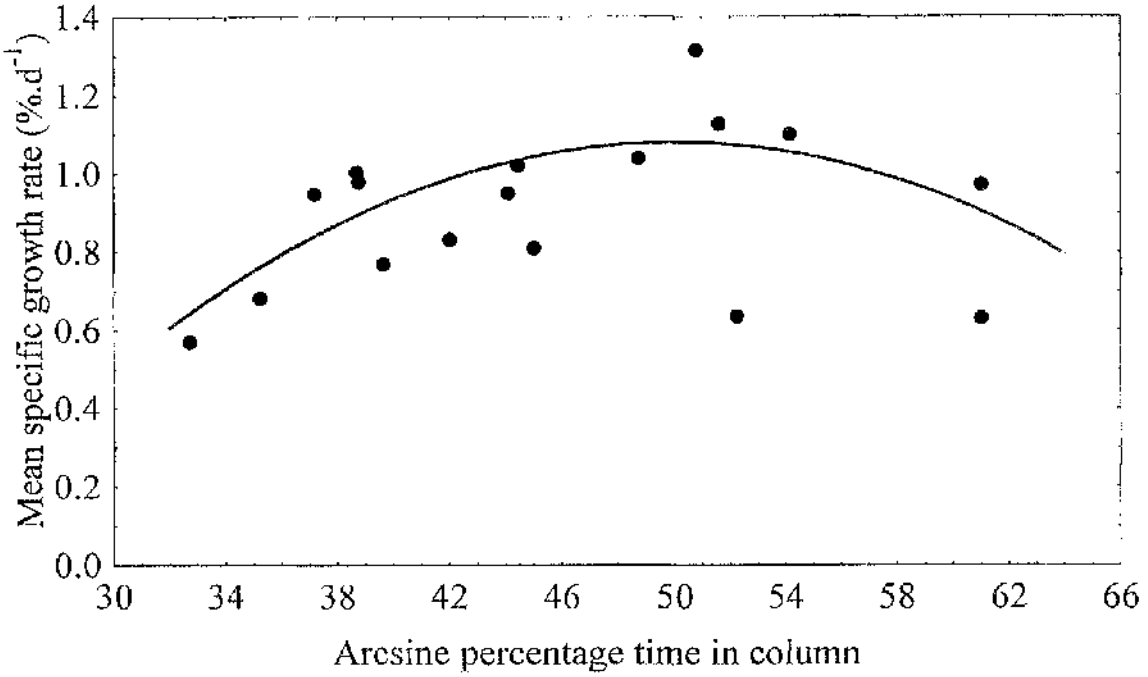


Fig. 4.5: The relationship between arcsine transformed percentage time in water column and mean specific growth rate (%.d^{-1}) over 8 weeks for the fed group in experiment I. See text for the polynomial regression equation.

4.3.1.3 Individual variation and performance in the experimental group (group 2)

In the experimental group, residual standard metabolic rate had no effect on subsequent aggression during the period of either reduced (r^2 = -0.044, n = 24, p = 0.847) or *ad lib.* (r^2 = 0.118, n =10, p = 0.176) feeding. Similarly, percentage time in the water column had no effect on growth, unlike in the control group (r^2 = -0.047, n = 24, p = 0.922).

The only predictor of growth in the reduced food period of the experimental group was each fish's distance from the upstream mesh divider (i.e. the food source). Distance from this point was calculated on the basis of the data on the zone occupied by each fish during observation sessions: a fish's main feeding station was taken to be the single zone in which it spent the greatest amount of its time (based on scan sample data). The fish were very site faithful, spending an average of 34.06±1.43 (S.E.)% of their observed time in one particular zone. These zones were where the fish would ultimately return to, after bouts of feeding and aggression in the other zones, or after being temporarily displaced by other fish.

Mean growth (%.d^{-1}) of fish during the reduced food period decreased significantly with distance of their main feeding station from the food source (r^2 = 0.201, n = 22, p< 0.05, Fig. 4.6). The preferred site of 13 out of 22 fish was in the middle of the most downstream pool, approximately 2.45m downstream of the food source (Fig. 4.6). However, residual standard metabolic rate (r^2 = 0.044, n = 24, p = 0.166), net aggression (r^2 = -0.043, n = 24, p = 0.831), and initial size of fish (r^2 = 0.005, n = 24, p = 0.300) had no effect on their proximity to the food source.

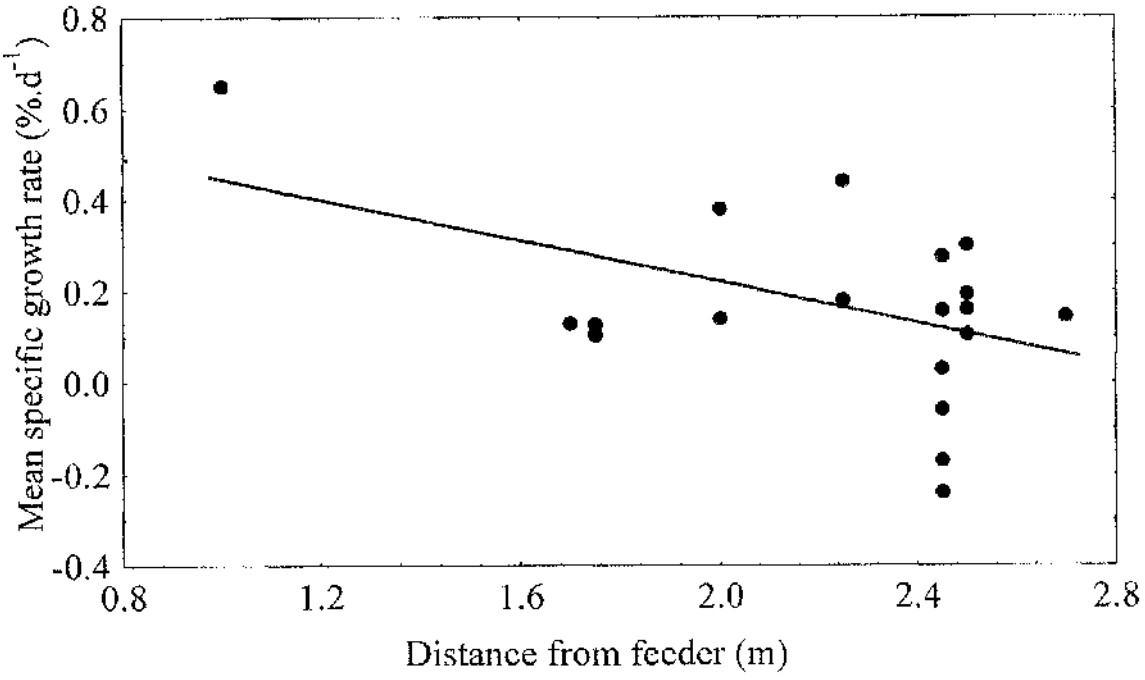


Fig. 4.6: The relationship in the experimental group between distance (m) of a fish's preferred feeding station (see text) from the upstream mesh (i.e. the food source) and mean specific growth rate (%.d^{-1}) during the reduced food period of experiment I.

Those fish surviving into the period of *ad. lib.* food tended to maintain the same relative positions with respect to each other, despite a general shift closer towards the food source (Fig. 4.7). Growth rates of survivors did not differ significantly from those that subsequently died: mean growth rate of survivors was 0.224±0.074 (S.E.)%.d^{-1} (n=10), whereas those that died had been growing at 0.132±0.045 %.d^{-1} (n=14; t-test: $t = -1.09$, d.f. = 21, $p = 0.288$).

Did physiological parameters influence growth performance, after controlling for the effect of distance from the food source in the period of reduced food? I examined this by calculating the expected growth for each fish given the distance from the feeder of its most frequently adopted position (from the regression equation to Fig. 4.6). Residual growth was calculated in a similar manner to residual standard metabolic rate (see chapter 2 - methods), as the residual from this regression line, negative values denoting a fish doing worse than expected for its particular location, positive values denoting a better than expected performance.

There was a negative relationship between residual standard metabolic rate and residual growth calculated in this way, those fish with high residual standard metabolic rates growing less than expected given their position in the artificial stream ($r^2 = 0.143$, $n = 18$, $p<0.05$, Fig. 4.8). However, since residual growth data was derived from a regression based on skewed data (Fig. 4.6), conclusions must be treated tentatively. Despite this, Fig. 4.6 was a good depiction of how salmon organise themselves in space, since their despotic nature would force most of the fish to take up crowded, subordinate positions in the artificial stream.

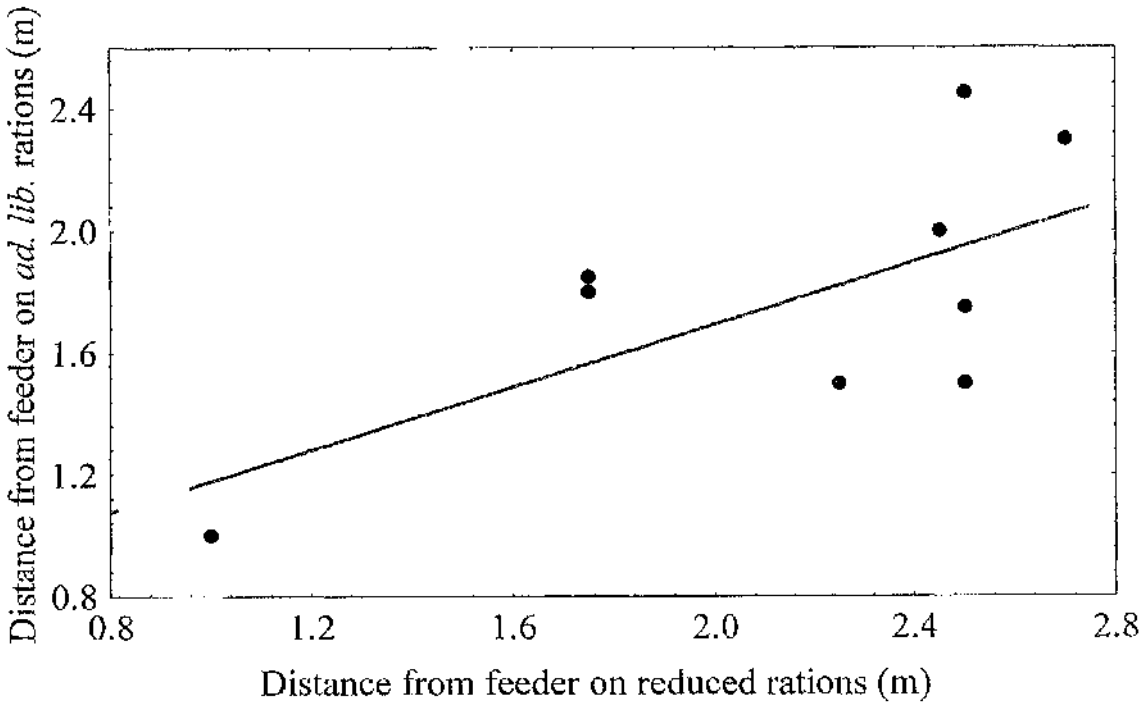


Fig. 4.7: The relationship between the preferred feeding station (distance (m) from the upstream mesh) of group 2 fish during the reduced and *ad lib.* food periods of experiment 1 ($r^2 = 0.363$, $n = 10$, $p < 0.05$).

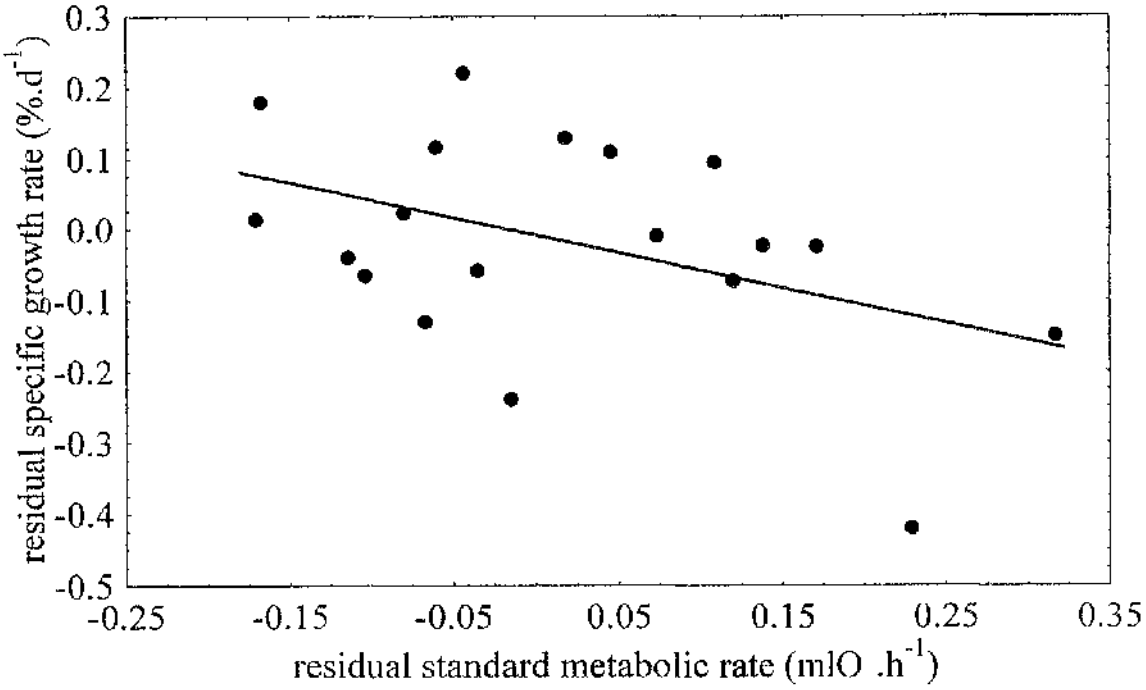


Fig. 4.8: The relationship between residual standard metabolic rate ($mlO_2.h^{-1}$) and mean residual specific growth rate ($\%.d^{-1}$) given each fish's preferred feeding station, during the reduced food period of group 2 in experiment I. See text for further explanation.

4.3.2 Results for experiment II

Of the 14 fish introduced in group 1, six subsequently defended large territories (mean area = 0.50±0.06 (S.E.) m^2). The remaining eight fish were constrained to one riffle area, also 0.50m^2 in area. From the next two introduced groups (17 and 11 fish respectively), only one fish from group 2 obtained a territory, also 0.5m^2 in area. Thus once all the groups had been introduced, only seven fish were in possession of large territories, and a disproportionate number of these (n = 6) belonged to group 1 (goodness of fit test: $\chi^2 = 10.54$, 2 d.f., $p < 0.01$). As the artificial stream prevented any emigration, the remaining 35 fish were all constrained on the same riffle, where the maximum area defended by one fish was 0.03m^2. Hereafter these fish are termed 'non-territorial' while those defending areas of greater than 0.40m^2 are termed 'territorial'.

Of the fish in group 1, those obtaining a territory were significantly larger than the non-territorial fish (fork length of territory holders = 55.08±1.12mm (n = 6); non-territorial fish = 50.11±0.67mm (n = 8), ANOVA; $F_{(1,12)} = 16.34$, $p < 0.005$, Fig. 4.9). Larger fish in group 1 tended also to be more aggressive than smaller fish, in that they initiated more attacks than they received ($r^2 = 0.219$, n = 13, $p<0.05$, Fig. 4.10). While this was partly due to territorial fish being significantly more aggressive than their counterparts (mean net aggression of territory holders and non-territorial fish was 0.005±0.002 (= S.E.) acts $fish^{-1}min^{-1}$ (n = 7) and -0.001±0.001 acts $fish^{-1}min^{-1}$ (n = 35) respectively, Mann-Whitney U test: U= 7.00, $p<0.05$), there was also a relationship between size and aggression in non-territorial fish (see later). There was no relationship, however, between residual standard metabolic rate and net aggression ($r^2 = -0.004$, n = 14, $p = 0.348$).

