

Juhani Pirhonen

Some Effects of Cultivation
on the Smolting of Two Forms
of Brown Trout (*Salmo trutta*)



UNIVERSITY OF JYVÄSKYLÄ

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ABSTRACT

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Yhteenveto: Viljelytekijöiden vaikutuksista meri- ja järvitaimenen (*Salmo trutta*) smolttiutumiseen

Diss.

Effects of feed restriction and stress on smolting of hatchery reared *Salmo trutta* were studied under experimental conditions. The handling periods in these two experiments took place over the summer and autumn, which is believed to be the sensitive period for the physiological decision of smolting. Possible changes in physiology and behaviour were observed during the following spring and summer. Smolting was not significantly affected by these handling procedures. However, drastic changes in movement behaviour of individually tagged trout during May and June were observed. Before mid-May downward migration suddenly increased, peaked at the end of May and beginning of June, and abruptly ceased in the mid-June when the temperature rose above 10°C. The behavioural pattern of both sea trout and brown trout was similar. The speed of the migration during the most intense period was almost equal to the speed of water, and most movement took place during daylight irrespective of the water temperature. This result was supported by the observation that both 1+ and 2+ brown trout feed most avidly during the daylight hours. During the smolting period also typical changes in gill Na⁺, K⁺-ATP-ase activities were observed. Highest gill Na⁺, K⁺-ATP-ase activities were measured at the end of May, when those were significantly higher in brown trout than in sea trout.

Key words: behaviour; condition factor; feed intake; gill Na⁺, K⁺-ATP-ase; growth; restricted feeding; *Salmo trutta*; smolting; smolt migration; stress.

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LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following original papers, which will be referred to in the text by Roman numerals I-V.

- I Pirhonen, J. & Forsman, L. Effect of prolonged feed restriction on size variation, feed consumption, body composition, growth and smolting of brown trout. Aquaculture (in press).
- II Forsman, L., Pirhonen, J. & Soivio, A. Effect of long term stress on the smolting of two forms of brown trout (*Salmo trutta* L.). Aquaculture (accepted).
- III Pirhonen, J., Koskela, J. & Jobling, M. 1997. Differences in feeding between 1+ and 2+ hatchery brown trout exposed to low water temperature. Journal of Fish Biology 50: 678-681.
- IV Pirhonen, J., Forsman, L., Soivio, A. & Thorpe, J. Movements of hatchery reared *Salmo trutta* during the smolting period, under experimental conditions. Aquaculture (accepted).
- V Pirhonen, J. & Forsman, L. Relationship between Na⁺,K⁺ -ATP-ase activity and migration behaviour of brown trout and sea trout (*Salmo trutta* L.) during the smolting period. Aquaculture (accepted).

1 INTRODUCTION

It is widely supposed that most salmonid fish species follow a more or less standard pattern of development, in which a juvenile stream phase is followed by a marine adolescent growing phase. Such a transition between environments involves a complex of physiological, morphological and behavioural changes, collectively called smolting. Consequently, a smolt is a juvenile salmonid in which all these changes occur during a relatively short period. Physiological and morphological changes precede the culmination of smolting, the smolt migration, during which the parr abandons the nursery river. Most research done on smolting with *Salmo* species has concentrated on Atlantic salmon, *Salmo salar* L., and relatively little is known of the smolting of brown trout, *Salmo trutta* L.

Brown trout typically smolts at the age of two years in Southern Finland but at the age of 3-4 years in Northern Finland (Huusko et al. 1990). However, there is much variation, specially between different trout forms. Anadromous sea trout and migrating freshwater resident brown trout are known to migrate extensively while nonmigrating brown trout stay in rivers for their entire life. This classification is only formal and also artificial because in general *Salmo trutta* is a very flexible group of different life strategies, and the difference is mainly in the proportion of nonmigrating individuals within a stock (Jonsson 1985, Koljonen 1989, Jonsson & Jonsson 1993).

1.1 Changes occurring during smolting

Smolting is a dynamic process starting with the changes in physiology and morphology preparing the parr for the marine environment. Physiological changes occur over an extended period of time and are environmentally

regulated. Migration, in turn, will be initiated by a proximal stimulus, when the fish are in a proper stage of migratory readiness (Solomon 1978, Hoar 1988). Migratory readiness will be increased by several factors as by photoperiod, temperature (Solomon 1982, Hoar 1988) and possibly lunar cycle (Mason 1975, Grau 1982) and the last stimulus for migration may include a sudden rise in temperature (Mills 1964), stream flooding (Solomon 1982) or a change in light level (Hayes 1953).

Physiological changes occurring before and during smolting include a clear rise in the concentration of several hormones (most notably thyroxine, growth hormone and cortisol) and in the gill Na^+, K^+ ATP-ase activity (Hoar 1988, Virtanen 1988, Boeuf 1993, Thorpe & Moore 1997). These changes have traditionally been interpreted as indicators or developmental requirements for the entry into seawater (McCormick & Saunders 1987). On the other hand it has also been proposed that these changes are evidence of seasonal reduction in effectiveness of hydromineral regulation in fresh water (Langdon & Thorpe 1985, Thorpe & Moore 1997).

As to behaviour, the parr are bottom oriented but during smolting switch into pelagic behaviour (Hoar 1976), or it could be said that individuals transfer their orientation away from fixed components and orient to one another (Thorpe 1982). During that time previously territorial parr will also start schooling. Those changes are accompanied by the development of saltwater preference and resistance (Hoar 1976, 1988, Iwata & Komatsu 1984, Iwata et al. 1985) and reduction in swimming activity (Thorpe & Morgan 1978, Smith 1982) and in swimming capacity (Virtanen & Forsman 1987, Graham et al. 1996).

1.2 Factors affecting smolting

Rising temperature and increasing photoperiod serve as important cues for the completion of smolting and especially for migratory activity (Clarke et al. 1996). Increasing daylength during the spring stimulates thyroid hormone activity and hypo-osmoregulatory ability (McCormick et al. 1987). However, changes occurring during smolting have been observed to be expressed in Baltic salmon also under constant conditions of light and temperature (Eriksson & Lundqvist 1982). Under such conditions the time from desmolting to the next smolting differs significantly from 1 year.

Despite that smolting is one of the cornerstones in the life cycle of salmonids, it is only an optional event (Thorpe 1994). The other choice the fish has is to mature and reproduce in the river without migrating (Thorpe 1986) because sexual maturation is an obligatory event for the continuation of a species. So in the first place the fish will try to reproduce, not to smolt (Thorpe 1994). Smolting and consequently migration from the relatively unproductive riverine habitat can therefore be considered a biological response of an animal whose maturation needs have not been met.

In salmon it has been hypothesised that there is a sensitive period during which a parr makes a physiological decision to smolt (Thorpe 1986, 1989,

Metcalfe et al. 1992). At present it seems most likely that that period takes place in salmon in the end of July or beginning of August, so it is about 9 months before the smolt migration period. Whether or not to smolt depends on the growth rate during that period, and the parr will carry on to smolt the following spring if the growth exceeds a genetically determined threshold level at that time. If the threshold is not exceeded, appetite declines (Metcalfe et al. 1986) and so food intake is reduced and growth rate declines. In consequence, within sibling populations the size distribution of individuals becomes bimodal (Thorpe 1977), the upper modal group representing potentially smolting fish, and the lower group representing non-smolts. Factors by which the growth rate is affected during the critical period are such as temperature, competition, food supply and social status (Thorpe et al. 1989, Metcalfe 1991, Metcalfe et al. 1992, Metcalfe 1994).

Migration is an opportunity for the fish and it is expressed under adverse conditions. In the case that the biological needs of an individual salmonid are not being met (Fig.1.) the fish will move away from its habitat. Smolt migration has been considered either as an active (Boeuf 1993, Fängstam 1993, Boeuf et al. 1994) or passive (Thorpe et al. 1988) process. Active migration would reflect attempts of the fish to find better feeding areas when the demand for the food is higher than supply. Passive migration would reflect the maladaptation of the fish which is pushed away from its present habitat.

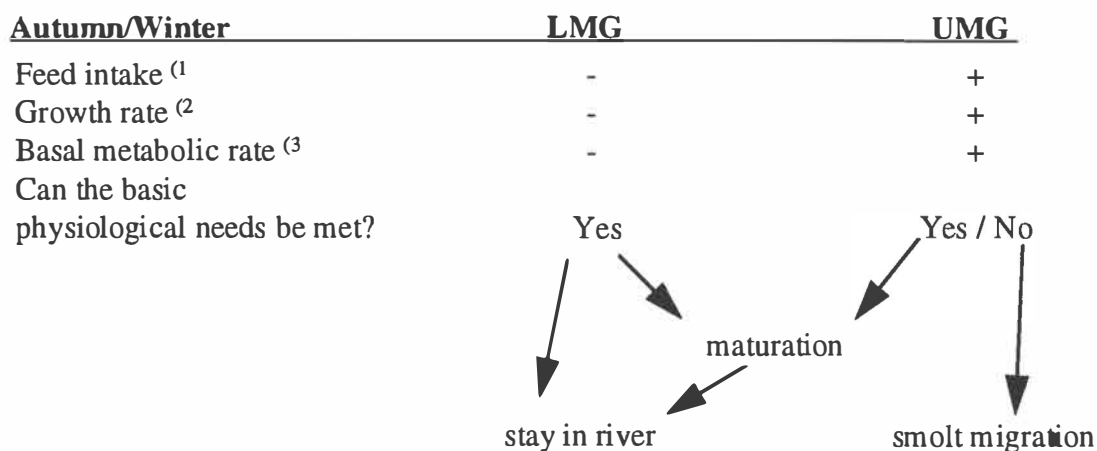


FIGURE 1 Differences in feed intake, growth rate and basal metabolic rate of lower (LMG) and upper modal groups (UMG) of Atlantic salmon. - or + indicates the relative level of each component in the two groups. Arrows indicate the strategy which the individuals most likely will apply during the following spring and autumn. Superscripts refer to the following references 1: Metcalfe et al. 1986, 2: Higgins & Talbot 1985, 3: Higgins 1985.

1.3 Smolting in hatchery conditions

It is known that smolting can be affected by manipulations in hatchery practice: *e.g.* cold water ($< 2^{\circ}\text{C}$) and low light intensity can delay the development of smolting, but warm water (10°C) instead can increase readiness to osmoregulate in seawater (Soivio *et al.* 1989a). However, smolting characteristics can also be altered under "normal" hatchery conditions by several other environmental factors. For example, thyroid hormone levels, which are known to show elevation at the smolting time, could be influenced by ration level (McCormick & Saunders 1990), current velocity (Youngson & Simpson 1984), fish density (Schreck *et al.* 1985) or tank size (Boeuf & Gaignon 1989).

Whether the hatchery smolts differ in smolting from their wild counterparts has been evaluated with Atlantic salmon in a few studies. Virtanen & Soivio (1985) reported that hatchery reared salmon had lower plasma thyroid hormone levels (both T_3 and T_4) and lower gill ATP-ase activity than the downstream migrating wild smolts. Piggins & Mills (1985) found that the proportion of 1+ salmon smolts increases from about 5 % in the wild to 40 % in the hatchery, and the wild smolts are also considerably smaller than hatchery-reared smolts of the same age. They also reported that the smolt rearing might cause abnormalities such as "giant" smolts and vertebral compaction, not reported in wild stocks. Dellefors (1996) reported that hatchery reared sea trout smolts had *e.g.* lower hypoosmoregulatory ability and lower plasma growth hormone levels than their wild counterparts.

1.4 Objectives and questions asked

It seems most probable that the physiological decision about smolting in an individual fish depends both on its genetic blue-print for development and the environmental opportunity to express that development. At present there is only relatively limited information concerning smolting of brown trout and hardly anything is known about the mechanisms affecting the smolting decision in this species. As brown trout and salmon are congeneric they are also rather similar in behaviour and physiology during the smolt stage. For example downstream migration pattern (Leonko & Chernitskiy 1986) and changes in osmoregulatory ability (Muona & Soivio 1992, Tanguy *et al.* 1994) during the smolting period are expressed at the same time and in the similar manner in these two species. One of the most notable differences between the two species is the difference in size distribution of the given population preceding smolting: under good growth conditions salmon show bimodal size distribution (Thorpe 1977) while that of trout is unimodal (Tanguy *et al.* 1994). The size distribution of Baltic salmon parr, at least at the Northern latitudes, has been shown to be unimodal (Eriksson *et al.* 1979). The baseline selected for this research was to evaluate whether the mechanisms leading to smolting in brown trout function in the same way as they have been reported to function in

salmon. One of the objectives of the study was also to obtain basic biological information of the smolting dynamics of *Salmo trutta*.

By altering the growth opportunity by different methods during the growth period we were also able to achieve information about the cultivation practices on general growth performance. Therefore the experiments were planned and carried out in order to evaluate

- the effects of cultivation practice on growth performance, smolting (Papers I and II) and feeding behaviour (Paper III)
- general patterns of smolting behaviour (Paper IV) and the possible link with the physiological changes (Paper V).

2 MATERIALS AND METHODS

A summary of the materials and methods is given here, and more detailed information about the techniques used is given in the individual papers.

All the experiments were carried out at Laukaa Fisheries Research and Aquaculture of the Finnish Game and Fisheries Research Institute (62°27'N, 25°55'E). The brown trout (Rautalampi strain) and sea trout (River Isojoki strain) used in the experiments were derived from the broodstocks held at the research station. The natural origin of the two trout stocks is at the same latitude in Finland. All the fish in papers I, II, IV, V were taken to the experiments at age 1+, and were 2+ when the smolting characteristics were evaluated. In paper III, both age classes were used at the same time, and no smolt characteristics were measured.

Smolting was partly evaluated conventionally by measuring certain physiological parameters (changes in muscle water, Cl^- , Na^+ and Mg^{2+} during sea water exposure (Papers I and II). Sea water exposures were carried out at c. 10°C and in 320 litres of water by mixing balanced sea salt (Instant Ocean by Aquarium Systems) to give a final salinity of 3 ‰. Fresh water controls were kept in individual restrainers in the cultivation tanks. Blood and muscle samples were taken and analysed as described by Soivio and Virtanen (1980, 1985).

The other considerable part of the evaluation of smolting consisted of monitoring movement behaviour before, during and after the smolt migration period. This monitoring was done in an annular flume (width 7 m, depth 30 cm) (Papers I, II, IV, V). All the fish in the experiment were implanted with PIT tags (passive integrated transponder, Destron/IDI, 400 kHz) into the body cavity one week prior to the start of the monitoring. The tank and the equipment used is described in detail in Paper IV.