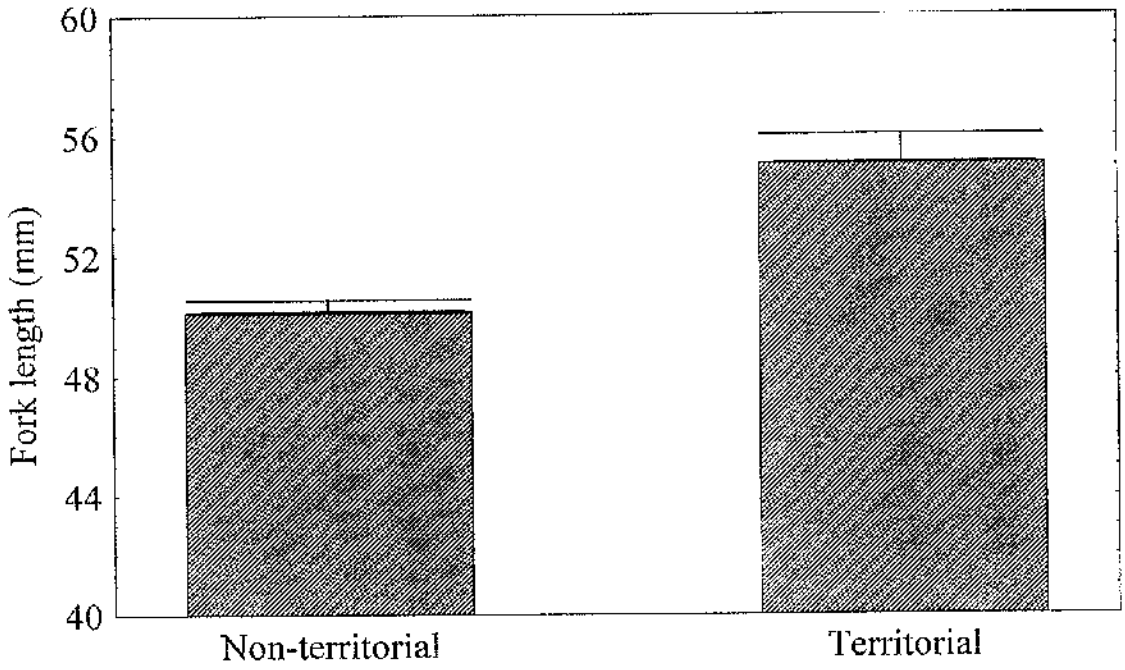


Fig. 4.9: Differences in initial fork length (mm) between territorial and non-territorial fish for group 1 fish in experiment II. Error bars denote standard errors.

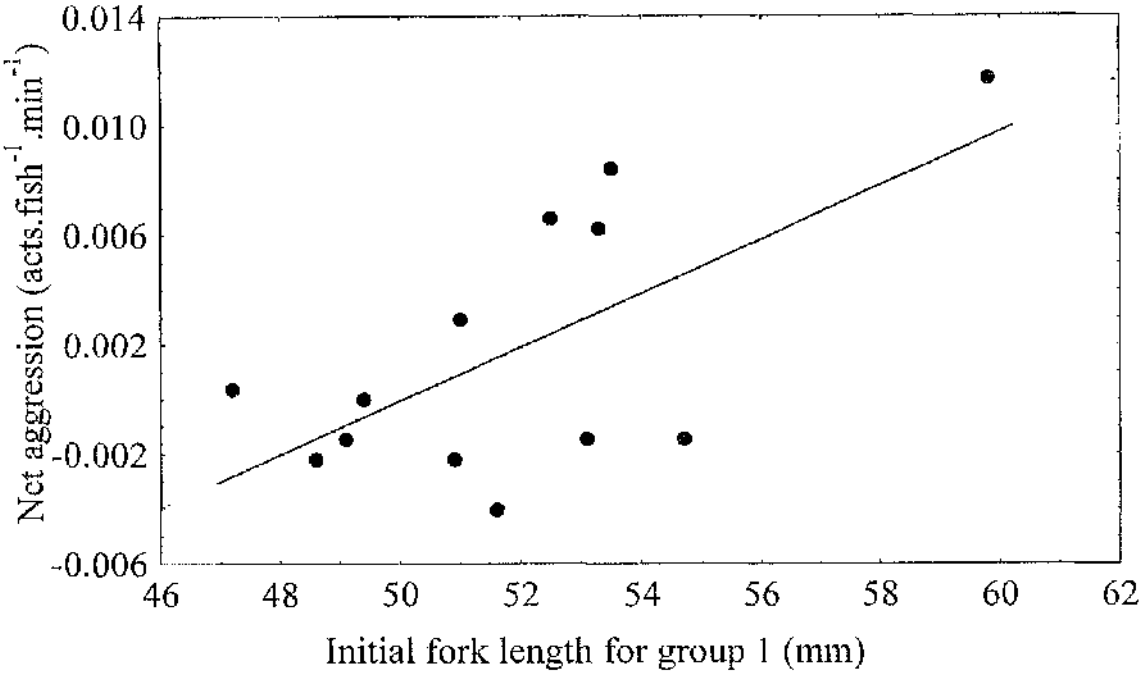


Fig. 4.10: The relationship between initial size (fork length (mm)) and net aggression (acts.fish^{-1}.min^{-1}) for group 1 of experiment II.

To investigate whether those fish from group 1 that obtained territories chose superior sites, 12 sites along the artificial stream were sampled for prey drift and water velocity (Table 4.5). Sites 1-6 and 10 corresponded to a territory holders' position, the sampling net being held at the point most frequently occupied by the territory holder. Sites 7 and 8 corresponded to upstream and downstream of the riffle area occupied by 83.3% of the fish, and 9, 11 and 12 were unoccupied. Using the dry weight of food collected per minute per litre of water flowing past the site as a measure of territory quality, there were no significant differences in quality between the 6 sites the territory holders in group 1 chose as territories and the 6 sites (including the 3 unoccupied sites) the remaining fish were forced to occupy (mean quality of territories = 0.136±0.003 $mg.l^{-1}$ (n = 6), mean quality of remaining sites = 0.174±0.006 $mg.l^{-1}$ (n = 6), ANOVA; $F_{(1,10)} = 0.401$, $p = 0.541$). This is despite 6 out of the 7 territorial fish belonging to group 1, and therefore having the greatest opportunity to sample various sites.

However, territory holders did benefit from a greater food intake. Fish with territories fed at a significantly greater rate than non-territorial fish (territory holders = 6.33±1.11 feeding movements $fish^{-1}min^{-1}$ (n = 7), non-territorial fish = 4.58±0.33 feeding movements $fish^{-1}min^{-1}$ (n = 35); ANOVA: $F_{(1,37)} = 3.64$, $p = 0.05$). This may be due to the monopoly on food items that each territory holding fish will have; despite no apparent preference for the best sites, territory holders had exclusive access to a large foraging area. Conversely, each of the non-territorial fish on the riffle had to share an area similar in size to a territory with 34 competitors. By recording the positions of fish, the percentages of total drift available to that position (assuming that all drift was available for consumption by the fish; Table 4.5) and the percentage of that drift available to individual fish after correction for the number of neighbouring fish also

Table 4.5: Profitability of different potential feeding positions in the artificial stream in experiment II.

Site no. (type of fish present)	Dry weight (mg) min^{-1} ±1.0 (S.E.)	Percentage of total sampled drift per site (%)	Water velocity ($l.min^{-1}$)± S.E.	Dry weight per litre ($mg.l^{-1}$)
1 (territorial)	3.0	7.89	186.0±13.3	0.016
2 (territorial)	1.0	2.63	111.6±18.6	0.009
3 (territorial)	4.0	10.53	874.2±16.2	0.005
4 (territorial)	1.0	2.63	111.6±18.6	0.009
5 (territorial)	3.0	7.89	297.6±18.6	0.010
6 (territorial)	2.0	5.26	130.2±5.7	0.015
7 (non-territorial)	7.0	18.42	223.2±24.8	0.031
8 (non-territorial)	3.0	7.89	260.4±3.7	0.011
9 (unoccupied)	2.0	5.26	279.0±13.3	0.007
10 (territorial)	4.0	10.53	130.2±9.3	0.031
11 (unoccupied)	4.0	10.53	130.2±9.3	0.031
12 (unoccupied)	4.0	10.53	558.0±18.6	0.007

exploiting the same site, it was possible to test whether territorial fish benefited from their exclusive access to a food supply. In group 1, growth rate increased significantly with the percentage of food available to individual fish (Spearman's Rank correlation, $R_s = 0.639$, $n = 14$, $p < 0.05$, Fig. 4.11). Analysis was restricted to group 1 fish, since they experienced the same initial conditions and were very similar in initial size. They also experienced the largest variation in food availability, since most of the territorial fish came from this group.

Despite the majority of fish being constrained to the riffle, there seemed to be a distinct hierarchy within this group of non-territorial fish. During each observation session, positions of individual fish within the group were recorded in terms of whether they were at the front, middle or back of the riffle. In this way I could estimate the percentage of time spent by fish in these positions; the front of the riffle was assumed to be the preferred feeding station. Net aggression correlated with initial fork length for the fish on the riffle ($r^2 = 0.095$, $n = 35$, $p < 0.05$, Fig. 4.12). Initial fork length was the fork length (mm) of the fish from all 3 groups measured on the day group 3 was introduced, to remove any bias of using fork lengths for groups 1 and 2 measured prior to the introduction of group 3. Initially larger fish also spent significantly more time at the front of the riffle than small ones (Spearmans rank correlation: $R_s = 0.415$, $n = 35$, $p<0.05$, Fig. 4.13), presumably as a consequence of their greater aggression. Initial fork length also correlated with an index of prey available to individual fish. The index was created by multiplying the percentage time spent at the front of the riffle by the amount of prey drift there: the more time spent at the front of the riffle, the larger the amount of food potentially obtained by individual fish. Therefore initially larger fish may potentially have acquired more food through spending more time at the front of

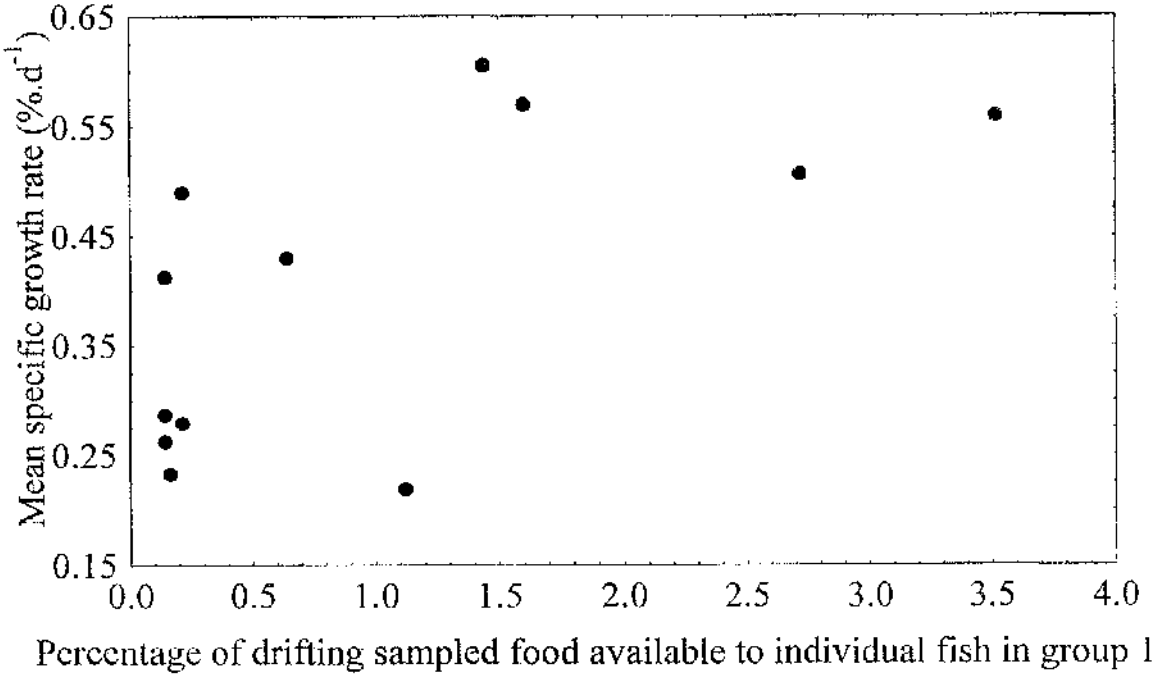


Fig. 4.11: The relationship between the percentage of the total food potentially available to individual fish and their mean specific growth rate (%.d^{-1}) in group 1 of experiment II.

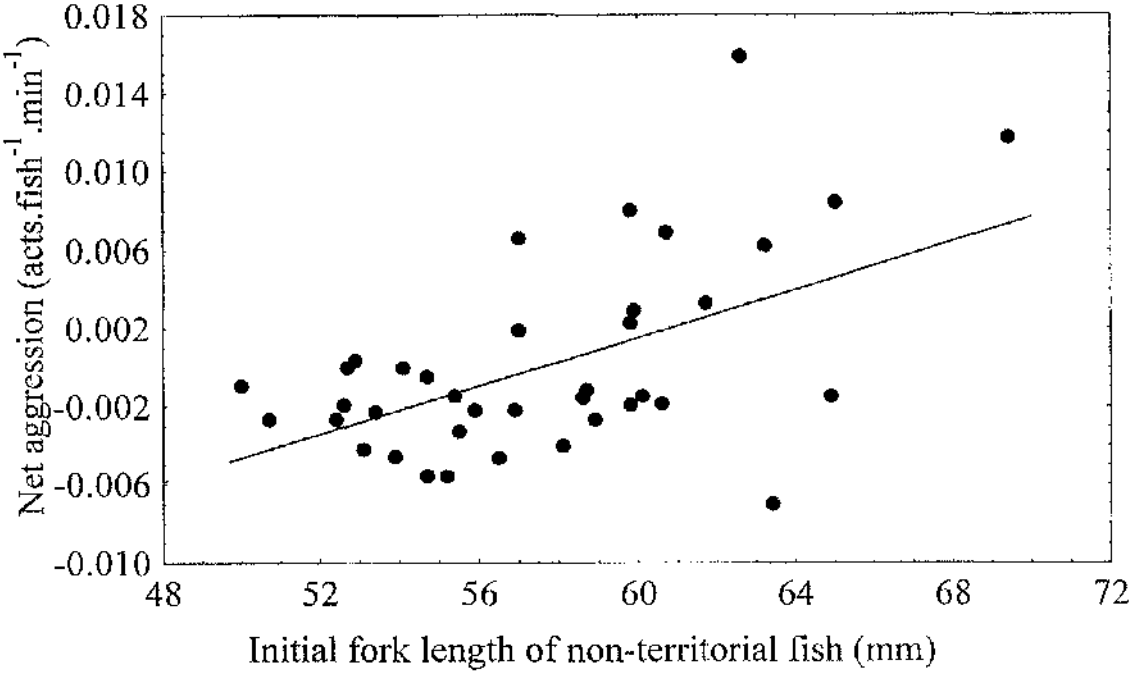


Fig. 4.12: The relationship between initial fork length (mm) and subsequent net aggression (act.fish^{-1}.min^{-1}) for non-territorial fish in experiment II.

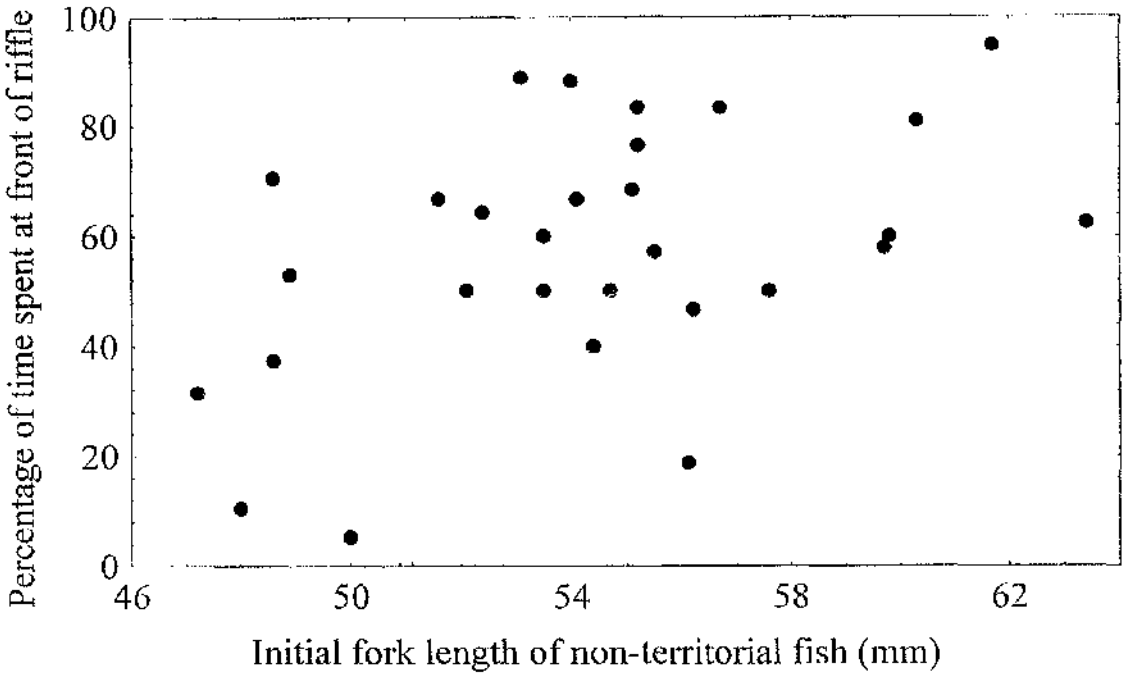


Fig. 4.13: The relationship between initial fork length (mm) and percentage of time spent at the front of the riffle for non-territorial fish in experiment II.

the riffle. There was indeed a correlation between time spent at the front of the riffle and subsequent mean specific growth rate (Spearman's rank correlation: $R_s = 0.442$, n = 35, $p<0.05$, Fig. 4.14).

Group 1 on the whole grew faster than the other two later-arriving groups, presumably due to a prior residence effect, whereby they were more likely to obtain territories (mean specific growth rates over the course of the experiment: group 1 = 0.411±0.038(S.E.)%, group 2 = 0.340±0.039%, and group 3 = 0.260±0.061%. One-way ANOVA between groups: $F_{(2,30)} = 2.699$, p = 0.05; Tukey post-hoc comparison of means shows a significant difference (p = 0.05) between groups 1 and 3, Fig. 4.15). However, there were no significant differences in growth rate between the groups when the territorial fish were removed from the analysis (mean specific growth rate of non-territorial fish: group 1 = 0.335±0.040%, group 2 = 0.333±0.042%, and group 3 = 0.260±0.061%. ANOVA: $F_{(2,24)} = 0.74$, p = 0.487).

At the end of the experiment in October, six fish had a fork length of greater than 75mm and were destined for the Upper Modal Group (UMG; Thorpe, 1977). Five of these salmon were from the group of six surviving territory holders, compared with only one out of 35 non-territorial fish (goodness of fit test; $\chi^2 = 24.440$ at 1 d.f., $p<0.001$). Four of the territorial fish destined for the UMG came from group 1, the other from group 2. The non-territorial fish destined for the UMG was also from group 2. A higher proportion of the UMG therefore belonged to group 1 (4 out of 12), compared to groups 2 and 3 (2 out of 14 and 0 out of 15 respectively, Fig. 4.16) although it was not quite significant (goodness of fit test; $\chi^2 = 4.000$ at 2 d.f., p = 0.10).

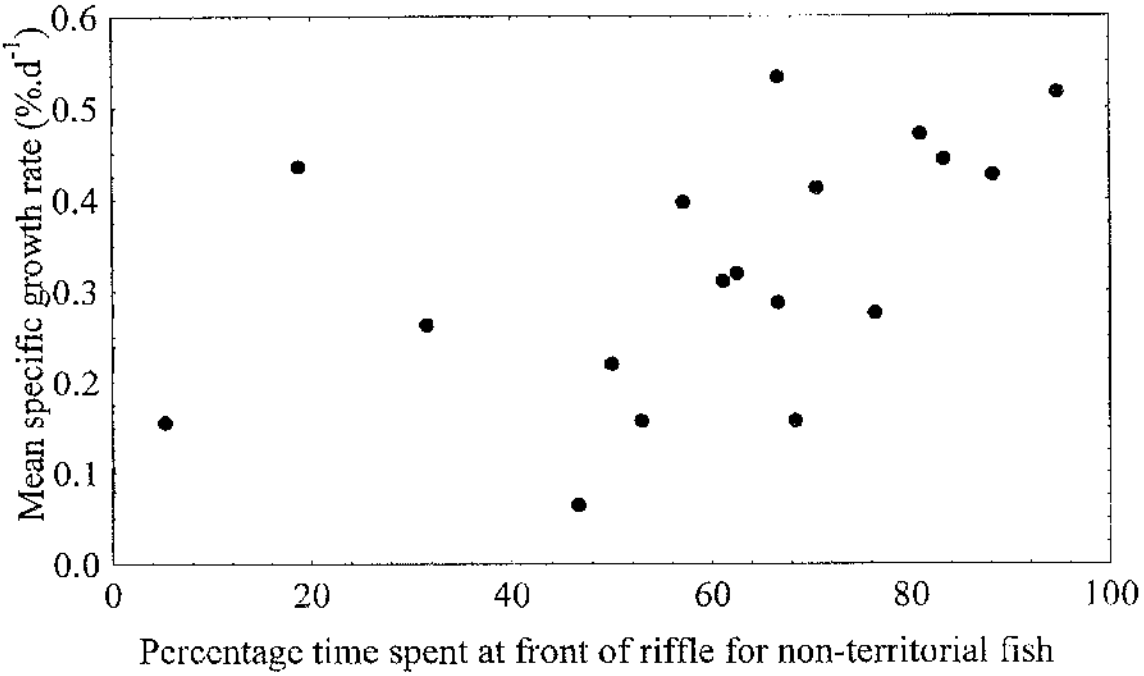


Fig. 4.14: The relationship between the percentage of time spent at the front of the riffle for non-territorial fish and mean specific growth rate (%.d^{-1}) in experiment II.

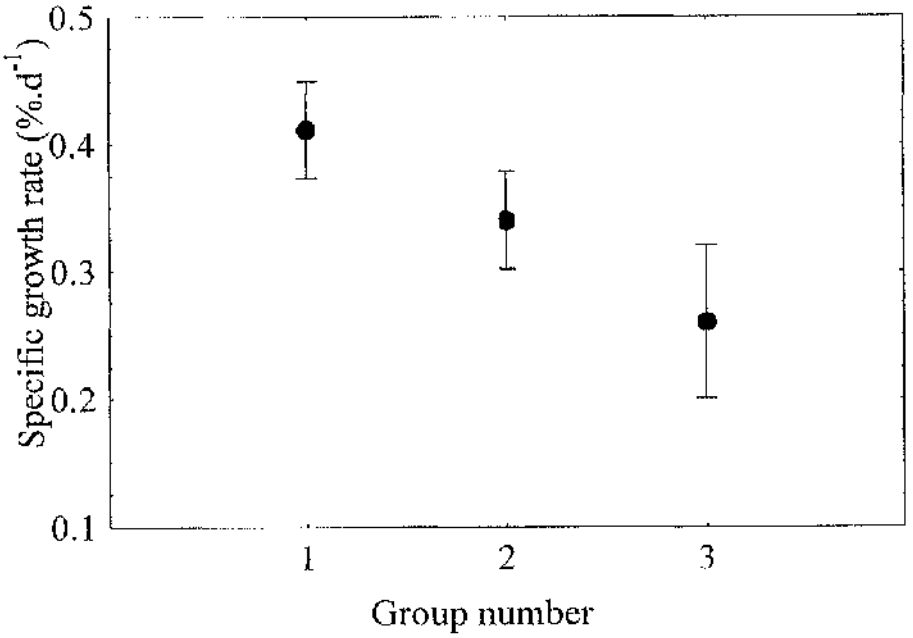


Fig. 4.15: Differences in mean specific growth rate (%.d^{-1}) between the 3 groups in order of their introduction into the artificial stream in experiment II; n = 14, 17, and 11 fish respectively. Error bars denote standard errors.

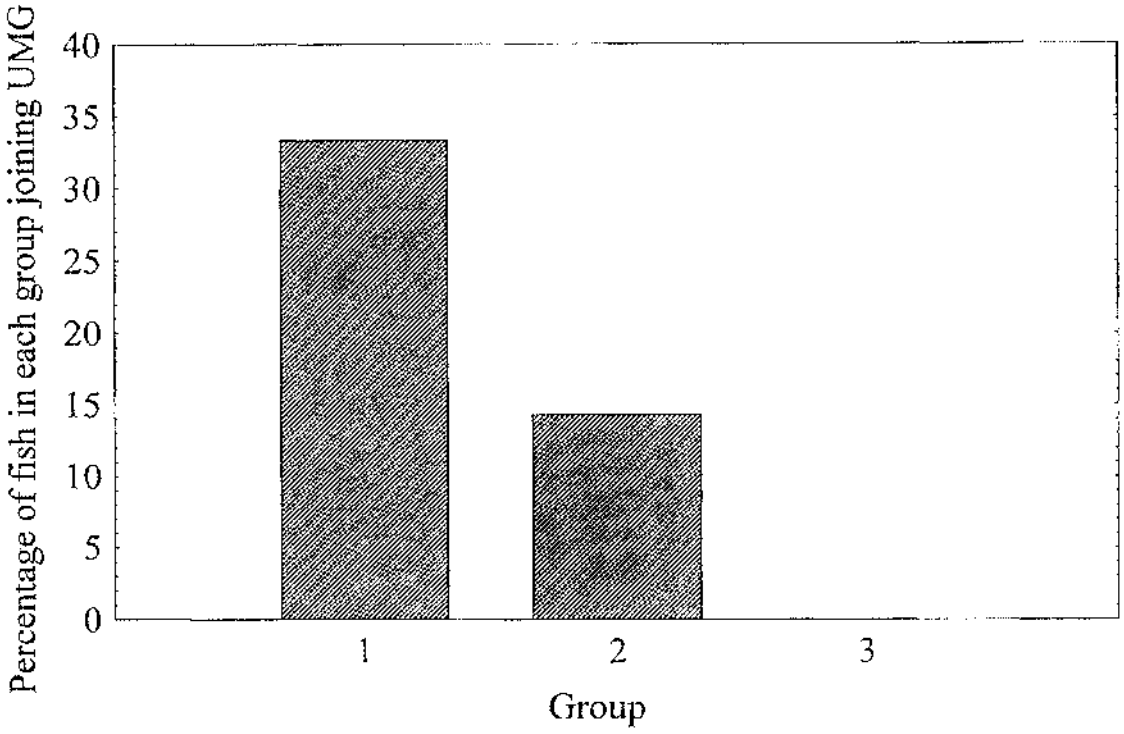


Fig. 4.16: The percentage of fish from each group destined for the Upper Modal Group (fork length> 75mm at the end of experiment II).

4.4 Discussion

4.4.1. Group effects on growth in experiment I

Juvenile salmon in group 2 unsurprisingly had significantly lower growth rates throughout the reduced food period. However, their gradual loss of condition implies that they attempted to maintain structural growth, measured as fork length, at the expense of weight. Weatherley & Gill (1981) showed with rainbow trout that the effects of slow growth resulting from reduced rations, as experienced here by group 2, resemble those of severe starvation. When a fish starves, its length changes little, implying that fish are composed of two different tissue types- reserve weight and structural weight. Fatty reserves and remobilizable musculature constitute reserve weight, whereas structural weight is composed of skeletal, circulatory and nervous tissues and cannot be remobilised (Broekhuizen *et al.*, 1994). Fork length is thus a measure of structural weight. Nicieza *et al.* (1991) described a threshold length in juvenile salmon, below which individuals could not smolt. Moreover, larger smolts have higher survival rates, measured as return rates, and higher growth rates while at sea (Eriksson *et al.*, 1987; Lundqvist *et al.*, 1988; Lundqvist *et al.*, 1994). As reserve weight can be quickly recovered during compensatory growth, it may be prudent for juvenile salmon to maintain skeletal growth at the expense of fatty tissue and musculature.

4.4.2. Individual variation and performance in groups 1 and 2 (experiment I)

Net aggression was found to increase with residual standard metabolic rate in the control group (group 1). Metcalfe *et al.* (1995) found that a higher residual standard metabolic rate conferred dominance in pairwise contests, but the mechanism conferring dominance remained unclear. Several studies have shown that competitive ability influences growth and subsequent smolting strategy in juvenile Atlantic salmon (Metcalfe, 1989, 1991), but these were also pairwise contests in small tanks. Aggression has been shown to confer dominance in juvenile brook charr in real streams, which in turn leads to the acquisition of superior territories and subsequently greater feeding rates (Grant, 1990), and dominance was shown to confer superior growth rates in three species of salmonid in an artificial stream (Fausch, 1984). The present study illustrates, in a semi-natural setting, that physiology (variation in standard metabolic rate) plays a role in social status through its effect on aggression. Percentage time in the water column also varied significantly with residual standard metabolic rate, the relationship being described by a U-shaped polynomial curve. This implies that fish with a low residual standard metabolic rate, with low net aggression, spent similar amounts of time in the water column to high residual standard metabolic rate fish with high net aggression. Given their differences in aggression, this possibly suggests that the fish with negative net aggression values (i.e. fish that were attacked more often than initiating attacks themselves) were kept off the substratum by more aggressive dominant individuals, which spent a similar amount of time off the substratum to maintain their dominance through aggression. The situation of fish with markedly different levels of aggression but spending similar amounts of time in the water column

corresponds to the observations on juvenile coho salmon by Puckett and Dill (1985). They identified different behavioural strategies, e.g. territorial fish, spending most of their time in a defended area, and 'floaters', which were unable to defend a territory and existed in the spaces between territories. Floaters were attacked more through entering the territorial space of more aggressive fish and subsequently spent more time off the substrate 'floating'. This also corresponds to observations of rainbow trout where subdominant fish were forced to maintain increased levels of activity due to saturation of territories by more dominant trout (Li & Brocksen, 1977). More aggressive, territorial fish would benefit from spending large amounts of time in the water column since this allows them either to feed or to defend their territories, a high cost-high return strategy that involves more aggression because they are competing for food in the water column with other dominant fish (Metcalfe, 1986).

Mean growth rate initially increased with the percentage of time spent in the water column, but decreased in those fish spending very high proportions of time spent off the substratum, suggesting an optimum percentage of time to spend off the substratum foraging and being aggressive. Intermediate levels of both aggression and time spent in the water column may result in reduced routine metabolic costs and hence greater growth efficiency (Paloheimo & Dickie, 1965). Similar findings were described by Metcalfe (1986), where the optimum strategy in subordinate fish was to minimize energy expenditure rather than maximize food intake through greater time spent in the water column.

Unlike group 1, in group 2 there were no significant relationships between residual standard metabolic rate and aggression or time spent in the water column. The only predictor of growth in the group 2 fish was the distance from the food source for each

fish; almost 60% of the fish spent most of their time in close proximity to each other in the most downstream pool, and grew less than the fish on the riffles and in the upstream pool. Potential profit declined with increasing distance from the food source, as the probability of food depletion by upstream fish increased. Compared to group 1, the majority of group 2 fish opted for the low energetic cost of staying in the low current speed environment of a pool. Aggression gradually increased during the period of reduced food; this has been suggested as a mechanism to increase territory size in salmonids when food is scarce (Symons, 1968; Slaney & Northcote, 1974; Dill *et al.*, 1981). However, most of the fish did not hold large territories, instead they spent most of their time close together in the pool. Rather, the increase in aggression may have been due to increased intruder pressure (since there were fewer fish in the pool after the group were put onto *ad lib.* food), a result of the fish opting for the low energetic cost of living in the pool. Moreover, increased intruder pressure has been suggested as causing smaller defended territories in brook trout (McNicol & Noakes, 1984) and coho salmon (Dill *et al.*, 1981). Furthermore, high densities of fish (as found in the pool) have been suggested as influencing dominance relationships in a study on juvenile largemouth bass; when confined to a small area the social order became relatively simple and uncomplicated by dominance relations based on relative aggression (Fleming & Johansen, 1984).

Although there was no dominance hierarchy based on aggression, initial size or residual standard metabolic rate, fish surviving into the *ad lib.* food period responded to the change in food regime by moving further upstream (upstream positions being more profitable; Fausch, 1984), but tended to maintain position relative to each other. Therefore a hierarchy based on position and subsequent growth was at work.

Throughout the period of reduced food each fish had experience of its relative position, and possibly this experience resulted in the fish maintaining their positions with respect to each other. The social structure may thus have been maintained by prior experience rather than current assessment, in a similar sense to salmonids using experience to settle contests rather than a continued assessment of fighting ability, which reduces the cost of aggression to both participants (Abbott *et al.*, 1985). Because the fish spread out upstream when put onto *ad lib.* rations, intruder pressure was reduced and aggression subsequently decreased.

It was shown for the group 1 fish that a high residual standard metabolic rate can increase an individual's success through an increase in aggression. However, after calculating expected growth for each fish in group 2 it was found that the higher the residual standard metabolic rate, the lower the actual growth, given a fish's position. Fish with higher standard metabolic rates (a higher metabolic turnover) will have a higher cost of living (Priede, 1985). When food abundance is high, as in group 1, a high metabolic turnover may allow allocation of resources to both growth and aggression (Titus, 1990). However in group 2 (low food abundance), the same high metabolic turnover that ordinarily confers a behavioural advantage becomes a disadvantage; instead the environment favours individuals with a lower metabolic turnover and hence lower energy demands for growth and survival.

4.4.3 Individual variation and performance in Experiment II

In this experiment, almost half of the first group of introduced fish obtained and defended large territories, the remaining fish in the group being constrained to an area approximately the size of one large territory, along with almost all of the fish from the subsequent two groups. This result strengthens the evidence that prior residence affects the outcome of intraspecific interactions. Similar findings have been documented for other species of salmonid in artificial streams: first emerging coho salmon fry had 'settler's rights' to the environment and created and maintained a size gap between themselves and later emerging fry (Mason & Chapman, 1965); the first juvenile rainbow trout introduced to an artificial stream also established a permament size gap compared with later introductions of trout (Chandler & Bjornn, 1988). Prior residence also affects interspecific interactions, a similar phenomenon being documented between chinook salmon and brown trout (Glova & Field-Dodgson, 1995), and between coho salmon, brook trout, and brown trout (Fausch & White, 1986). However, these studies used longer time intervals between early and late fish, e.g: 22 days in both Mason & Chapman (1965) and Chandler & Bjornn (1988). This gave fish time to create a size advantage. In this study the time intervals were much shorter: 7 days between each group, 14 days in total for all the fish to be introduced. All fish were of similar size, showing that prior residence alone, and not the size advantage it may subsequently confer, has a strong influence on which individuals obtain territories. Prior residence is thus a superior competitive asymmetry distinct from any physical advantage attributable to it (see chapter 3).