Gill Na^+, K^+ -ATP-ase activity was measured from the fish in the flume (Paper V). For the analyses a 2x3 mm piece of the first gill arch was taken from

anaesthetised fish by a biopsy. All the samples were stored in liquid nitrogen until analysis. Na^+, K^+ -ATPase activity was analysed by the method described by Schrock et al. (1994). The activity of this enzyme has been considered as one of the most valuable indices of smolting status in salmonids (Boeuf et al. 1985, Hoar 1988, Boeuf 1993) and the new nonlethal microsample method allowed us to sample the fish without sacrificing them. This made it possible to continue monitoring the behaviour of the sampled individuals.

Feed intake was measured using an X-radiographic technique (Talbot & Higgins 1983, Jobling et al. 1993a) with X-ray dense glass balls as the marker (ballotini, Jencons Ltd., U.K.). After the incorporation of ballotinis, standard curves were prepared by X-raying known weights of the marked feed and counting the numbers of ballotinis present. Feed intake measurements were made by providing the marked feed during a certain time, followed immediately by anaesthetisation of the fish (MS-222), X-raying (Siemens Nanodor X-ray machine, Agfa Structurix D7 film), weighing (to 0.1 g), measuring the total length (to 0.1 cm) and identifying individuals (from the stream tank) by reading the PIT tag. X-ray plates were then developed and the amounts of feed consumed by the individual fish were then estimated from the numbers of ballotinis present in the gastrointestinal tract.

Proximate body water, lipid and protein composition (Papers I and II) were analysed from the individual fishes by standard methods. Body energy content (Paper I) was estimated on the basis of calorific content of fat (38.0 kJ g^{-1}) and protein (28.6 kJ g^{-1}) (Jobling 1993).

3 RESULTS AND DISCUSSION

3.1 Feeding and growth performance in *Salmo trutta*

3.1.1 Effects of prolonged feed restriction (Paper I)

The feed restriction period (31 May - 1 November) produced almost two fold differences in mean wet weight between the group fed to satiation twice a day (control; ww on 1 Nov. 88.7 g) and fed only twice a week (TW; 48.3 g). The third treatment group, fed once a day (OD), was intermediate. After the experimental period all the groups were fed for 4 hours per day in excess. No compensatory growth was observed in the previously feed restricted groups. This result indicates that even if fish, as higher vertebrates, were able to compensate for the retarded growth (Dobson & Holmes 1984, Jobling et al. 1993b, Hayward et al. 1997) that compensation is hardly expressed at low water temperatures. Dobson & Holmes (1984) argue that compensatory growth would occur throughout the year in rainbow trout (*Oncorhynchus mykiss*), but it is relatively small at temperatures below 9°C.

The effects of feeding frequencies on uniformity in feed intake and fish size within a tank were evaluated with the help of the coefficient of variation (CV), which allows comparisons of the relative amount of variation in populations having different means (Sokal & Rohlf 1981). High levels of interindividual variation in feed intake have been linked to competition or aggressive behaviour among individuals, whereas high rates of feed intake and low variation in intake are thought to reflect good feeding conditions (Davis & Olla 1987, McCarthy et al. 1992, Jobling & Koskela 1996). The CV values of feed intake for the OD groups (fed for 30 min per day) were slightly higher or

similar to the values reported for rainbow trout fed full rations for one hour (CV 25 - 30 %, McCarthy et al. 1992; CV 38 - 56 %, Jobling & Koskela 1996). The CV of intake in the TW and control groups were lower and higher, respectively, than that of OD groups. This suggests that the more often the fish are fed to excess the bigger is the CV of intake.

Low variation in feed intake in the TW groups would have been expected to contribute to lower variation in weight within a tank when compared to the treatments with higher variation in feed intake. However, the CV of weight was very similar in all the treatment groups within each sampling occasion. This result suggests that large variation in food intake between individuals is the result of large intra-individual variation in food intake especially in the control groups but also to some extent in the OD groups. Therefore it was concluded that differences in the feeding frequency will not cause size hierarchies in a group of brown trout.

Previously it has been observed in plaice (*Pleuronectes platessa*) (Jobling 1982) and in rainbow trout (Ruuhonen & Grove 1996) that gastric capacity increases as the feeding frequency decreases. Also our results suggest that the fish fed most infrequently were able to increase their gastric capacity, and therefore the fish were able to acclimate to infrequent feeding. This acclimation was seen as a rapid increase in condition factor and also the growth rate increased close to the rates of the control fish. The lower growth rate of the OD groups suggests that the minimum time to satiate brown trout increases with fish size, which is in accordance with the results of Elliott (1975a,b).

Taken together, by increasing the time between feedings we were able to decrease the variation of food intake between the individuals, but the variation in weight was not affected, possibly due to large intra-individual variation in food intake. This suggests that under a liberal feeding regime irrespective of the feeding frequency no clear-cut hierarchies are formed in a group of brown trout. Because the food conversion ratio and growth rates were poorer in the feed restricted than in the control groups it is therefore advisable to use relatively long feeding time per day for the efficient culture of brown trout.

3.1.2 Effects of long term stress (Paper II)

Under hatchery conditions fish are exposed to several different stressors including handling, severe crowding, grading and prophylactic treatments. Environmental stress can place a load on the physiologic system that impairs to some degree the ability of the fish to perform certain activities (Schreck 1981). For example, long-term stress is known to suppress fish growth (Pickering 1990), reduce the quality of gametes (Campbell et al. 1992, 1994), disturb immune system (Barton et al. 1987, Pickering & Pottinger 1987) and possibly smolting and migration (Wedemyer & McLeay 1981, Schreck 1982, Patino et al. 1986).

In this experiment both sea and brown trout were stressed by draining the tank completely for three minutes 1-4 times per week between 29 July and 14 November. At the beginning of the experiment the stressed brown trout did not gain weight at the same rate as all the other groups (Fig. 2): they were

significantly smaller on the first of September than all the other groups (ANOVA, $F_{(3,8)}=6.75$, $p = 0.014$). After that stressed brown trout were able to grow even slightly faster than the other groups and from 6 October onwards no differences were observed. Proximate body composition (moisture, fat, protein) did not differ between the treatments at any occasion (days 0, 62, 130, 235 from the beginning).

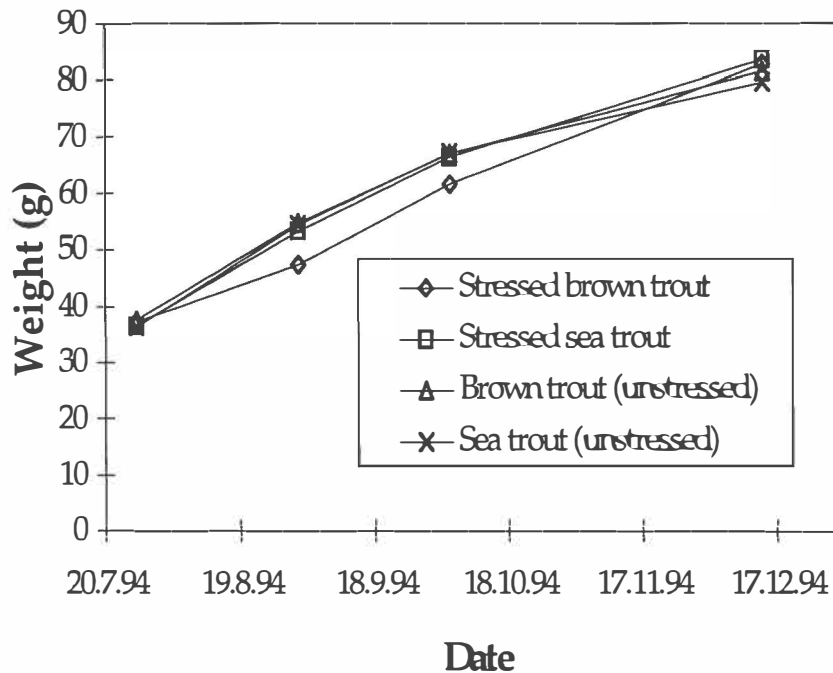


FIGURE 2 Weight increment of the four groups in the stress experiment.