Across all groups, aggression correlated significantly with size and not with residual standard metabolic rate as shown in experiment I. This may be due to prior residence being such a strong asymmetry in gaining territories, coupled with relatively small numbers of fish in each group, masking any effects differences in standard metabolic rate might have. In salmonids, there is often a clear correlation between status and size (Jenkins, 1969), possibly because dominant fry grow faster (Huntingford *et al.*, 1990), and dominant fish tend to hold the most profitable positions (Fausch, 1984). However, it is unclear whether increased aggression is a consequence of territory ownership or a cause; increased aggression on establishing a territory has been described as the competitive threat hypothesis. For example, Dill (1978) described juvenile coho salmon attacking larger intruders at a greater distance than equal sized or smaller fish, and Abbott *et al.* (1985) demonstrated in rainbow trout that dominants increased their levels of aggression towards subordinates after subordinates had increased their weight by up to 13%, making them more of a perceived competitive threat. This behavioural plasticity would obfuscate the quality of individuals attaining territories, since they might become aggressive as a consequence. Furthermore, most studies are based on observations of already established territory holders, and cannot disassociate the effects of territory quality and phenotypic quality on an individual's behaviour. However, the results from the present study showed a good relationship between size and aggressiveness between the 'non-territorial' fish constrained to the riffle. This provides further evidence of the correlation between status and size. Furthermore, it suggests that increased aggression was not a consequence of larger fish obtaining territories in group 1, but a cause. In addition, it is probable that the larger territorial fish obtained their increased size as a consequence of being more aggressive in the

hatchery tanks prior to the start of the experiment (Metcalfe & Thorpe, 1992*b*; Metcalfe *et al.* 1992).

Although the larger, more aggressive fish in group 1 did obtain and defend large territories, they did not appear to choose the most profitable sites in terms of water velocity and particulate drift, as has been documented before in several studies (Fausch, 1984; Grant, 1990). These earlier studies have provided evidence for the assumption that higher quality individuals will obtain territories, and the best territories will belong to those of highest rank (Maynard Smith, 1974; Arcese, 1989). However, in these studies the competitors had prior knowledge of the potential territories, so that superior competitiors could exploit the best territories as they became vacant (Stamps & Krishnan, 1994). In the present experiment the fish had no knowledge of potential territory quality before introduction to the artificial stream. Consequently, there may be a cost in searching for the best territory; with no prior knowledge of the environment there may be a risk in taking time to sample sites, as these sites may at the same time become occupied and defended by conspecifics. A similar conclusion was made in a study on pied flycatchers (Slagsvold *et al.*, 1988), where the synchronous arrival of competing females on breeding grounds in spring results in their showing a pattern of restricted searching for mates, as it is very important to start breeding as soon as possible, for a delay in breeding means a reduction in reproductive success (Harvey *et al.*, 1985). Similarly, after emergence, juvenile salmon are all searching for territories at approximately the same time, due to fairly synchronous emergence (Gustavson-Marjanen & Dowse, 1983; also see Chapter 3); this may also curtail sampling time. Moreover, in salmonids the social structure can be very stable for months after territory acquisition (Jenkins, 1969), so it will not be in an individual's best interests to

risk failure to secure a territory due to sampling time. This may explain why territorial fish in group 1 fail to exploit the most profitable sites, despite having the greatest sampling opportunity (and the least competition).

However, although territorial fish did not occupy superior sites, they did feed at significantly greater rates than fish constrained to the riffle. This concurs with previous studies (Grant, 1990), in which by keeping neighbours farther away, the aggressive territorial fish decrease competition for drifting prey and increase their own feeding rate. Conversely, the 34 non-territorial fish were constrained to an area similar in size to one large territory and suffered feeding rate depensation as a result. Furthermore, territorial fish benefitted from their exclusive access to a food supply: group 1 fish grew faster if they had a greater exclusivity to passing prey items, territorial fish having the most exclusive access to food. This complements earlier studies that hypothesise that more aggressive fish have a higher gross gain rate than less aggressive fish (Puckett & Dill, 1985; Grant, 1990).

There seemed to be a distinct hierarchy within the non-territorial fish. Larger fish were more aggressive and spent more time at the upstream end of the riffle (the preferred feeding site; Fausch, 1984), monopolising more potential prey and growing faster. This is unlike the result from experiment I, where the social hierarchy was less pronounced under greater intruder pressure and reduced rations. Therefore relatively plentiful food may be an environmental cue that prompts a fish to maintain a feeding station with aggression, so strengthening a hierarchy, unlike the case for fish on reduced rations in experiment I. Brown's (1964) economic defendability theory suggests that an animal should only defend a feeding station or territory if the energetic benefits (food intake) outweigh the costs (time and energy involved in aggression, risk

of energy). Here it can be hypothesised that in the poor environment experienced by the experimental group in experiment I the costs in maintaining an aggression-based hierarchy outweighed the benefits of obtaining what little food there was, whereas in experiment II the environment was rich enough to favour an aggression-based hierarchy amongst the fish constrained to the riffle.

The mean growth rates of group 1 fish in experiment II were higher than those of the other two groups, due to the territorial fish mostly belonging to this group. Moreover, most of the fish which had the greatest probability of joining the Upper Modal Group and smolting after one year belonged to this group, and were territorial; most territorial but virtually no non-territorial fish entered the Upper Modal Group. This is further evidence, but in the semi-natural setting of an artificial stream, that ability to obtain a preferred feeding station and withstand competition influences the age at which juvenile salmon migrate to sea (Metcalfe, 1989; 1991).

Chapter 5: Aggression and growth depression in juvenile salmon - the consequences of variation in metabolic rate.

5.1 Introduction

Intraspecific competition is a potentially serious problem in salmonid aquaculture. Competitive interactions for food are a major source of growth rate variation under aquaculture conditions, since they result in aggressive individuals consuming a disproportionate amount of food and accelerating their growth relative to less aggressive individuals. The principal effects are increasing variance and skew of the size distribution of fish (Brett, 1979; Kinghorn, 1983; Jobling, 1985; McCarthy *et al.*, 1992; Ryer & Olla, 1996). Differences in growth manifest themselves quickly and the size disparity increases, exacerbating the monopolization of food by large fish (Olla *et al.*, 1992) and suppressing the feeding activity of subordinates (Metcalfe, 1989). Furthermore, if growth rate is more dependent on competitive ability than physiological efficiency, selection for faster growing fish will favour more aggressive and competitive fish, rather than those that maximise the efficiency of growth (Weatherley, 1976; Doyle & Talbot, 1986; Swain & Riddell, 1990). However, selection studies on medaka showed a reduction in aggression when selecting for faster growing fish in a high interaction environment (Ruzzante & Doyle, 1991; 1993). This was thought to be due to relatively unaggressive, indifferent fish growing faster, since agonistic interactions are energetically costly (Li & Brocksen, 1977; Metcalfe, 1986). The markedly different findings of Ruzzante & Doyle may have been due to the high

population densities at which the selection experiments were carried out, selection for fast growth being more effective at higher population densities.

Several methods have been developed to reduce aggression in an aquaculture situation. In juvenile chum salmon, Davis & Olla (1987) showed that a high food ration resulted in less variation in growth than intermediate and low rations, competition for food being lower when food is more abundant. Resource patterning (the spatial and temporal distribution of food) also influences the intensity of agonistic interactions; aggression is more intense if food is distributed from a single, defensible point source (allowing a dominance hierarchy to be established), whereas if the food is dispersed and indefensible no dominance hierarchy is developed and aggression is lower (Olla *et al.*, 1992; Grant, 1993; Ryer & Olla, 1996). Increasing current flow also reduces aggression. Costs of aggression are greater in a fast current, since more energy must be expended when fish move to initiate an attack (Grant & Noakes, 1992). Fish living in fast currents may therefore reduce their aggression to reduce total energy expenditure. Fish swimming against a strong current are also more polarised and so their trajectories are less likely to cross (a common cause of interactions). Such a reduction in aggression with increasing current flow has been shown experimentally with brook charr (McNicol & Noakes, 1981; East & Magnan, 1987) and arctic charr (Christiansen & Jobling, 1990; Jobling *et al.*, 1994; Adams *et al.*, 1995) in aquaculture conditions.

However, an alternative method of reducing aggression would be to remove the fish most predisposed to aggression, thus improving the growth rate of the remaining fish. It is clear that larger fish are more dominant in hatchery tanks (Wankowski & Thorpe, 1979; Abbott & Dill, 1989; Metcalfe, 1994), but larger size is probably a consequence of dominance and not a cause (Huntingford *et al.*, 1990; Metcalfe *et al.*, 1992). As

rearing is often initiated with juvenile salmonids of uniform size, the initial factors that allow fish to out-compete others of the same size is relatively unclear. A recent study demonstrated that more dominant juvenile salmon in pair-wise experiments had higher relative standard metabolic rates, after controlling for body size (Metcalfe *et al.*, 1995). If such a relationship between standard metabolic rate (SMR) and dominance persists in a hatchery tank environment, it may be possible to select out the potentially dominant fish by measuring their standard metabolic rate and removing those fish with very high relative standard metabolic rates. Moreover, Ruzzante & Doyle (1991) suggested that their faster growing, non-aggressive medaka (see above) may have had a relatively more efficient standard metabolism (*sic.*) than their more aggressive conspecifics, implying that individual variation in physiology can have consequences on individual growth, mediated by behaviour.

Therefore, the aims of this chapter are to investigate any links between relative standard metabolic rate and intensity of agonistic interaction in a hatchery tank environment by varying the ratios of juvenile salmon with high and low relative standard metabolic rates. I also investigated the effect of differences in aggression between groups on subsequent average growth and growth variation.

5.2 Methods

In August 1995, the standard metabolic rates (SMR) of 70 0+ juvenile salmon derived from a pair of sea-run adults were measured at a constant temperature of 9°C. The residual standard metabolic rates of individual fish were then calculated (see

Chapter 2) and each fish was categorised as 'high' or 'low', according to whether it had a positive or a negative residual standard metabolic rate. Ten fish were excluded, as their standard metabolic rate equalled the predicted value (i.e: their residual was zero). The 60 remaining fish consisted of 30 high and 30 low standard metabolic rate fish; these two categories of fish were kept in separate holding tanks and fed *ad. lib.*, prior to individually marking their ventral sides with combinations of alcian blue dye spots at the start of the experiment.

The experiment used 3 circular tangential flow tanks (diameter = 0.5m), whose water depth was maintained at 0.2m using standpipes. The floor of each tank consisted of radial black and white stripes to create a more heterogeneous substratum, since this promotes the establishment of territories (Mikheev *et al., in press*). Twenty high SMR fish were placed in one tank, and 20 low SMR fish were placed in another. The third tank held 10 high and 10 low SMR fish. This group is referred to as the control since it contained approximately the same normal distribution of residual standard metabolic rates as the stock population. The tanks were deep sided and were raised off the ground, so that the fish were unable to see directly anyone standing adjacent to them. Behavioural observations were therefore made from a vantage point 1m away, with the aid of an overhead angled mirror. At no time during observations did the observer stand over or go nearer to the tanks. Compared with their startled behaviour when a hand was moved over the tanks, being observed with the mirror did not seem to alarm the fish.

During August and September 1995 observations were carried out twice daily (in the morning and afternoon) over 34 days; these consisted of observing each tank of salmon for 10 minutes and noting the total number of aggressive interactions between

fish. Each tank received *ad lib.* pelleted food from an automatic feeder every 30 minutes, 24 hours a day; the food was delivered from a point source to encourage aggression. In addition, the salmon were hand fed the same food five minutes before each observation. Initially, it was not possible to ascribe any aggressive interaction to any one individual fish as the fish were marked only on their ventral sides for individual identification during weighing and measuring. Therefore only absolute levels of aggression could be measured for each tank. However, towards the end of the experiment individual fish could be identified to an extent, as size differences became more apparent; data were then collected separately for three size categories of fish (large, medium, and small). Aggressive interactions consisted of charges, chases, and nips. Charges consisted of a rapid, direct and unambiguous motion towards another fish, chases followed a charge and consisted of pursuit resulting in the displacement of the attacked fish from its original position, and nips were any biting motion made by the aggressor towards another fish. These normally occurred after a chase (Abbott *et al.*, 1985; Adams *et al.*, 1995). Charges alone were the most common form of aggression, making up 80% of the total number of observed interactions. The remaining 20% consisted of charges followed by a chase, or charges followed by both a chase and a nip. Due to mortalities during the course of the experiment, aggression was standardised for between-tanks analysis as the number of aggressive interactions. $fish^{-1}$. min^{-1}. At the end of the experiment 17 salmon remained in both the 'low' and control groups, and 15 salmon remained in the 'high' group.

The salmon were anaesthetised, weighed (to the nearest 0.01g) and measured (fork length, to the nearest 0.1mm) once every two weeks to calculate individual specific growth rates (SGR) using the equation:

$$SGR = 100((\ln.W_{(2)} - \ln.W_{(1)})/ t) \quad \text{(Eq. 5.1)},$$

where $W_{(1)}$ = initial weight (g), $W_{(2)}$ = final weight (g) and t = time elapsed in days. Mean specific growth rate and the distribution of individual growth rates could then be compared between the tanks.

Following each two-weekly measurement, groups were put into a different tank from the ones they were in before to remove possible tank effects. In this way the 3 groups spent at least one week during the experiment in each tank.

5.3 Results

At the start of the experiment, mean fork length and weight for the 'high' group was 45.56±1.193 (S.E.)mm and 0.92±0.07g (n = 20) respectively. The 'low' group measured 45.24±1.49mm and weighed 0.93±0.09g (n = 20), and the control group measured 49.50±0.99mm in fork length and weighed 1.19±0.07g (n = 20). The weights of the 'high' and 'low' fish within this control group did not differ significantly from each other ('high' fish weight = 1.19+0.07g (n = 10), 'low' fish weight = 1.20+0.07g (n = 10); one way ANOVA, $F_{(1,18)} = 0.001$, $p = 0.974$). Residual standard metabolic rates were calculated from a regression equation of a double logarithmic plot of standard metabolic rate (SMR, $mlO_2.h^{-1}$) against salmon weight (W, g) for a sample of 227 juvenile salmon:

$$\ln(SMR) = -2.71 + 0.65.\ln(W) \quad \text{(Eq. 5.2)}$$

($r^2 = 0.412$, n = 227, $p<0.005$; some of the fish used to establish this relationship were also used in the experiments of chapter 3).

The 20 juvenile salmon with positive residual standard metabolic rates in the 'high' group had a mean residual of 0.039±0.006 (S.E.)$mlO_2.h^{-1}$, the 20 fish in the control group had a mean residual of 0.015±0.019$mlO_2.h^{-1}$, and the 20 fish with negative residual standard metabolic rates in the 'low' group had a mean residual of -0.020±0.002$mlO_2.h^{-1}$. Residual standard metabolic rates between the 'high' and 'low' groups were, of course, significantly different (one-way ANOVA across all three groups; $F_{(2,57)} = 5.05$, $p<0.05$, Tukey post-hoc comparison of means: 'high' vs. 'low', $p<0.05$; Fig.5.1).

There were no significant differences between aggression rates measured during the morning and afternoon (Wilcoxon's matched pairs test, comparing rates on the same day; 'high' group: $Z = 0.809$, $p = 0.418$; control group: $Z = 1.483$, $p = 0.138$; 'low' group: $Z = 0.761$, $p = 0.447$), so morning and afternoon aggression rates for each group were pooled for subsequent analysis. Mean values of aggression for each tank were: 'high' group = 0.059±0.009 (S.E.)$acts.fish^{-1}.min^{-1}$, control group = 0.047±0.005, and 'low' group = 0.022±0.002. Aggression in the 'low' group was significantly lower than both the 'high' and control groups, but there were no significant differences between the control and 'high' groups (Repeated measures ANOVA: $F_{(2,66)} = 10.35$, $p< 0.005$. Tukey post-hoc comparison of means: 'high' vs. 'low', $p< 0.0005$; control vs. 'low', $p< 0.01$; control vs. 'high', $p = 0.243$, Fig. 5.2).