Campbell et al. (1992) has shown that rainbow trout did not acclimate to stress (in terms of plasma cortisol) induced in a similar manner as we did. At the end of their 9 month experiment they couldn't show significant differences in weight between the stressed and control groups. In conformity with this, Pickering and Stewart (1984) concluded that after a long term crowding experiment of brown trout, growth was not suppressed due to chronic elevation of circulating corticosteroids. Pickering (1989) has concluded that acclimation may take several weeks after the blood cortisol levels have been elevated in response to a chronic stress in brown trout, for example under a crowded environment. The stress we induced, however, was acute and repeated for a prolonged period, which can be expected to delay acclimation when compared to a constantly crowded tank.

In our experiment the growth was retarded for a few weeks in stressed brown trout but not in stressed sea trout. It seems most likely that our trout were able to acclimate to the tank draining to some extent and that different stocks differ in the tolerance to the same stressor. Towards the end of the experiment the trout seemed to get used to tank draining since they were relatively relaxed and did not jump as much as in the beginning of the study

when handled in the same way. One reason for decreased activity during the stress was probably also the declining temperature.

3.1.3 Day-night behaviour of 1+ and 2+ trout (Paper III)

This experiment was carried out to verify the result of the mainly daytime activity in the stream tank (Paper IV), even though most of the previously published papers (Cunjak 1988, Fraser et al. 1993, 1995, Griffith & Smith 1993, Heggenes et al. 1993) have shown that juvenile Atlantic salmon and brown trout were mainly nocturnal under low water temperature. However, also daytime activity during the winter has been observed in juvenile brown trout (Müller 1969a,b, Eriksson 1973, Cunjak & Power 1986a).

In our experiment we found that both 1+ and 2+ trout feed most avidly during the daylight hours, but there were differences in foraging behaviour between the two age groups. More of the 1+ than the 2+ trout fed during the hours of darkness, especially during the latter stages of the experiment. The 1+ fish also tended to consume a greater proportion of their daily ration at night.

These results appear to contrast with reports that small trout are almost exclusively nocturnal at low temperature (Griffith & Smith 1993, Heggenes et al. 1993). The diurnal activity we observed may, in part, have been due to the fact that the fish had been fed during daylight hours since start-feeding. However, our experimental design differed in one, possibly very significant, way from Fraser's et al. (1993, 1995) experiments with juvenile salmon: in our experiment the fish were kept in total darkness during the night while Fraser and associates offered some 0.05 lx during the night. This light intensity is much above the visual threshold of coho salmon (Thorarensen et al. 1989) or schooling fish species (Wardle 1993). Fraser & Metcalfe (1997) have observed only minimal feeding rates of juvenile Atlantic salmon below 0.01 lx during winter. Thus, total darkness may in part explain the relatively low feeding activity of our trout during the night. However, feeding in total darkness from the bottom of the tank should be possible, as has been shown with Arctic charr (*Salvelinus alpinus*) and salmon (Wallace et al. 1988, Jørgensen & Jobling 1992).

Our result of the higher intake at night of the 1+ than the 2+ fish supports the hypothesis that large fish are less susceptible to predation than are smaller conspecifics (Milinski 1993). Thus, if the switch to nocturnal activity at low temperature is a predator-avoidance tactic this behaviour may be expected to be expressed more strongly by small, juvenile salmonids than by larger conspecifics. A switch to nocturnal foraging at low temperatures may be a behavioural strategy to reduce the risk of capture by diurnally-active, warm-blooded, visual predators (Fraser et al. 1995, Valdimarsson & Metcalfe 1998). The fact that larger trout remain active, and feed more avidly than smaller conspecifics during daylight hours lends support to this idea.

3.2 Changes during smolting in *Salmo trutta*

3.2.1 Movement behaviour (Paper IV)

3.2.1.1 Behaviour within a day

In contrast to most of the previous findings of the mainly nocturnal activity of the parr at low ($< 7^{\circ}\text{C}$) temperatures (Österdahl 1969, Thorpe & Morgan 1978, Tytler et al. 1978, Cunjak 1988, Thorpe et al. 1988, Rimmer & Paim 1990, Fraser et al. 1993, Heggenes et al. 1993, Moore & Potter 1994, Thorpe et al. 1994, Fraser et al. 1995, Hvidsten et al. 1995, Thorpe & Moore 1997) our trout were most active during the daylight hours all over the spring irrespective of the temperature (Paper IV). The information of the movement behaviour in natural environments is lacking for the two stocks used, but there are several studies which support the present result (Eriksson 1973, 1975, Cunjak & Power 1986a, Eriksson & Alanärä 1992).

It seems most probable that age-dependent changes had taken place (section 3.1.3.) but also differences between species and stocks may have contributed to the selected behaviour. Rimmer et al. (1983), for example, noted that in summer Atlantic salmon juveniles were always above the streambed but when the temperature fell below 10°C the salmon were found exclusively in sheltered substrate chambers beneath surface streambed stones. Observations in that study were made only during the daytime which possibly indicates that salmon switched to nocturnal behaviour under declining temperatures. Brown trout, in turn, were never found overwintering beneath rocks in Credit River in Ontario (Cunjak & Power 1986a), and neither was brook trout (*Salvelinus fontinalis*). On the other hand, in another small river in Quebec, small brook trout spent winter within the substrate, but larger trout were unable to do that because of their size (Cunjak & Power 1986b). Eriksson (1973, 1975, also Eriksson & Alanärä 1992) has found that both salmon and trout exhibit diurnal activity during winter but turns first into crepuscular (most active at dusk and dawn) and further into nocturnal activity towards the end of May. Fängstam (1993) and Fängstam et al. (1993) have shown smolt migration of Baltic salmon to occur during the daylight in an experimental flume, but that migration mainly took place at temperatures above 10°C .

Gregory & Griffith (1996) found that under clear water conditions fish hid more than they did under either surface ice or in turbid water, which suggested that "fish may have been less likely to conceal themselves when they were otherwise protected". This may partly explain the daytime activity of the fish in the present flume experiments, where the fish were sheltered indoors, and shielded from external disturbance by a black plastic sheet. Heggenes et al. (1993) noted that brown trout >25 cm long, unlike smaller individuals, were active during the daylight hours in winter. On that basis the present 20 cm trout would have been expected to be nocturnal at low temperatures, but Heggenes et al. (1993) also highlighted the importance of a coarse substratum as shelter, and that the lack of shelter may alter the movement patterns of fish considerably. The 100 rocks on the otherwise bare floor of our flume provided

no suitable refuges for trout during the day. We couldn't find any evidence that within the size range of the fish used there were any differences in day/night behaviour of big or small immature individuals.