To check whether these results were due to just a few very aggressive fish that had been included in the 'high' group only by chance, I separated the data from this group into 3 size classes of fish and allocated percentages of total observed aggression to each class during 24 trials at the end of the experiment (when fish could be reliably classified into size categories by eye; Table 5.1). The largest fish did tend to be the

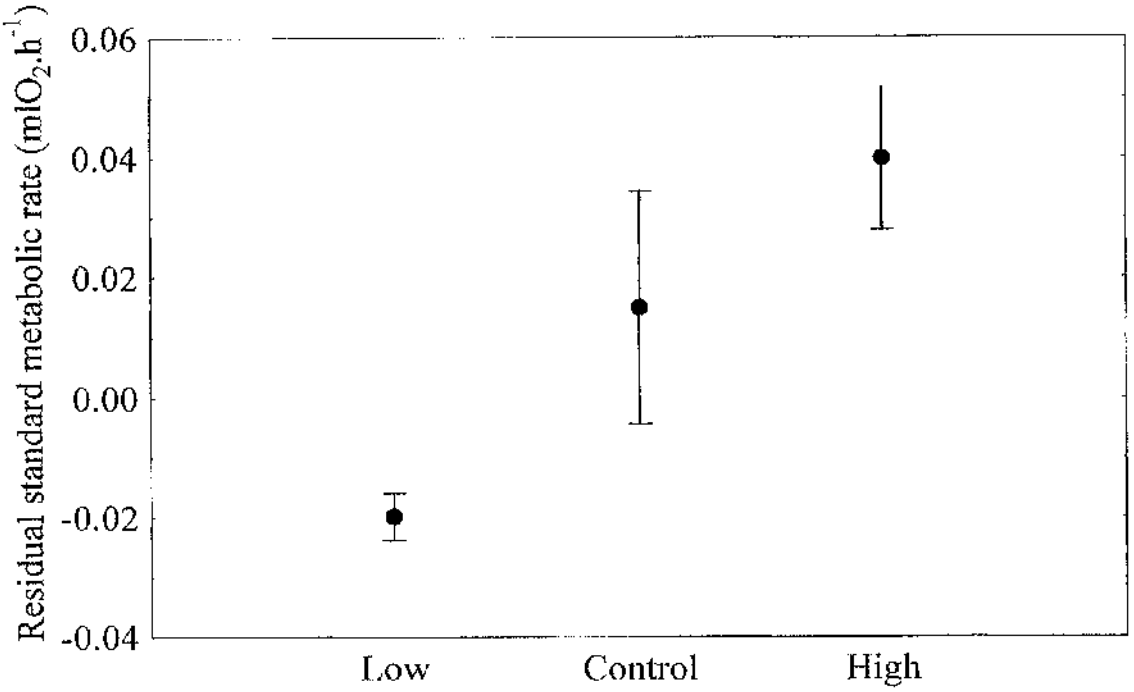


Fig. 5.1: The mean residual standard metabolic rates of the 'low' group (20 juvenile salmon with negative residual standard metabolic rates), the 'high' group (20 juvenile salmon with positive residual standard metabolic rates), and the control group (equal proportions of juvenile salmon with either positive or negative residual standard metabolic rates, n = 20). Bars denote standard errors.

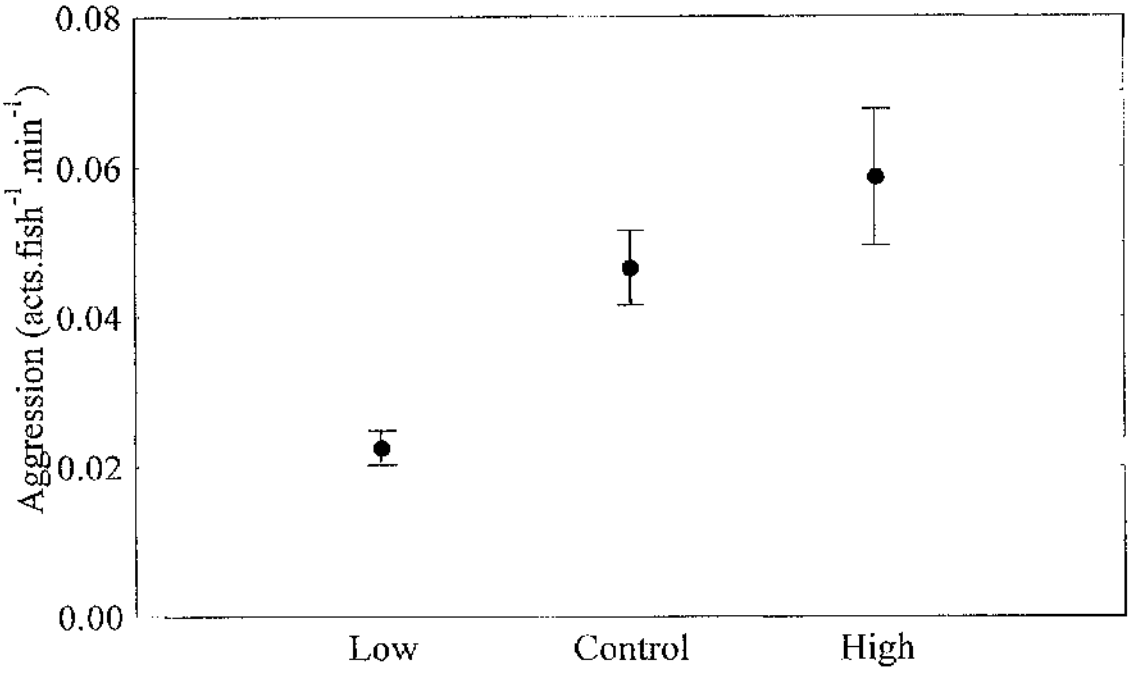


Fig. 5.2: Mean aggressive acts.fish^{-1}.min^{-1} in the 'low' group, the 'high' group, and the control group. Bars denote standard errors.

Table 5.1: The distribution of total observed aggression between 3 size classes of juvenile salmon in the 'high' (positive residual standard metabolic rate) group over 24 observations.

Size category (range in fork-lengths, mm)	Number of fish	Number of aggressive interactions	Percentage of total observed aggression contributed by size class
Small (51 - 60)	10	53	22.1
Medium (61 - 70)	4	98	40.8
Large (71 - 80)	1	89	37.1

most aggressive, although the remaining 14 salmon shared 62.9% of the total aggression in the group. Excluding the most aggressive fish, the amended mean aggression rate for the 'high' group was 0.037±0.008 acts.fish^{-1}.min^{-1}, which was still significantly greater than aggression in the low tank (Repeated measures ANOVA: $F_{(2,56)} = 15.14$, $p<0.005$. Tukey post-hoc comparison of means: 'high' vs. 'low', $p< 0.05$). Therefore the high levels of aggression associated with the 'high' group would seem to be due to the fish being generally more aggressive, rather than the chance inclusion of an aggressive fish.

Mean specific growth rates over the course of the six week experiment by weight for each tank were 0.781±0.068(S.E.)%.d^{-1} ('high' group), 0.639±0.047%.d^{-1} (control group) and 0.747±0.041%.d^{-1} ('low' group). There were no significant differences between tanks in mean growth rate (Kruskal-Wallis one-way ANOVA; $H_{(2,n=49)} = 3.20$, $p = 0.202$, Fig. 5.3). However, the distribution in growth rates was markedly different between tanks, since growth in the 'high' group was very skewed compared to the other two treatments (Fig. 5.4). By measuring the skewness and its standard error, I could establish whether the frequency distributions were skewed by testing them against the null hypothesis that skew equalled zero (i.e.: the distribution was normal; Sokal & Rohlf, 1981). The skewness of each group was: 'high'group, 1.327±0.580 (S.E. of skewness); control group, 0.087±0.550; 'low' group, 0.376±0.550. Only the 'high' group differed significantly from normal (two-tailed $t_s = 2.288$, $p<0.05$), both the control and 'low' groups being approximately normal ($t_s = 0.158$, $p>0.05$ and $t_s = 0.684$, $p>0.05$ respectively). This implies that a few individuals were growing relatively fast in the 'high' group, at the expense of the majority of juvenile salmon in that group.

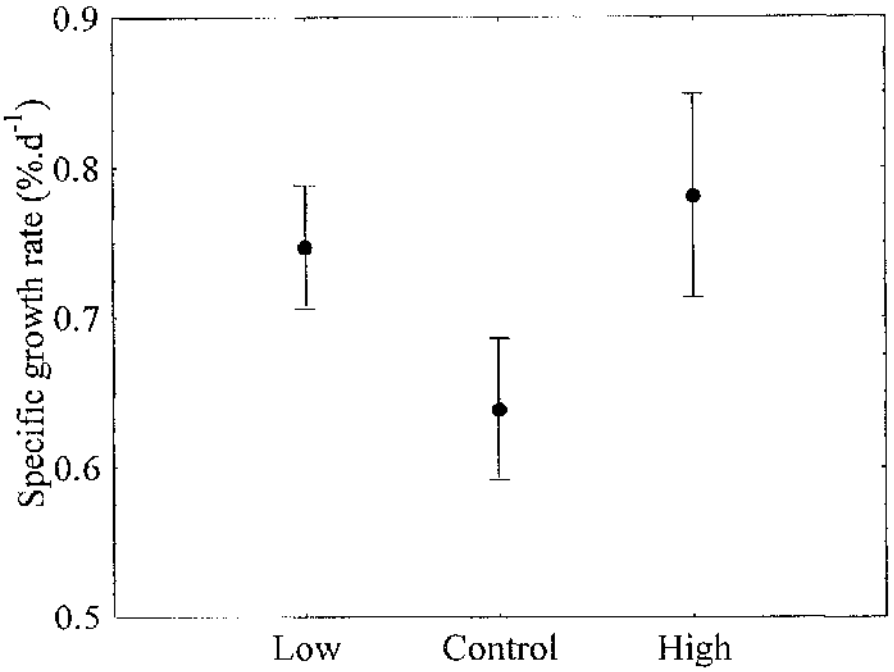


Fig. 5.3: Mean specific growth rates (%.d^{-1}) for the 'low' group, the control group, and the 'high' group. Bars denote standard errors.

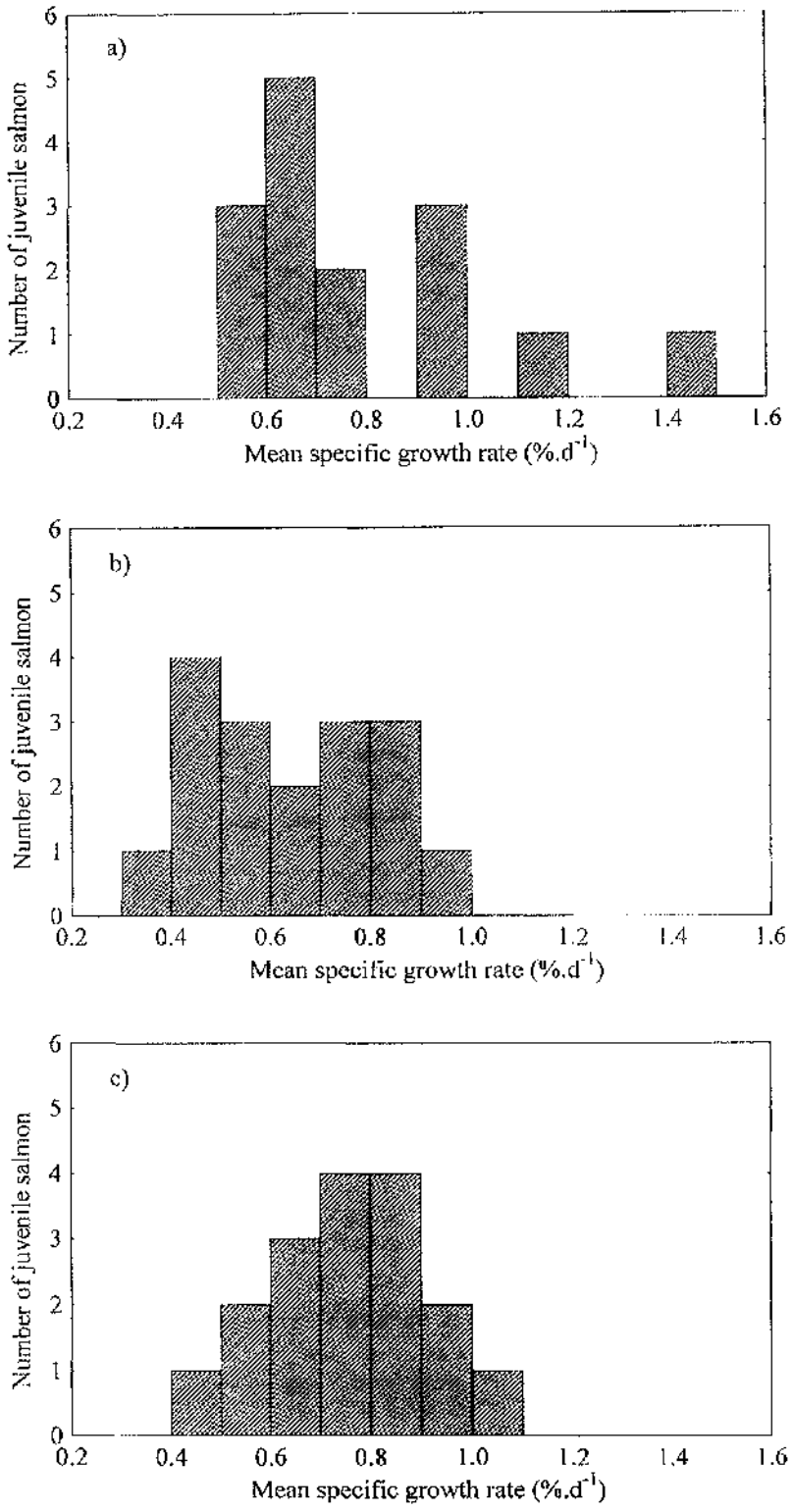


Fig. 5.4: The frequency distribution of mean specific growth rates (%.d^{-1}) in (*a*) the 'high' group (juvenile salmon with positive residual standard metabolic rates), (*b*) the control group (group with equal proportions of juvenile salmon with either positive or negative residual standard metabolic rates), and (*c*) the 'low' group (juvenile salmon with negative residual standard metabolic rates), over the course of the experiment.

5.4 Discussion

There was an overall significant difference in mean residual standard metabolic rate between the three groups, and mean aggression increased as the proportion of fish with high residual standard metabolic rates increased. The highest levels of aggression, observed in the 'high' metabolic rate group, were not due to the chance inclusion of an aggressive fish, since removing the most aggressive fish in that group would only reduce aggression by 37% i.e., still resulting in the group being significantly more aggressive than the 'low' group. It is apparent that segregating fish on the basis of relative standard metabolic rate significantly reduced aggression for the 'low' group, although the potentially dominant fish in the 'high' group tended to fight amongst themselves. This concurs with a previous study (Metcalfe *et al.*, 1990) that makes a distinction between absolute and relative status, whereby absolute status is defined as the fish's inherent ability to dominate conspecifics in a large group, and relative status as the fish's ability to be dominant in a smaller group, dependent on the quality of that group. Fish in the 'low' group, although showing the same potential range in relative status as those in the 'high' group, were probably lower in absolute status through their lower relative standard metabolic rates. This low absolute status is reflected in their low levels of aggression (cf. Abbott *et al.*, 1985). Conversely, fish in the 'high' group, while covering the complete spectrum of relative social status amongst themselves, may have had a greater mean absolute status through their relatively high standard metabolic rates. This too is reflected in their greater aggression. This parallels the study by Metcalfe *et al.* (1990), in which the group consisting of low absolute

status fish showed a less clearly defined hierarchy, and the fish of low relative status in that group did not experience growth depensation.

Average growth was not improved by segregating high and low residual standard metabolic rate fish. However, growth variation in the 'high' group was significantly skewed, presumably due to the greater proportion of more competitive individuals, greater intensity of agonistic interactions, and subsequently stronger dominance hierarchy. Dominant fish tend both to grow faster and to suppress the feeding of subordinates (Jobling, 1985; Metcalfe, 1991; Ryer & Olla, 1996). Consequently, very few fish from this group grew quickly. None of the fish from the control and 'low' groups grew as fast as the fastest growing fish in the 'high' group, but their growth variation was more normally distributed. Furthermore, they may have been less stressed as a result of lower levels of aggression, since aggression in salmonids also increases physiological stress in subordinates, when measured either as levels of brain chemicals (e.g.: monoamines and derived metabolites; Winberg *et al.*, 1991), or elevated metabolic rates (Pickering, 1992). Moreover, in a study on arctic charr, fish that had been subjected to aggressive encounters and had bite marks on their fins grew less well than fish without bite marks (Christiansen & Jobling, 1990). It is unclear from the present experiment, however, whether the poor growth of subordinates was due to aggression-induced stress or an inability to acquire food. Fish in the control tank did not have significantly different aggression rates from those in the 'high' tank, but nonetheless showed less growth depensation. Therefore, it can be implied that growth depensation in the 'high' tank was due to inability of the subordinates to acquire food, rather than to stress. Both dominant and subordinate fish are victims of attack and concominant stress (Abbott & Dill, 1989; Adams *et al.*, 1995), so we can assume that

fish in the control and 'high' tank were equally stressed, leaving the inability of subordinate fish to acquire food as a possible explanation for the greater growth depensation of fish in the 'high' tank.

However, there is a case for reducing stress if not improving mean growth in hatchery tanks through lowering aggression (Christiansen & Jobling, 1990; Winberg, 1991; Pickering, 1992; Adams *et al.*, 1995). Segregating fish through measuring individual standard metabolic rates is labour intensive and impractical on a commercial scale, although it gives an indication of relative potential dominance amongst fish of uniform size. It has been observed, however, that juvenile salmon with high relative standard metabolic rates absorb their yolk sacs quicker, and start eating exogenous food sooner (Metcalfe *et al.*, 1995; Chapter 3). Therefore it may be possible to crudely screen for those fish with very high standard metabolic rates by identifying those that have absorbed their yolk sacs relatively early. Removing these fish may eliminate potential despots in a hatchery tank.