Jobling et al. (1998) have recently found that at 2.7 - 3.0°C both 2+ Baltic salmon and 2+ brown trout feed predominantly during daylight hours, and they suggested that this behaviour reflected either the effects of domestication or ontogenetic changes in foraging activity. In accordance to this our results (Paper III) indicate that both 1+ and 2+ hatchery brown trout fed during the day and at night at low temperatures but the major part of the daily ration was consumed during daylight hours and that 1+ trout had greater feeding activity at night than the 2+ fish. On the basis of these results we can assume that our trout in the flume were also feeding mainly during daylight hours and therefore it is possible that the diel changes in movement activity were a consequence of their inherent activity associated with feeding.

3.2.1.2 Seasonal changes in behaviour

The trout in the flume tank showed a change in their behaviour typically occurring during the parr-smolt transformation (Paper IV). There was a clear rise and decrease in the extent of movement in the mid-May and in the mid-June, respectively. Both the start and specially the end of the run occurred very abruptly and relatively simultaneously in all the individuals, and the most intense period in the flume lasted for about one month. Jonsson & Ruud-Hansen (1985) have investigated salmon smolt migration in river Imsa and there over 90% of the smolts descended during one month, a result similar to that of Hvidsten et al. (1995) in central Norway. Leonko & Chernitskiy (1986) compared the smolt migration of Atlantic salmon and sea trout in Kola Peninsula for seven years and the annual dynamics of migration were rather similar between the two species, actually more similar than intraspecific migration patterns in different years. The duration of migration when 90% of the sea trout smolts had descended lasted from 18 to 31 days depending on the year (Leonko & Chernitskiy 1986). During a period of seven years Bohlin et al. (1993) caught 90% of the sea trout smolts with an average of 29 days each year.

In our experiment no threshold temperature induced the movement but downstream displacement increased as soon as temperature started to rise. Movement was most intense between 6 and 10°C, values somewhat lower than those reported elsewhere for movement of trout (Chelkowski et al. 1994, Moore & Potter 1994) and salmon (Österdahl 1969, Fried et al. 1978, McCleave 1978, Jonsson & Ruud-Hansen 1985, Fängstam et al. 1993). Several reasons have been suggested as predictors for the initiation of migration. Those have been such as the number of degree-days above 4°C from March 1 (Bohlin et al. 1993), an annually varying threshold temperature (Solomon 1978), the combined effect of several physical stimuli, not only to a threshold temperature (Hvidsten et al. 1995) or a combination of temperature increase and temperature level in the river during the spring (Jonsson & Ruud-Hansen 1985). There seems to be no consensus by which means the migration is initiated, but it is most likely that there are several cues inducing the start of the run, and temperature rise is

probably an important instigating factor in that complex. Photoperiod is regarded as most usual synchroniser of seasonally changing physiological processes, e.g. smolting (Hoar 1988).

I would also argue that there really should not be any absolute value of any physical cue for the initiation of movement applicable to all trout, since arrival time at the sea is restricted to a very limited period. For all members of the population within the whole length of a single river system to arrive at the river mouth within that time window, individual fishes are going to have to start moving downstream progressively earlier the further they are from the sea. Also environmental factors, especially temperature, differ in the upper reaches from those of the river mouth. So, at least in theory, the specific cues for particular individuals should relate to the location and physical conditions of their particular juvenile habitats.

3.2.2 Physiology

3.2.2.1 Gill Na^+, K^+ -ATP-ase activity (Paper IV)

Our attempt here was to demonstrate whether gill Na^+, K^+ -ATPase activity and downstream migration correlate, and the possible difference in that enzyme activity between brown trout and sea trout. Despite of the general accordance of the correlation between the smolt migration and gill Na^+, K^+ -ATPase activity, this does not seem to be always the case. But above all, as far as we know such a correlation has not been demonstrated earlier at an individual level, and the present experimental setup allowed us to investigate that possible correlation. However, we could not find any significant indices of such a correlation. No correlation between fish size and Na^+, K^+ -ATPase activity was observed. The mean Na^+, K^+ -ATPase activity was significantly higher in the end of May in brown trout than in sea trout, but no significant differences were observed on 11 May or 11 July. The highest measured values in the Na^+, K^+ -ATPase activity were observed at the same time as the migration activity peaked. Soivio et al. (1989b) observed a significantly higher Na^+, K^+ -ATPase activity in sea trout (River Ii stock) than in Rautalampi strain brown trout. The enzyme activities measured for brown trout did not clearly peak in the end of May (Soivio et al. 1989b) and were also somewhat lower than those of our trout.

The present non-significant correlation between migration and the Na^+, K^+ -ATPase activity can be explained by the findings of Ewing & Birks (1982) and Ewing et al. (1980) with chinook salmon (*Oncorhynchus tshawytscha*). They demonstrated that migration tendency and elevated Na^+, K^+ -ATPase activity did not necessarily take place simultaneously. Ewing and Birks (1982) concluded that even if gill Na^+, K^+ -ATPase activity is often correlated with migration their relationship is not causal, and these two changes possibly are simply concurrent events (Langdon 1985).

3.2.2.2 Plasma ions and muscle water (Papers I and II)

Plasma ion concentrations and muscle water content were measured from the fish left in the cultivation tanks while their PIT-tagged counterparts were taken into the flume in February for behavioural monitoring. The results of these analyses show the typical pattern of decreasing plasma ion concentrations and improved capacity to retain water balance in sea water in the course of the spring (Soivio et al. 1989a,b), especially for sea trout. The values in fresh water were very similar both in sea trout and brown trout but during the sea water exposure brown trout appeared to have poorer hypo-osmoregulatory capacity than sea trout.

3.3 Cultivation practice and smolting (Papers I and II)

It is commonly known that by altering certain environmental factors (photoperiod, temperature, salinity, hatchery practice) we can contribute to smolting (Virtanen 1988). By photoperiodic manipulations it is possible to produce out-of-season smolts (Hoar 1988, Clarke et al. 1996), but in the present study we attempted to switch smolting on/off by giving the groups of trout different growth opportunities during the expected sensitive period.

In the experiment described in Paper I we couldn't show any major influence of the food restriction on smolting. In Atlantic salmon it has been observed that the greater the opportunity for growth in July and August the greater is the proportion of young Atlantic salmon maintaining growth (Thorpe et al. 1989) and therefore being able to smolt and migrate the following spring (Metcalf et al. 1992, Thorpe et al. 1992, Metcalfe 1994). Also in young brown trout the growth rate is important in determining whether an individual migrates or stays, but there are genetic differences between individuals and populations (Jonsson 1982, 1989, Jonsson & Jonsson 1993). The present results of the smolting of brown trout may indicate that the feed restriction was not severe enough to depress smolting because the genetically determined threshold level in growth rate had been passed (Thorpe et al. 1992, Metcalfe 1993, Jonsson & Jonsson 1993) or that the restriction did not take place at the right time of the year. If the physiological decision for smolting in brown trout takes place slightly later (August/September) than in Atlantic salmon (July/August), it is possible that our trout had made their positive decision at that time. During those months the growth rates in all the treatments were relatively high (over 1% day⁻¹) because of the acclimation to the new feeding routine. Pirhonen & Forsman (unpublished) have also found that total food deprivation for three weeks in either June - July or in August did not affect smolting of brown trout. That result also suggests that the critical period for smolting decision may be taken at different time in trout than in salmon.

Neither in the stress experiment (Paper II) couldn't we achieve clear evidence of the effect of cultivation practice on smolting. In the stressed brown trout group, the ones with retarded growth at the beginning of the experiment (Fig. 1), the peak of migration was less pronounced than in the three other

groups. However, significant differences in movement activity between the stressed and unstressed groups were not found and the possibility that the differences actually existed cannot be rejected because of the low statistical power.

3.4 Differences in smolting between trout and salmon: hypotheses for the future research

Whether or not the physiological decision for smolting in trout is taken at the same time as in salmon was one of the basic hypotheses to be tested for this work. However, during this work I did not compare smolting between the two species experimentally. Therefore the comparisons I discuss here are based in the part of salmon on the published literature.

In two papers (Papers I and II) we could not show any clear indication of the sensitive period for the smolting decision in trout, because all the treatment groups tended to smolt in a very similar manner. These results suggest that the mechanism leading to the smolting decision in trout differs from that of salmon. In the light of the present results I will hypothesise the possible pathways where the future research could be concentrated to affect smolting of brown trout.

Hypothesis 1: S1 trout by accelerating hatching

Previously it has been shown in salmon that once an individual fish has made the decision to smolt, it has selected its path of development and that decision is irreversible (Metcalf 1994, Thorpe & Metcalf, in press). On that basis it can be assumed that the trout in my experiments had passed that critical time for smolting decision. The other possibility can be that the threshold level needed to smolt is at a different level in trout than in salmon. In trout no individuals are smolting at the 1+ age, but practically all are smolts at the 2+ age, if not maturing. A similar situation would occur, at least theoretically, in salmon if the hatching and first feeding took place relatively late in the first summer and growth rate was low during the sensitive period for smolting. Under moderate development conditions when first feeding is in early summer and growth rate higher during the sensitive period, a part of the salmon population will maintain high rates of growth and a bimodal size distribution will be formed (Thorpe 1986). This assumption leads me to hypothesise that it should be possible to express bimodal size distribution also in trout during the first summer if the hatching and first feeding were accelerated. Based on the present results it seems that by arresting the growth during the second summer it is difficult to avoid the fish turning into smolts, if the sensitive period for smolting decision in trout is taken at the same time as in salmon.

Hypothesis 2: The effect of competition for food on smolting in brown trout

The size distribution in the salmon population becomes bimodal during the late spring and autumn when appetite declines in lower modal group (LMG) individuals. That is believed to be, at least partly, a result of the impairment of feeding efficiency of LMG fish in the presence of competitors (Metcalf 1989, 1991). However, no bimodality has been observed in trout (Tanguy et al. 1994, Chelkowski 1995). Therefore, my hypothesis is that in a trout population there is possibly either very little competition between individuals or if competition exists, all the individuals are strong and able to compete for the available resources. However, if the CV of weight within a tank is a good indicator of existing competition, it seems likely that in my trout tanks a spectrum of competitive abilities existed. Unlike the situation in salmon where competition may suppress the poorer competitors to the point of going anorexic, all my 2+ trout individuals had presumably exceeded whatever threshold was necessary to maintain growth, and even though the poorest competitors amongst them may have had a hard time, it was not enough to suppress their appetites.

4 CONCLUSIONS

I was able to demonstrate with the experiments described in the five papers the general pattern of behaviour of smolting brown trout under laboratory conditions. Also typical changes during the smolting period in physiology were observed. The results indicated that the way how decision for smolting is taken in brown trout most likely differs from the way reported for salmon. The knowledge of the ways leading to the smolting decision in salmon was used as a baseline in the planning of the experiments.

Arresting the growth rate of trout during the second summer does not seem to decrease the probability for smolting during the following spring. This led me to conclude that the decision for smolting in trout needs to be taken at a different time than in salmon (July - August). The other possibility is that the growth, even if arrested, still exceeded the genetically determined threshold level during the critical period for the smolting decision.

It was also observed that the trout, irrespective of their age and temperature, were mainly active during the daylight hours, which is a result somewhat contradictory to the previous observations of the mainly nocturnal activity at low temperatures. This result, however, could be due to their inherent activity associated with feeding. All the experiments were also protected from any external disturbances and thus it is possible that the fish were less likely to hide (*i.e.* become nocturnal) if they felt themselves otherwise protected.

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YHTEENVETO

Viljelytekijöiden vaikutuksista meri- ja järvitaimenen (*Salmo trutta*) smolttiutumiseen

Suurimmalla osalla lohikalalajeista (suvut *Salmo*, *Oncorhynchus* ja *Salvelinus*) on pääpiirteissään samanlainen elämänkierto. Poikasvaiheensa nämä kalat viettävät joessa (tässä vaiheessa nimitys jokipoikanen), jonka jälkeen ne vaeltavat mereen tai järveen syönnökselle. Syönnösvaiheen aikana lohikalat kasvavat nopeasti, saavuttavat sukukypsyyden ja palaavat takaisin kotijokeensa kudulle. Vaihetta, jolloin poikanen jättää kotijokensa, kutsutaan smolttiutumiseksi, ja vastaavasti kalaa tuossa vaiheessa joko vaelluspoikaseksi tai smoltiksi. Ennen smolttiutumista ja sen aikana kalassa tapahtuu fysiologisia, morfologisia ja käyttäytymismuutoksia. Varsinainen smolttivaellus, jonka tarkka ajankohta riippuu paljolti ympäristöolosuhteista, tapahtuu oloissamme yleensä touko-kesäkuussa.

Vaellus paikasta toiseen on eläimen biologinen vaste epäedullisissa olosuhteissa, joissa sen tarpeet eivät tyydyty. Myös smolttivaelluksen on esitetty johtuvan tästä syystä. Jokiympäristö on turvallinen lastenkamari, mutta kohtalaisen vähätuottoinen ympäristö. Kalan tärkein tehtävä on kuitenkin suvun jatkaminen, ja sukutuotteiden kehittäminen vaatii paljon energiaa. Se ei taas onnistu joessa, jossa kala ei saa riittävästi ravintoa. Niinpä kala vaeltaa kunnes sen kulloisetkin tarpeet tyydyttyvät. Osa koiraista pystyy kuitenkin tulemaan sukukypsiksi jo jokipoikasvaiheessa, ja siitä syystä ne eivät vaellakaan, vaan jäävät jokeen kudulle. ”Päätös” siitä, milloin kukin kalayksilö lähtee smolttivaellukselle, tapahtuu ilmeisesti jo paljon ennen varsinaista vaellusta. Lohella on havaittu, että tuo päätös tehdään vaellusta edeltävän vuoden heinä-elokuun vaihteessa, eli n. 9 kuukautta ennen smolttivaellusta.

Väitöskirjatutkimuksissani olen selvittänyt kahden eri taimenmuodon, meri- ja järvitaimenen, smolttiutumiseen liittyviä muutoksia, sekä sitä,

voidaanko taimenen smolttiutumista säädellä viljelyolosuhteita muuntelemalla. Smolttiutumisaikaa säätelemällä voitaisiin vaikuttaa taimenistutusten onnistumiseen ja kannattavuuteen. Olettamuksena tutkimuksissa on ollut, että päätös smolttiutumisesta tapahtuu samaan aikaan kuin lohella. Taimenten smolttiutumista arvioitiin seuraamalla yksilömerkittyjen kalojen käyttäytymistä keinotekoisessa joessa ja fysiologisia muutoksia kevään ja kesän aikana.