Aggressiveness is known to be a heritable trait in salmonids (Taylor, 1990; Dunbrack *et al.*, 1996). Furthermore, this study shows variation in aggression to have a basis in intraspecific variation in physiological state. It complements previous studies on salmonids, in which induced differences in physiology were found to predict differences in competitive ability and subsequent dominance: Johnsson & Bjornsson (1994) and Johnsson *et al.* (1996) showed that injections of exogenous growth hormone positively affected dominance in rainbow trout, although there was no evidence that dominance was correlated with endogenous growth hormone levels. None the less, the above studies and this experiment suggest a link between physiology, subsequent behaviour and growth. Given the heritability of aggressiveness

and its suggested physiological basis, it may be feasible to select out potential despots through monitoring rates of yolk-sac absorption.

Chapter 6: Changes in standard metabolic rate after the onset of size bimodality in juvenile Atlantic salmon.

6.1 Introduction

During the first six months of life, sibling populations of juvenile Atlantic salmon diverge into those fish that will migrate to sea as smolts the following spring, and those that will defer migration for a further year. They are recognizable on the basis of size; by late autumn the initially unimodal length-frequency distribution has diverged into a clearly bimodal distribution, the upper mode fish (Upper Modal Group, UMG) subsequently migrating to sea as one-year old smolts, or S1's, and the lower mode fish (Lower Modal Group, LMG) remaining in freshwater for a further year and deferring migration until at least the following spring (S2's; Simpson & Thorpe, 1976; Thorpe, 1977; Thorpe *et al.*, 1980). Although these size differences are apparent in the autumn, the initiation of differential growth rates occurs in June/July, evidenced by changes in the relative rates of RNA and DNA synthesis in skeletal muscle at that time (Villarreal, 1983; Thorpe, 1987). Moreover, the appetite of fish destined for the Lower Modal Group decreases by late August (Metcalfe *et al.*, 1986), whereas the Upper Modal Group maintain their appetite and growth (Metcalfe *et al.*, 1988).

Given that the growth rates of the two modal groups are so markedly different, studies have been carried out on whether metabolism differs between the modal groups and also between smolts (S1) and parr of the same age that are deferring migration (S2). Because the discovery that juvenile salmon become segregated into a bimodal length-frequency distribution prior to smolting is comparatively recent, more work has been done on the consequence of the bimodal distribution, i.e. metabolic differences

between smolts and juvenile salmon remaining in freshwater. Baraduc & Fontaine (1956) showed that resting oxygen consumption per unit weight at 8°C was 30% higher in smolts when compared to salmon deferring migration. Power (1959) reported the opposite below 13.5°C, but above that temperature smolts had higher weight-specific resting metabolic rates. Higgins (1985) also showed that smolts have greater standard metabolic rates, after allowing all fish to evacuate their guts and taking oxygen consumption measurements continuously over 24 hours. Maxime *et al.* (1989) also showed weight-specific standard metabolic rate to be higher in smolts than parr.

However, few comparisons have been made between the two modal groups prior to smolting. Higgins (1985), in addition to his work on smolts, recorded higher weight-specific standard metabolic rates in Upper Mode than Lower Mode juvenile salmon, once the bimodal split had become pronounced. Wright *et al.* (1990) implied a lower metabolic rate in Lower Mode fish on the basis of slower rates of otolith accretion in these fish; otolith growth was more closely linked to metabolic rate than somatic growth (Mosegaard *et al.*, 1988). This was directly tested by Wright (1991), who found that otolith accretion and standard metabolic rate were indeed both lower in the Lower Modal Group.

However, the above studies did not track individual fish from both modal groups from the onset of bimodality through to the spring. This chapter presents a time course of measurements of standard metabolic rate from fish of both modal groups over a period of seven months, and aims to highlight the dynamics of changing standard metablic rates in both modal groups over a period of time when the ambient water temperature decreased sharply before rising again. Individual variation in standard metabolic rates is measured on a weight-independent basis, rather than a weight-

specific one, by calculating deviations of the observed standard metabolic rate away from a value predicted from a weight vs. standard metabolic rate regression equation (residual standard metabolic rates; see Chapter 2). This method of measuring individual variation in metabolic rate between individuals has been espoused by McNab (1988), Daan *et al.* (1990), and Metcalfe *et al.* (1995), and avoids the problem of interpreting results from fish of markedly different size ranges (the two modal groups), when large fish respire much less than small fish on a weight-specific basis (Schmidt-Nielsen, 1984). Data are also presented on the consistency of these residual values for each individual, given that the faster growing fish in the Upper Modal Group are increasing in size, and will have a progressively greater predicted standard metabolic rate at each sampling period.

6.2 Methods

Rather than tracking ambient water temperature and measuring the standard metabolic rates of the same fish at a different temperature each time, the standard metabolic rates of 62 juvenile Atlantic salmon were measured 6 times from November 1994 to June 1995 at 13°C. Sampling dates were 10-14th November, 10-14th December, 20-24th January, 18-21st March, 7-8th May, and 3rd June, with a mean inter-sampling period of 41±6d. Ambient water temperatures at times of sampling were 9.4±0.3, 7.7±0.2, 4.9±0.2, 4.3±0.2, 9.8±0.2 and 12.5°C respectively; salmon were kept at ambient water temperature between sampling periods. Fish from both modal groups were all treated similarly, and standard metabolic rate was measured as described in

Chapter 2. Each fish was individually marked with a combination of alcian blue dye spots to aid identification, and fish were fed *ad lib.* with commercial pelleted food in a holding tank between measurements. Fish were assigned to modal groups on the basis of size, those fish with a fork length greater than 75mm in November (first sampling period) being assigned to the Upper Modal Group (n = 27 of the 62 fish), following Metcalfe *et al.* (1988). Fork length (mm) and weight (g) were measured after each measurement of oxygen consumption in order to calculate specific growth rate ($\%d^{-1}$).

6.3 Results

As juvenile salmon were measured at 13°C throughout the experiment, temperature differences between the measuring temperature and ambient temperature for each sampling period (November, December, January, March, May and June) were 3.6, 5.3, 8.1, 8.7, 3.2 and 0.5°C respectively. The growth rates of the fish over the winter indicated that the original assignment to modal groups in November was 100% accurate. Mean weights for the two modal groups during the 6 sampling periods are presented in Table 6.1. Due to mortalities there were no UMG fish in the sixth sampling period. Regression equations of standard metabolic rate against weight (both axes were natural log. transformed) of both modal groups for each sampling period are given in Table 6.2i, and significance values for each regression equation are presented in Table 6.2ii.

Table 6.1: Mean weights of UMG and LMG juvenile salmon at the time of the six sampling periods over 7 months.

Sampling period	UMG mean weight±S.E.(g) (n)	LMG mean weight±S.E.(g) (n)
November	6.68±0.47 (27)	1.99±0.10 (35)
December	6.76±0.46 (24)	2.12±0.10 (28)
January	7.84±0.50 (24)	2.32±0.11 (22)
March	10.30±0.67 (24)	2.49±0.12 (17)
May	16.90±1.02 (21)	3.20±0.24 (14)
June	*	4.40±0.39 (10)

*: no data for UMG in June due to mortalities.

Table 6.2i: Regression equations for the double-logarithmic relationship between standard metabolic rate ($mlO_2.h^{-1}$) and weight (g) in Upper and Lower Modal Group juvenile salmon during each sampling period. Also given are the results of ANCOVA analyses comparing regression intercepts and mass exponents.

Sampling period	Intercept		Mass exponent		ANCOVA	
	LMG	UMG	LMG	UMG	Intercept	Mass exponent
November	-1.731	-1.708	0.621	0.748	$F_{(1,59)}$= 1.21, p= 0.28	$F_{(1,59)}$= 0.32, p= 0.58
December	-1.482	-2.688	0.324	1.314	N/A	$F_{(1,45)}$= 10.61, p< 0.005
January	-1.847	-2.742	0.970	1.431	$F_{(1,42)}$= 3.15, p= 0.08	$F_{(1,41)}$= 2.18, p= 0.15
March	-2.200	-2.317	1.260	1.202	$F_{(1,38)}$= 0.83, p= 0.37	$F_{(1,37)}$= 0.03, p= 0.87
May	-2.323	-1.834	0.842	0.872	$F_{(1,32)}$= 8.76, p< 0.01	$F_{(1,31)}$= 0.189, p= 0.89

Table 6.2ii: Significance values of the double-logarithmic regression equations of standard metabolic rate ($mlO_2.h^{-1}$) against weight (g) in Upper and Lower Modal Group juvenile salmon during each sampling period.

Sampling period	UMG	LMG
November	r^2= 0.555, n= 27, p< 0.001	r^2= 0.228, n= 35, p< 0.005
December	r^2= 0.485, n= 24, p< 0.001	r^2= 0.087, n= 28, p= 0.06
January	r^2= 0.676, n= 24, p< 0.001	r^2= 0.601, n= 22, p< 0.001
March	r^2= 0.706, n=24, p< 0.001	r^2= 0.368, n= 17, p< 0.01
May	r^2= 0.726, n= 21, p< 0.001	r^2= 0.571, n= 14, p< 0.005
June	*	r^2= 0.376, n= 10, p< 0.05

*: no data for UMG in June due to mortalities.

Regression equations of standard metabolic rate ($mlO_2.h^{-1}$) against salmon weight (g) for both modal groups within each sampling period differed significantly in slope only during December (Fig. 6.1*a*) and in elevation only during May (Fig 6.1*b*, Table 6.2i & 6.2ii).

However, comparisons of regression lines between the two modal groups are difficult since there was such a size difference between the two groups of fish. In order to compare fish of different modal groups but comparable sizes and acclimation temperatures I contrasted the standard metabolic rate vs. weight relationships of Lower Modal Group fish in May (when they weighed an average of 3.20±0.16g, range 2.01 - 5.47g) with that of the Upper Modal Group in November (mean weight = 6.68±0.47g, range 2.72 -11.59g). Regression equations between standard metabolic rate ($mlO_2.h^{-1}$) and weight (g) for both groups (see Table 6.2ii) did not differ significantly in slope ($F_{(1,38)} = 0.11$, $p = 0.754$). However, the two groups differed significantly in elevation ($F_{(1,38)} = 20.24$, $p<0.0001$, Fig. 6.2). This implies that LMG fish in May were consuming oxygen at a lower rate than UMG fish of the same size in November.

To determine the effects of time of year and modal group on the residual standard metabolic rates, I calculated residuals of each measurement from the pooled 'common' regression line of oxygen consumption on weight, calculated by using all measurements across all sampling periods. The common regression equation of standard metabolic rate ($\dot{V}O_2$, $mlO_2.h^{-1}$) against weight (W, g; both axes were natural log. transformed) was

$$\dot{V}O_2 = 0.96.W - 1.98 \qquad \text{(Eq. 6.1)}$$

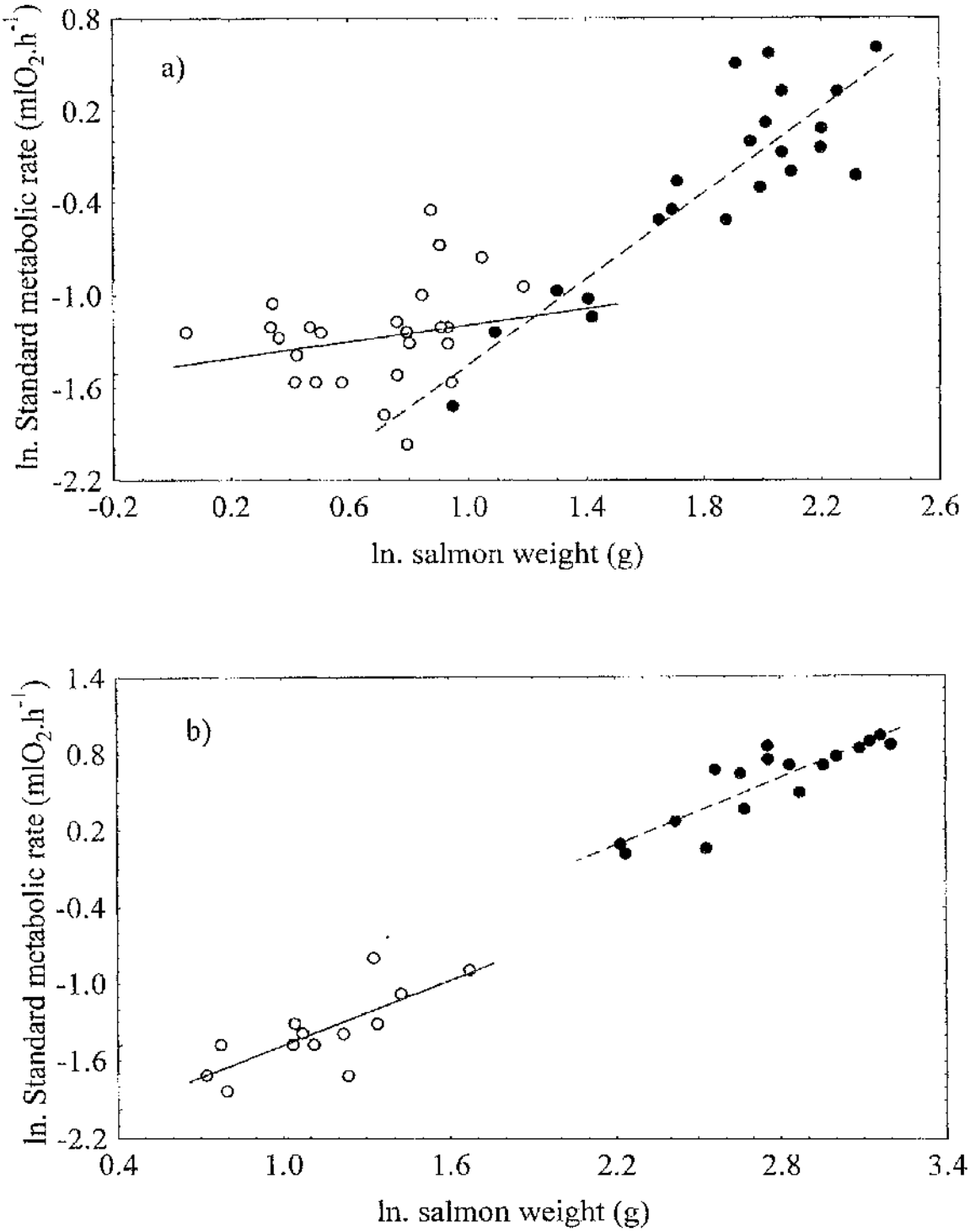


Fig. 6.1: Relationship between salmon weight (g) and standard metabolic rate ($mlO_2.h^{-1}$) for UMG (•) and LMG (o) fish in (*a*) December and (*b*) May (both axes natural log. transformed).

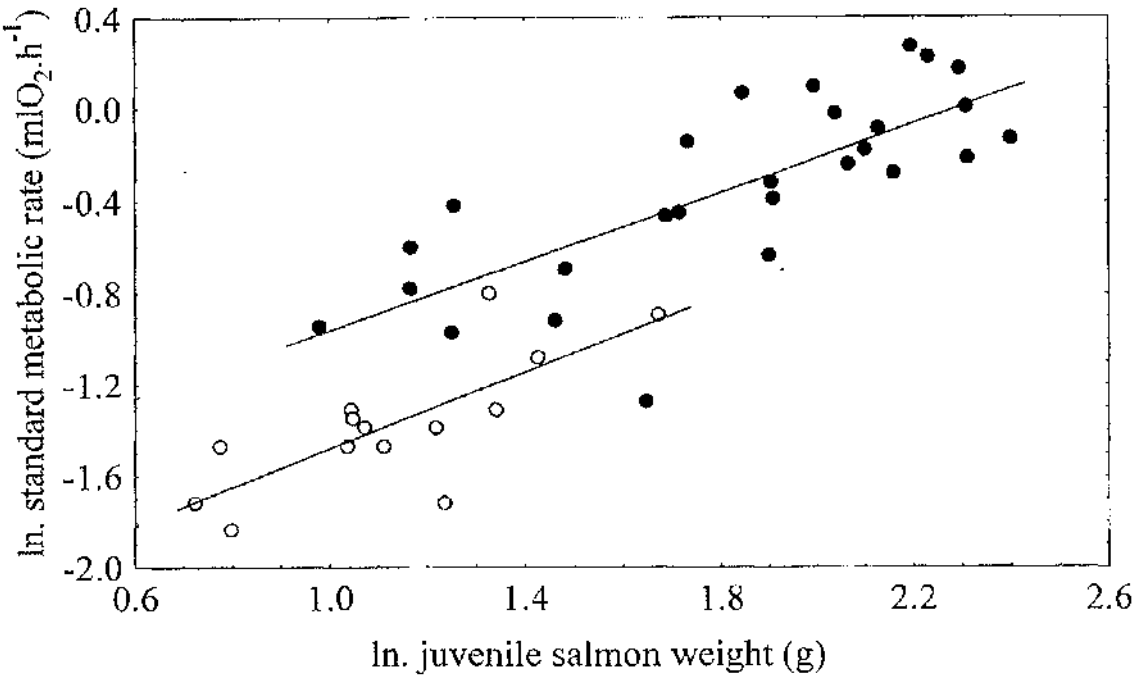


Fig. 6.2: Relationship between salmon weight (g) and standard metabolic rate ($mlO_2.h^{-1}$) for UMG salmon in November (•) and LMG fish in May (o). See text for statistical comparison).