Kokeet tehtiin siten, että 1-vuotiaiden taimenten kasvuedellytyksiä heikennettiin kasvukauden aikana, jolloin päätöksen smolttiutumisesta oletettiin tapahtuvan. Kokeissa kalojen ruokintakertojen määrää vähennettiin tai kaloja stressattiin useita kertoja viikossa laskemalla altaasta vesi pois kolmeksi minuutiksi. Ruokintakertojen vähentäminen hidasti huomattavasti kalojen kasvua, mutta kalojen rasittaminen ei juurikaan vaikuttanut niiden kasvuun. Vaikka koekaloilla oli suuriakin kokoeroja smolttiutumisaikana, en kuitenkaan havainnut em. käsittelyjen vaikuttavan millään tavalla kalojen smolttiutumiseen seuraavana keväänä. Näiden tulosten pohjalta on oletettavaa, että päätös smolttiutumisesta tapahtuu taimenella eri aikaan kuin lohella. Toinen mahdollisuus on, että käsittelyt eivät olleet tarpeeksi tehokkaita vaikuttaakseen smolttiutumiseen.

Koeolosuhteissa pystyin osoittamaan selvät käyttäytymismuutokset smolttiutumisaikana yksilömerkityillä taimenilla, joiden liikkeet keinotekoisessa joessa tallentuivat tietokoneelle. Ennen toukokuun puoliväliä kalojen vaellusaktiivisuus kohosi nopeasti, huipentuen touko-kesäkuun vaihteessa. Kesäkuun puolivälissä vaellus loppui kokonaan. Sekä meri- että järvitaimen käyttäytyivät samalla tavalla koko seurantajakson, mutta fysiologisten mittauksen mukaan meritaimen pystyy säätelemään suolatasapainoaan merivedessä järvitaimenta paremmin. Sukukypsyt koiraat vaelsivat koealtaassa selvästi vähemmän kuin ei-sukukypsät kalat. Vaellusseurannan aikana kaloilta mitattiin kolmesti kiduksen Na^+, K^+ -ATP-aasientsyymin aktiivisuutta. Tämän entsyymin aktiivisuuden on todettu kohoavan smolttiutuvilla kaloilla, joskaan sen varsinaisesta merkityksestä ei olla aivan varmoja. Na^+, K^+ -ATP-aasiaktiivisuus oli korkeimmillaan toukokuun lopussa, jolloin myös vaellus oli kiihkeimmillään. Tuolloin järvitaimenen entsyymiaktiivisuus oli korkeampi kuin meritaimenella. Entsyymiaktiivisuudella ei kuitenkaan ollut korrelaatiota yksilöllisen vaellusaktiivisuuden kanssa.

Suurin osa kalojen vaelluksesta ja liikehännästä tapahtui päiväsaikaan lämpötilasta riippumatta. Tämä tulos poikkesi pääosin aiemmista havainnoista lohikalojen yöaktiivisuudesta alhaisissa ($< 7^\circ\text{C}$) lämpötiloissa. Tämän tuloksen varmistamiseksi vertailtiin myös 1- ja 2-vuotiaita taimenia ja niiden vuorokautista ruokailukäyttäytymistä talvilämpötiloissa. Ruokailuaktiivisuuden selvittämiseksi käytettiin röntgenmenetelmää, jossa kaloille syötettiin rehua, johon oli sekoitettu röntgenkuvissa erottuvia pieniä lasikuulia. Tulos osoitti taimenten syövän suurimmaksi osaksi valoisana aikana kalan koosta riippumatta. Tulokseni viittaavat siihen, että taimenten päiväaktiivisuus johtuu niiden päiväaikaisesta ruokailukäyttäytymisestä, mikä on mahdollisesti seurausta niiden aikaisemmin kokemista laitosolosuhteista.

REFERENCES

- Barton, B.A., Schreck, C.B. & Barton, L.D. 1987. Effect of chronic cortisol administration and daily acute stress on growth, physiological conditions, and stress responses in juvenile rainbow trout. *Dis. Aquat. Org.* 2: 173-185.
- Boeuf, G. 1993. Salmonid smolting: a pre-adaptation to the oceanic environment. In: J.C. Rankin and F.B. Jensen (eds), *Fish ecophysiology*: 105-136. Chapman and Hall, London.
- Boeuf, G. & Gaignon, J.-L. 1989. Effects of rearing conditions of growth and thyroid hormones during smolting of Atlantic salmon, *Salmo salar* L. *Aquaculture* 82: 29-38.
- Boeuf, G., Le Roux, A., Gaignon, J.L. & Harache, Y. 1985. Gill ($\text{Na}^+\text{-K}^+$)-ATPase activity and smolting in Atlantic salmon (*Salmo salar* L.) in France. *Aquaculture* 45: 73-81.
- Bohlin, T., Dellefors, C. & Faremo, U. 1993. Timing of sea-run brown trout (*Salmo trutta*) smolt migration: effects of climatic variation. *Can. J. Fish. Aquat. Sci.* 50: 1132-1136.
- Campbell, P.M., Pottinger, T.G. & Sumpter, J.P. 1992. Stress reduces the quality of gametes produced by rainbow trout. *Biol. Reprod.* 47: 1140-1150.
- Campbell, P.M., Pottinger, T.G. & Sumpter, J.P. 1994. Preliminary evidence that chronic confinement stress reduces the quality of gametes produced by brown trout. *Aquaculture* 120: 151-169.
- Chelkowski, Z. 1995. Biological characteristics of sea trout smolts (*Salmo trutta* m *trutta* L.) grown from fry released in the stream Osówka. *Acta Ichth. Pisc.* 25: 19-32.
- Chelkowski, Z., Chelkowska, B. & Ciupinski, M. 1994. Period of downstream migration of sea trout (*Salmo trutta* L.) smolt grown in Gowienica River. *Acta Ichthyol. Pisc.* 24: 145-152.