(r^2 = 0.834, n = 245, $p<0.0001$, Fig. 6.3). This represented fish ranging in size from 1.00g to 24.37g (mean weight = 5.79±0.31g). Changes in residual standard metabolic rate for each modal group over the six months are presented in Fig. 6.4. Time of year had a significant effect on residual standard metabolic rate for both the UMG and LMG (Repeated measures ANOVA, $F_{(4,64)}$ = 9.34, $p<0.0001$ and $F_{(4,52)}$ = 9.40, $p<0.0001$ respectively). Furthermore, residual standard metabolic rates for UMG salmon were significantly greater than those for LMG salmon in January and March, but there was no difference in May. Conversely, residual standard metabolic rates for LMG salmon were significantly greater than those for UMG salmon in November (Table 6.3). The interaction term (time of year x modal group) also had a significant effect on residual standard metabolic rate ($F_{(4,222)}$ = 6.25, $p<0.0001$), implying that time of year had a bigger effect on one modal group, namely the UMG (Fig. 6.4).

Individual fish within modal groups had consistently high or low residual standard metabolic rates, as indicated by Kendall's coefficient of concordance (a non-parametric test of association between residual values for each fish from each month) of the residuals from each sampling period calculated from the pooled regression equation (Eq. 6.1; Kendall's coefficient of concordance for UMG = 0.414 (n = 17, 4 d.f.) and LMG = 0.413 (n = 14, 4 d.f.), both were significant at $p<0.001$). Fig. 6.5 shows that many of the fish did maintain a relatively similar residual standard metabolic rate over the seven months. However, while fish from both modal groups were consistent in their relative rankings of residual standard metabolic rates, individual fish from the UMG showed significantly greater monthly variation in residual standard metabolic rate, standard deviations being significantly higher in the UMG than the LMG (mean

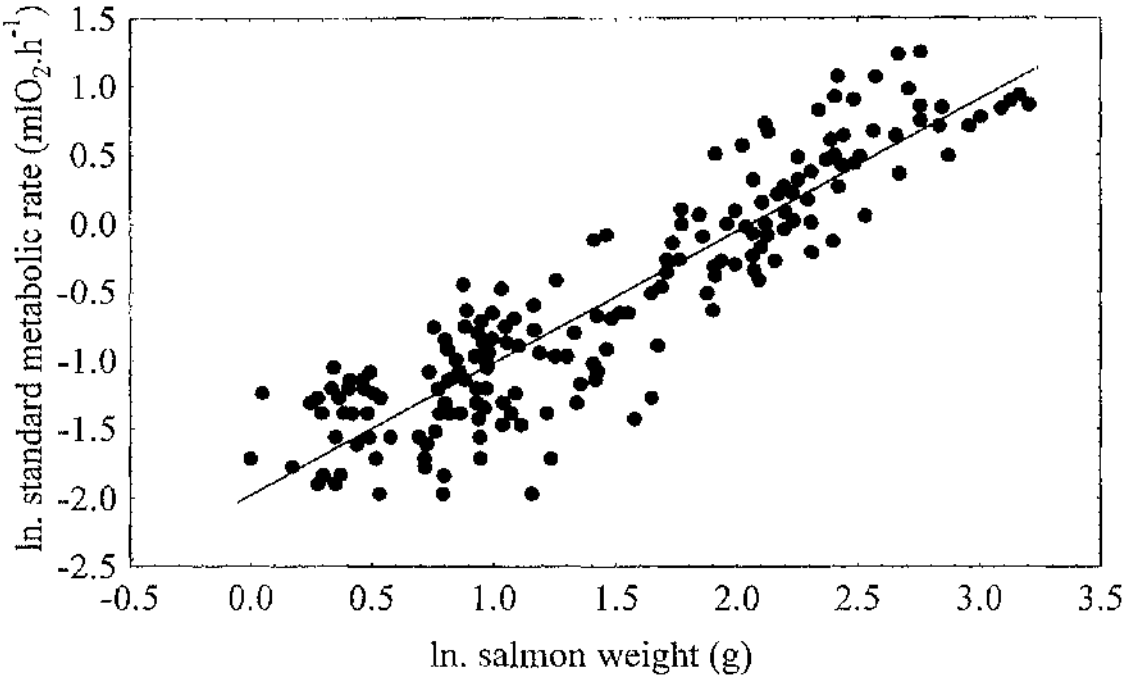


Fig. 6.3: Relationship between salmon weight (g) and standard metabolic rate ($mlO_2.h^{-1}$) pooling all six sampling periods (both axes natural log. transformed).

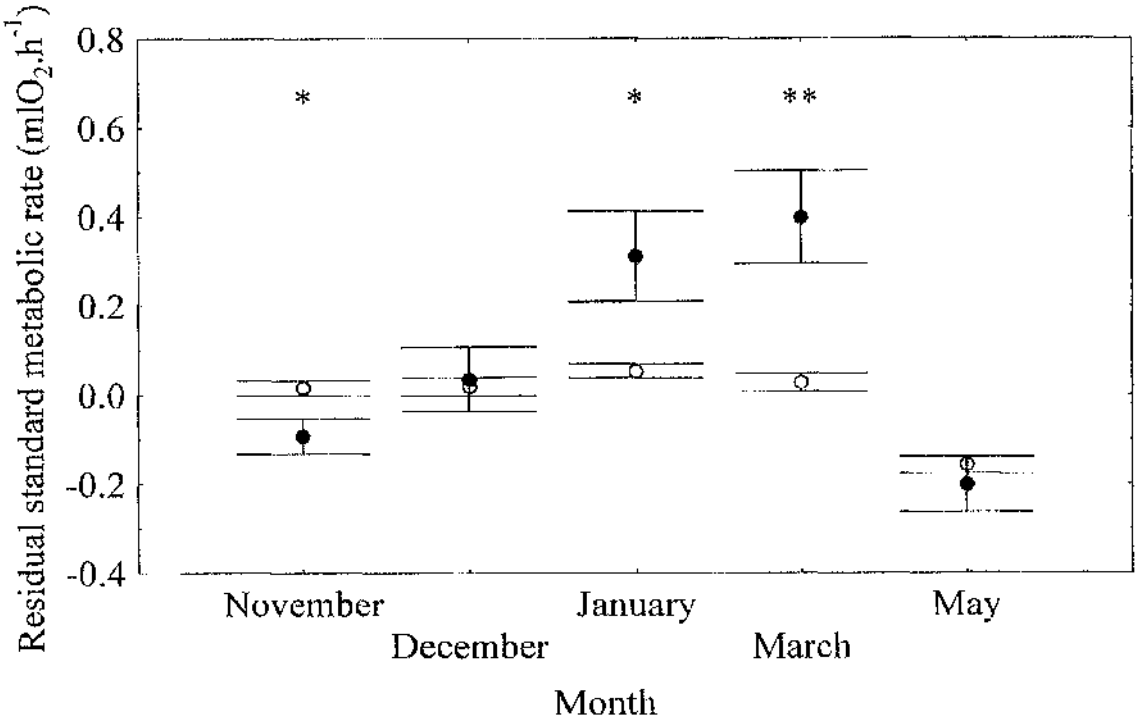


Fig. 6.4: Changes in residual standard metabolic rate ($mlO_2.h^{-1}$) for UMG (•) and LMG (o) juvenile salmon by month. Significant differences between modal groups (see Table 6.3) are represented by asterisks: *, $p < 0.01$; **, $p < 0.005$. Bars denote standard errors.

Table 6.3: One-way ANOVA's between residual standard metabolic rates of the Upper and Lower Modal Groups during each sampling period.

Sampling period	One-way ANOVA
November	$F_{(1,60)} = 7.54$, $p<0.01$
December	$F_{(1,47)} = 0.06$, $p = 0.807$
January	$F_{(1,43)} = 6.02$, $p<0.01$
March	$F_{(1,39)} = 8.75$, $p<0.005$
May	$F_{(1,33)} = 0.33$, $p = 0.568$

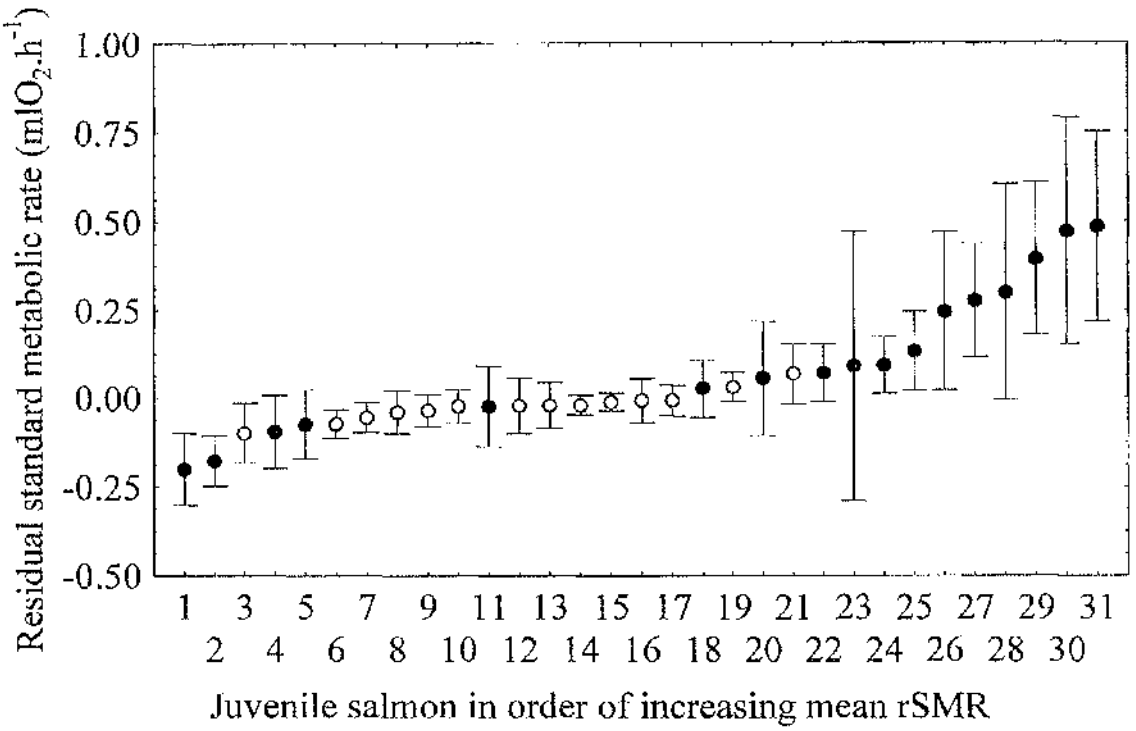


Fig. 6.5: Mean residual standard metabolic rate ($mlO_2.h^{-1}$) for UMG (•) and LMG (o) juvenile salmon surviving until May, ranked in order of increasing mean, calculated from Eq. 6.1. Bars denote standard errors.

UMG S.D. = 0.377±0.053 (S.E.), n = 17, mean LMG S.D. = 0.119±0.011, n = 14; one-way ANOVA, $F_{(1,29)} = 18.87$, $p<0.0005$).

When juvenile salmon from both modal groups were combined, a significant correlation was observed between an individual's mean residual standard metabolic rate (calculated from Eq. 6.1) and specific growth rate by weight over the seven months (%d^{-1}; Spearman's Rank correlation, $r_s = 0.515$, n = 31, $p<0.005$). However, within modal groups mean growth between November and May did not correlate significantly with residual standard metabolic rate (LMG, $r_s = -0.257$, n = 14, p = 0.375; UMG, $r_s = 0.056$, n = 17, p = 0.830). Rather, mean growth differed significantly between modal groups: over the entire period (from November to May) mean specific growth rate in the UMG was 0.236±0.009%d^{-1} (n = 17), and in the LMG was 0.067±0.015%d^{-1} (n = 14, one-way ANOVA: $F_{(1,30)} = 100.27$, $p<0.0001$). Data for specific growth rates in both modal groups are presented in Table 6.4; as expected the UMG grew significantly faster than the LMG throughout the experiment.

Table 6.4: Mean specific growth rates in weight for UMG and LMG juvenile salmon between 5 sampling periods over 6 months, with significance values from one-way ANOVA.

Sampling period	Mean specific growth rate (%.d^{-1}±S.E.)		ANOVA
	UMG	LMG	
November-December	0.149±0.033	0.014±0.022	$F_{(1,46)}$= 12.93, p<0.001
December-January	0.148±0.010	0.037±0.015	$F_{(1,41)}$= 37.10, p<0.0001
January-March	0.203±0.008	0.004±0.008	$F_{(1,39)}$= 278.90, p<0.0001
March-May	0.442±0.019	0.210±0.040	$F_{(1,33)}$= 33.28, p<0.0001

6.4 Discussion

The Upper Modal Group grew faster than the Lower Modal Group throughout the winter, although fish in the lower mode had increased their growth rate by May. This is consistent with previous studies on the time-divergence in length between modal groups (Thorpe *et al.*, 1980; Thorpe *et al.*, 1982; Higgins, 1985). The first differences in weight-specific metabolic rate between the two modal groups of juvenile salmon were apparent in December, when the regression equations of standard metabolic rate against weight for both modal groups differed significantly in slope (Upper Modal Group mass exponent = 1.314, Lower Modal Group mass exponent = 0.324). This difference in measured oxygen consumption occurred earlier than that recorded by previous studies (Higgins (1985), Maxime *et al.* (1989) and Wright (1991) all carried out their studies in late winter-spring). However, my results agree with the general findings of the above studies in that the Upper Modal Group usually have higher weight-specific standard metabolic rates than the Lower Modal Group. No further weight-specific metabolic differences were reported until May, when a significant difference in elevation between the regression equations for both modal groups was apparent (UMG intercept = -1.834, LMG intercept = -2.323). Despite fish from both groups being markedly different in size, this implies that Upper Modal Group salmon of similar size to Lower Modal Group salmon are still consuming oxygen at a greater rate on a mass-independent basis. Higgins (1985) found that upper mode salmon had significantly larger hearts as a function of body weight than lower mode fish, pointing to a difference in respiratory activity between the two groups. This may explain the difference in standard metabolic rates in December. However, by May the Upper

Modal Group are about to smolt; Higgins (1985) found no difference in heart size between smolts and parr, whereas Poupa *et al.* (1974) found an increase in relative heart weight after migration, preceded by a thickening in the ventricular shell of the smolts. Higher metabolic rates in the Upper Modal Group in winter and prior to smoltification, possibly due to increasing heart size, have been suggested as pre-adaptations to future long distance marine migrations with associated high metabolic demands (Armstrong & West, 1994).

However, the difference in regression lines recorded in May (Fig. 6.2*b*) provides only weak evidence of weight-specific differences in standard metabolic rate, due to the disparity in size between the two modal groups. Differences in standard metabolic rate between fish of different modal groups but of comparable size were directly examined by comparing Upper Modal Group salmon in November with Lower Modal Group fish in May. The regression equations of standard metabolic rate against weight for both groups of fish differed only in elevation, directly showing that the Upper Modal Group have significantly higher weight-specific standard metabolic rates than Lower Modal Group fish of comparable size.

Differences in regression equations between groups of fish (namely, the Upper and Lower Modal groups) give only an indirect impression of how the metabolism of individual fish from both groups changes over time. Therefore, individual deviations away from an oxygen consumption value predicted by a regression equation of standard metabolic rate against weight (residual standard metabolic rate) were used as a measure of individual variation. Both modal group and time of year had significant effects on residual standard metabolic rate. Moreover, time of year had a greater effect on the Upper Modal Group (Fig. 6.4). While mean monthly residual standard

metabolic rates in the Lower Modal Group remained relatively static, residuals for fish in the Upper Mode steadily increased until March before decreasing to a value similar to that of the Lower Mode by May. This variation in the Upper Modal Group may be a consequence of the Upper Modal Group's metabolic responsiveness to temperature change; Power (1959) found that weight-specific standard metabolic rate was lower in smolts than in fish deferring migration below 13.5°C, but was higher above that temperature. He therefore hypothesised that they were metabolically more responsive to temperature change. Conversely, residual standard metabolic rates in the Lower Modal Group are relatively invariant throughout the winter; they may be demonstrating a suppressed metabolic response relative to the Upper Modal Group, in a similar fashion to their suppressed food intake and growth during winter (Simpson & Thorpe, 1976; Higgins, 1985).

However, it is possible that the apparent seasonal changes in metabolic rate may instead be due to differences in the optimal temperature for enzymatic activity. Studies of the enzymes involved in respiration has shown differences in enzyme efficiency between the two modal groups. Lactate dehydrogenase (LDH), an enzyme that converts pyruvate to lactate during glycolysis has been extensively examined in studies of thermal adaptation. Graham (1994) showed that LDH in Upper Modal Group salmon becomes seasonally adapted, so that the reduction of pyruvate to lactate is most efficient at current environmental temperatures, whereas Lower Modal Group fish show much less of a seasonal adaptation. Enzyme efficiency is measured with the Michaelis constant (K_m), and is most efficient when enzyme-substrate affinity is highest and K_m is low. In the present experiments, fish would have been acclimated to the ambient temperature regime but metabolic rates were always measured at 13°C.

Therefore in mid-winter Upper Modal Group fish might have had an elevated metabolic rate because the temperature at which oxygen consumption was measured was significantly higher than the temperature to which they were acclimated, so that for the short duration of the measurement of metabolism their metabolic enzymes were working inefficiently. In May and November, when the difference between ambient and sampling temperatures was relatively small (approximately 3.0°C), the Upper Mode residual standard metabolic rates were lower and more similar to those of the Lower Modal Group. This suggests more efficient functioning of their metabolic enzymes during the measurement period. Conversely, since such seasonal enzyme adaptation is not apparent in the Lower Modal Group (Graham, 1994), one would not expect the residual standard metabolic rate of those fish to vary significantly throughout the time sampled.

However, differences between individuals in their residual standard metabolic rates were fairly consistent from month to month in both modal groups. The reproducibility of measurements may reflect the fact that the standard metabolic rate is a fixed minimum rate of oxygen consumption, below which physiological function is impaired (Priede, 1985). It has been hypothesised that deviations of basal metabolic rates away from an allometric predicted value in a variety of taxa are due to relative organ masses. This has been shown in several species of birds, where residuals of basal metabolic rate were correlated with residuals of metabolically active organs such as the heart and kidneys (Daan *et al.*, 1990). In mammals, no association was found between relative basal metabolic rate and relative brain size, although this did not preclude organs directly involved in energy mobilization having an effect on relative basal metabolic rate (McNab & Eisenberg, 1989). Therefore, it can be hypothesised that the

consistency of residual standard metabolic rates in both modal groups may be due to relative organ masses remaining broadly invariant within an individual throughout the sampling period, especially in the Lower Modal Group.

Variation in residual standard metabolic rate was significantly higher in the Upper Modal Group; this may be due to changes in relative organ size that have been reported for this modal group. By spring, fish in the Upper Modal Group have significantly larger hearts as a function of body weight than lower mode salmon (Higgins, 1985), and the greater variation in residual standard metabolic rate throughout the study may be a reflection of that, as individual upper mode fish are undergoing greater physiological change relative to the Lower Modal Group.

Chapter 7: General Discussion

7.1 Variation in standard metabolic rate and subsequent behaviour

One of the tenets of the hypothesis that higher relative standard metabolic rates confer dominance in juvenile salmon is that higher standard metabolic rates correlate with large metabolic scopes (Priede, 1985; Metcalfe *et al.*, 1995). However, this study suggests that active metabolic rate represents a ceiling for aerobic metabolic activity that gets lower as standard metabolic rate increases in juvenile salmon of a narrow size range. This is because the relationship between weight-specific standard and active metabolic rate displayed negative allometry. In addition, on a mass-independent basis (using individual deviations, or residuals, from allometric predictions of standard metabolic rate), factorial metabolic scope was negatively correlated with residual standard metabolic rate (Chapter 2). Both findings imply that if the standard metabolic rate is high, less metabolic scope for activity remains than if the standard metabolic rate is lower. This is contrary to the assumption in Metcalfe *et al.* (1995) that suggests that salmon with high relative standard metabolic rates have correspondingly greater metabolic scopes within which they can acquire dominance by carrying out greater activity such as aggression. However, the present study found that juvenile salmon with high relative standard metabolic rates were indeed more aggressive than fish with low relative standard metabolic rates, although the data imply that the more aggressive fish have a smaller metabolic scope.

Hayes *et al.* (1992) hypothesised that any correlation between metabolic rate and life-history arose from consequences of resource allocation. The principle of resource

allocation states that available energy is partitioned between maintenance, growth and reproduction (Gadgil & Bossert, 1970). This would manifest itself as variation in, for instance, mammalian litter size (a life-history variable) correlating with variation in costs of maintenance, or basal metabolic rate (Hayes *et al.*, 1992). The principle of resource allocation is analogous to partitioning the components of metabolism such as locomotor activity and feeding metabolism within the limits of standard and active metabolic rate (Brett & Groves, 1979; Priede, 1985). Therefore, increased allocation to one component such as maintenance reduces energy available for other uses (e.g. growth and reproduction), if total energy is fixed (Hayes *et al.*, 1992). In addition to higher relative standard metabolic rates reducing energy available to other components of metabolic scope, individuals with higher metabolic rates require more food (Titus, 1990; Clarke, 1992) to maintain their higher levels of maintenance. However, juvenile salmon with high standard metabolic rates, although requiring more food, appeared to maintain a lower feeding motivation when tested in isolation (Chapter 3). They achieved a higher dominance status, however, through greater aggression (whether in pairs or in groups, Chapters 3 & 4), and therefore were more likely to obtain a territory. By this means individuals with a high cost of maintenance could guarantee a reliable access to available food (Elliott, 1984; 1990), since salmonid social hierarchies are quite stable over time (Jenkins, 1969; Grant *et al.*, 1989).

In the territorial system of juvenile salmon, individuals of differing relative standard metabolic rates may employ alternative methods of balancing their energy budgets: salmon with high standard metabolic rates and hence smaller metabolic scopes employ greater aggression in order to guarantee a food source, at the expense of movements associated with foraging. Foraging movements, measured here as feeding motivation,

are themselves energetically costly (Puckett & Dill, 1985; Krohn & Boisclair, 1994). Since aggression increases the probability of acquiring a feeding territory in a salmonid social hierarchy (Fausch, 1984; Puckett & Dill, 1985; Grant, 1990), salmon with high costs of maintenance and limited metabolic scope may opt for using that scope primarily for aggression, affording them a territory within which they can then feed and maintain their high standard metabolic rate. However, territory holders within groups of salmon tested in an artificial stream did forage at greater rates than fish without territories (Chapter 3). This may be a consequence of territory size and not the motivational state of the territory holder, as neighbours will be kept further away, decreasing competition for passing prey items (Puckett & Dill, 1985; Grant, 1990).

Moreover, the relatively small metabolic scope of fish with high relative standard metabolic rates manifests itself further in an environment with little food. Juvenile salmon with high metabolic rates can afford to be aggressive when food is plentiful, and still allocate resources to somatic growth, especially as they may have already acquired a feeding territory. However, when food is in short supply high metabolic rate fish grow less well than predicted for a particular location; their high costs of maintenance prevent them from allocating as much resources to growth as conspecifics with low standard metabolic rate (Chapter 4). This is similar to Clarke's work on blennies (1992): roughhead blennies could live in poor areas of coral reef as they had lower costs of maintenance, whereas spinyhead blennies inhabited the more profitable areas through competitive exclusion.

The relationship between standard metabolic rate and behaviour was also apparent in hatchery tanks. Aggression was greater in the group containing only fish with high standard metabolic rates (Chapter 5). This is despite the variation in relative standard

metabolic rate and relative status between the fish probably being similar to that in the group containing only low standard metabolic rate fish, since relative status is the fish's ability to dominate and is dependent on the quality of the fish with which it interacts. Greater aggression amongst the high metabolic rate fish was therefore probably due to their higher absolute status, which is their inherent ability to dominate conspecifics and is independent of the quality of the conspecifics. An aim of this study was to improve mean growth in hatchery tanks. This was done by taking out the potentially dominant salmon with high standard metabolic rates which might monopolise disproportionate amounts of food. Mean growth was not significantly better in the group of low metabolic rate fish, but the distribution of individual mean growth rates was more even. This concurs with an earlier study (Metcalfe *et al.*, 1990), in which a group of fish with low absolute status showed a less clearly defined hierarchy, and the subordinates of that group did not experience growth depensation, allowing a more even distribution of growth rates.

7.2 Behaviour, prior residence and life-history strategies

In an artificial stream, relative standard metabolic rate correlated with net aggression and the percentage time spent in the water column: fish with high relative standard metabolic rates were both highly aggressive and very mobile in the water column (Chapter 4). Conversely, fish with low relative standard metabolic rates were relatively unaggressive yet spent similar amounts of time in the water column. This may correspond to different behavioural strategies outlined in earlier salmonid studies. One

strategy is that territorial fish actively defend an area, a high cost-high return strategy involving more aggression and competition for food in the water column with other territorial fish (Metcalfe, 1986). Another strategy is to 'float': 'floating' fish spend similar amounts of time in the water column as territorial fish as a consequence of being attacked. Floaters are unable to defend a territory and live in the spaces between territories (Li & Brocksen, 1977; Puckett & Dill, 1985). However, fish with standard metabolic rates and aggression rates intermediate between the two extremes spent a correspondingly intermediate time in the water column, and also grew faster than fish spending most of their time in the water column. Such fish may be employing a strategy of reducing routine metabolic costs and hence gaining greater growth efficiency (Paloheimo & Dickie, 1965; Metcalfe, 1986). These strategies, possibly employed depending on individual standard metabolic rate, may be partly responsible for population regulation in a stream. When the denisty of non-territorial fish is high, the largest territorial fish could spend so much time in territorial defence that there would be insufficient time to obtain an adequate energy intake (Elliott, 1993). Increasing defence costs have been hypothesised as eliminating larger juveniles at high initial fish densities, and increasing selection intensity for an optimum fish size (Elliott, 1990; 1993).

When prior residence was added as a factor in determining dominance (Chapters 3 & 4), it tended to swamp any effects of relative standard metabolic rate on subsequent behaviour. Introducing prior residence was an attempt to make the overall design of the experiments more natural. Although the majority of salmonid fry in a single redd emerge fairly synchronously over about three days (Gustavson-Marjanen & Dowse, 1983), the total emergence time can be several weeks long (Brännäs, 1987). In both

pairs and groups of fish, relative size was the next best predictor (after prior residence) of aggression and dominance. In the artificial stream, only fish from the first group to be introduced actually acquired and defended large territories. However, the size range between groups was quite small, showing that prior residence alone, and not necessarily the size advantage it may confer (e.g. Mason & Chapman, 1965; Chandler & Bjornn, 1988) had a strong influence on subsequent dominance. In addition, there was a correlation between aggression and size, the larger fish acquiring territories through increased aggression. This is consistent with previous studies (Jenkins, 1969; Fausch, 1984). The data implied that aggressive fish acquired territories, rather than that territory-holders subsequently became dominant, since there was also a clear correlation between aggression and size in fish which failed to acquire territories.

In experiments using only pairs of fish, the resident was dominant in the majority of cases, especially if it was larger, and an intruder would only acquire dominance if it was much larger (> 7%). This parallels the findings above, showing that size is a good indicator of status (Turner & Huntingford, 1986).

In the artificial stream, the first group of fish to enter the habitat grew faster, due to most of the territory-holders belonging to that group (Chapter 4). Moreover, these initial residents were on average more aggressive, and they were more likely to end up joining the Upper Modal Group. Although these fish did not have significantly higher standard metabolic rates, and instead appeared to acquire dominance through prior residence and relative size, there is still a strong argument for metabolic rate having an influence on subsequent life-history strategy: fish with higher metabolic rates are more dominant (due to their greater aggression) when there is no prior residence asymmetry, and aggression in hatchery tanks can be moderated by removing them (Chapter 5).

These results were found in both first-feeding salmon and juveniles that were several months old, so would appear to be persistent. More competitive dominant fish maintain high growth rates, and are subsequently more likely to enter the Upper Modal Group and smolt relatively early (Metcalfe *et al.*, 1989; 1990; Metcalfe, 1991). Furthermore, possibly due to variation in standard metabolic rate, some fish are intrinsically dominant, with an innate tendency for greater aggression (suggested by Huntingford *et al.*, 1990).

Numerous genetic studies have reported correlations between variation at enzyme coding loci and fitness-related characters such as metabolism, developmental rates, and growth (Pollard *et al.*, 1994). Research on rainbow trout has linked the PGM-1* allele with both faster developmental rates and greater aggression (Ferguson & Danzmann, 1985). This suggests a genetic component to the decision as to which life-history an individual will follow (e.g. time of maturation appears to be heritable, especially in the progeny of precociously mature male parr; Thorpe & Morgan, 1980). In addition, a variant of the same gene (PGM-1*r***b*) is associated with faster embryonic development, including earlier hatching and emergence, and larger body size in juveniles (Leary *et al.*, 1983; Ferguson & Danzmann, 1985). It has been shown that fish with high standard metabolic rates have faster rates of yolk-sac absorption, possibly leading them to also emerge earlier (Metcalfe *et al.*, 1995; Chapter 3). In juvenile salmon it is possible that variation in standard metabolic rate causing variation in emergence times and subsequent behaviour (by both prior residence effects and innate aggressiveness) may itself be driven by variants of a gene similar to that found in rainbow trout.

7.3 Metabolism in juvenile salmon

This study showed that individual relative standard metabolic rates were relatively invariant in both modal groups (Chapter 6). The reproducibility of measurements may reflect the hypothesis that standard metabolic rate is a fixed minimum rate of oxygen consumption, below which physiological function is impaired (Priede, 1985), and that standard metabolic rate was being successfully measured in this study. Its relative invariance and correlation with behavioural measurements demonstrated throughout the thesis suggests that behaviour is a consequence of variation in standard metabolic rate rather than a cause. Also, salmon subsequently shown to be dominant already have larger otoliths (an indicator of higher metabolic rate; Wright, 1991) at first feeding (Metcalfe *et al.*, 1992), several days before the onset of aggressive behaviour (Dill, 1977). It is certainly the case that social rank can have an effect on routine metabolic rate. Dominant fish have been observed to consume more oxygen than subordinates (Farr & Andrews, 1978; Haller, 1995) as a result of fighting and the stress of dominance. Furthermore, relatively unaggressive salmonids can reduce their routine costs and hence grow faster, as mentioned above (Paloheimo & Dickie, 1965; Metcalfe, 1986). However, these are measurements of routine metabolic rate, which is the day-to-day fluctuation of metabolic rate above the standard level measured in this thesis (Brett & Groves, 1979; Priede, 1985). It is unlikely, therefore, that variation in standard metabolic rate is a consequence of differences in behaviour.

However, oxygen consumption is only one measure of metabolism in fish, and it is naive to expect standard metabolic rate measured as oxygen consumption to singly

explain initial differences in individual behaviour. Oxygen consumption is only one of many physiological features which vary between individuals. Life-history strategies are strongly dependent on early growth rates (Metcalfe *et al.* 1988; Thorpe *et al.*, 1989), and individual costs of maintenance (measured here as oxygen consumption) have been shown to affect growth (Chapter 4). This implies that there are differences in growth efficiency due to differences in relative standard metabolic rate. Such differences in growth efficiency may be due to individual differences in protein synthesis and degradation, another measure of metabolism. Inefficient, slower growing fish have a higher energetic cost of growth due to higher protein synthesis and degradation rates (McCarthy *et al.*, 1994). This would be an alternative measure of costs of maintenance, and since it is an important determinant of the growth performance of individual fish (McCarthy *et al.*, 1994), it would be a valid parameter to study in conjunction with life-history strategies and metabolic rate.

Appendix: List of Latin species names mentioned in text

Species name	Latin name	Chapter						
		1	2	3	4	5	6	7
Insecta:								
African dung beetle	*Scarabaeus laevistriatus*	•						
Bumble bee	*Bombus terricola*	•						
Amphibia:								
Dart-poison frog	*Dendrobates pumilio*			•				
Pisces:								
Arctic charr	*Salvelinus alpinus*		•			•		
Atlantic cod	*Gadus morhua*		•					
Atlantic salmon	*Salmo salar*	•	•	•	•	•	•	•
Brook charr	*Salvelinus fontinalis*				•	•		
Brown trout	*Salmo trutta*				•			
Chinook salmon	*Oncorhynchus tshawytscha*				•			
Chum salmon	*Oncorhynchus keta*					•		
Coho salmon	*Oncorhynchus kisutch*			•	•			
Convict cichlid	*Cichlasoma nigrofasciatum*			•				
Largemouth bass	*Micropterus salmoides*		•		•			
Medaka	*Oryzias latipes*					•		
Mouthbrooding cichlid	*Oreochromis mossambicus*			•				
Nile Tilapia	*Oreochromis niloticus*	•						
Northern pike	*Esox lucius*		•					

Species name	Latin name	Chapter						
		1	2	3	4	5	6	7
Rainbow trout	*Oncorhynchus mykiss*			•	•			•
Roach	*Rutilus rutilus*		•					
Roughhead blenny	*Acanthemblemaria aspera*	•			•			•
Siamese fighting fish	*Betta splendens*	•						
Spinyhead blenny	*Acanthemblemaria spinosa*	•			•			•
Zebra fish	*Brachydario rerio*		•					
Aves:								
Great tit	*Parus major*			•				
Pied flycatcher	*Ficedula hypoleuca*				•			
Mammalia:								
Coyote	*Canis latrans*	•						
Rat	*Rattus rattus*	•						

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