- Clarke, W.C., Saunders, R.L. & McCormick, S.D. 1996. Smolt production. In: Pennell, W. & Barton, B.A. (eds), *Principles of Salmonid Culture*: 517-568. *Developments in Aquaculture and Fisheries Science*, 29. Elsevier Science B.V. Amsterdam.
- Cunjak, R.A. 1988. Behaviour and microhabitat of young Atlantic salmon (*Salmo salar*) during winter. *Can. J. Fish. Aquat. Sci.* 45: 2156-2160.
- Cunjak, R.A. & Power, G. 1986a. Winter habitat utilization by stream resident brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*). *Can. J. Fish. Aquat. Sci.* 43: 1970-1981.
- Cunjak, R.A. & Power, G. 1986b. Seasonal changes in the physiology of brook trout, *Salvelinus fontinalis* (Mitchill), in a sub-Arctic river system. *J. Fish Biol.* 29: 279-288.
- Davis, M.W. & Olla, B.L. 1987. Aggression and variation in growth of chum salmon (*Oncorhynchus keta*) juveniles in sea water: effect of limited rations. *Can. J. Fish. Aquat. Sci.* 44: 192-197.
- Dellefors, C. 1996. Smoltification and sea migration in wild and hatchery-reared brown trout, *Salmo trutta*. Ph.D. Thesis, University of Göteborg, Sweden.
- Dobson, S.H. & Holmes, R.M. 1984. Compensatory growth in the rainbow trout, *Salmo gairdneri* Richardson. *J. Fish Biol.* 25: 649-656.
- Elliott, J.M. 1975a. Weight of food and time required to satiate brown trout, *Salmo trutta* L. *Freshw. Biol.* 5: 51-64.
- Elliott, J.M. 1975b. Number of meals in a day, maximum weight of food consumed in a day and maximum rate of feeding for brown trout, *Salmo trutta* L. *Freshw. Biol.* 5: 287-303.
- Eriksson, L.-O. 1973. Spring inversion of the diel rhythm of locomotor activity on young sea-going brown trout, *Salmo trutta trutta* L., and Atlantic salmon, *Salmo salar* L. *Aquilo Ser. Zool.* 14: 68-79.
- Eriksson, L.-O. 1975. Diel and annual locomotor activity rhythms in some fresh water fish species with special reference to the seasonal inversion in salmonids. Ph.D. Thesis, University of Umeå, Sweden.
- Eriksson, L.-O. & Alanärä, A. 1992. Timing of feeding behavior in salmonids. In: Thorpe, J.E. & Huntingford, F.A. (eds), *The importance of feeding behaviour for the efficient culture of salmonid fishes*: 41-48. *World aquaculture workshops, number 2*. The World Aquaculture Society, Baton Rouge, Louisiana.
- Eriksson, L.-O. & Lundqvist, H. 1982. Circannual rhythms and photoperiod regulation of growth and smolting in Baltic salmon (*Salmo salar* L.). *Aquaculture* 28: 113-121.
- Eriksson, L.-O., Lundqvist, H. & Johansson, H. 1979. On the normality of size distribution and the precocious maturation in a Baltic salmon, *Salmo salar* L. parr population. *Aquilo, Ser. Zool.* 19: 81-86.
- Ewing, R.D. & Birks, E.K. 1982. Criteria for parr-smolt transformation in juvenile chinook salmon (*Oncorhynchus tshawytscha*). *Aquaculture* 28: 185-194.

- Ewing, R.D., Fustish, C.A., Jonson, S.L. & Pribble, H.J. 1980. Seaward migration of juvenile chinook salmon without elevated gill (Na+K)-ATPase activities. *Trans. Am. Fish. Soc.* 109: 349-356.
- Fängstam, H. 1993. Individual downstream swimming speed during the natural smolting period among young of Baltic salmon (*Salmo salar*). *Can. J. Zool.* 71: 1782-1786.
- Fängstam, H., Berglund, I., Sjöberg, M. & Lundqvist, H. 1993. Effects of size and early sexual maturation on downstream migration during smolting in Baltic salmon (*Salmo salar*). *J. Fish Biol.* 43: 517-529.
- Fraser, N.H.C. & Metcalfe, N.B. 1997. The costs of becoming nocturnal: feeding efficiency in relation to light intensity in juvenile Atlantic salmon. *Functional Ecol.* 11: 385-391.
- Fraser, N.H.C., Metcalfe, N.B. & Thorpe, J.E. 1993. Temperature dependent switch between diurnal and nocturnal foraging in salmon. *Proc. Roy. Soc. Lond. Ser. B* 252: 135-139.
- Fraser, N.H.C., Heggenes, J., Metcalfe, N.B. & Thorpe, J.E. 1995. Low summer temperatures cause juvenile Atlantic salmon to become nocturnal. *Can. J. Zool.* 73: 446-451.
- Fried, S.M., McCleave, J.D. & LaBar, G.W. 1978. Seaward migration of hatchery reared Atlantic salmon, *Salmo salar*, smolts in the Penobscot river estuary, Maine: riverine movements. *J. Fish. Res. Bd. Can.* 53: 76-87.
- Graham, W.D., Thorpe, J.E. & Metcalfe, N.B. 1996. Seasonal current holding performance of juvenile Atlantic salmon in relation to temperature and smolting. *Can. J. Fish. Aquat. Sci.* 53: 80-86.
- Grau, E.G. 1982. Is the lunar cycle a factor timing the onset of salmon migration. In: Brannon, E.L. & Salo, E.O. (eds), *Proceedings of the salmon and trout migratory behavior symposium*: 184-189. School of Fisheries, Univ. of Washington, Seattle.
- Gregory, J.S. & Griffith, J.S. 1996. Winter concealment by subyearling rainbow trout: space size selection and reduced concealment under surface ice and in turbid water conditions. *Can. J. Zool.* 74: 451-455.
- Griffith, J.S. & Smith, R.W. 1993. Use of winter concealment cover by juvenile cutthroat and brown trout in the south fork of the Snake River, Idaho. *N. Am. J. Fish. Manag.* 13: 823-830.
- Hayes, F.R. 1953. Artificial freshets and other factors controlling the ascent and population of Atlantic salmon in the La Have River, Nova Scotia. *Bull. Fish. Res. Bd. Can.* 99.
- Hayward, R.S., Noltie, D.B. & Wang, N. 1997. Use of compensatory growth to double hybrid sunfish growth rates. *Trans. Am. Fish. Soc.* 126: 316-322.
- Heggenes, J., Krog, O.M.W., Lindås, O.R., Dokk, J.G. & Bremnes, T. 1993. Homeostatic behavioural response in a changing environment: brown trout (*Salmo trutta*) become nocturnal during winter. *J. Anim. Ecol.* 62: 295-308.
- Higgins, P.J. & Talbot, C. 1985. Growth and feeding in juvenile Atlantic salmon (*Salmo salar* L.). In: Cowey, C.B., Mackie, A.M. & Bell, J.G. (eds), *Nutrition and Feeding in Fish*: 243-263. Academic Press Inc. London.

- Higgins, P.J. 1985. Metabolic differences between Atlantic salmon (*Salmo salar*) parr and smolts. *Aquaculture* 45: 33-53.
- Hoar, W.S. 1976. Smolt transformation: evolution, behavior and physiology. *J. Fish. Res. Bd. Can.* 33: 1234-1252.
- Hoar, W.S. 1988. The physiology of smolting salmonids. In: Hoar, W.S. & Randall, D.J. (eds), *Fish Physiology*, Vol XIB: 275-343. Academic Press Inc. London.
- Huusko, A., Van der Meer, O. & Koljonen, M.-L. 1990. Life history patterns and genetic differences in brown trout (*Salmo trutta* L.) in the Koutajoki river system. *Pol. Arch. Hydrobiol.* 37: 63-77.
- Hvidsten, N.A., Jensen A.J., Vivås, H., Bakke, Ø. & Heggberget, T.G. 1995. Downstream migration of Atlantic salmon smolts in relation to water flow, water temperature, moon phase and social interaction. *Nordic J. Freshw. Res.* 70: 38-48.
- Iwata, M. & Komatsu, S. 1984. Importance of estuarine residence for adaptation of chum salmon (*Oncorhynchus keta*) fry to sea water. *Can. J. Fish. Aquat. Sci.* 41: 744-749.
- Iwata, M., Ogura, H., Komatsu, S., Suzuki, K., Nishioka, R.S. & Bern, H.A. 1985. Changes in salinity preference of chum and coho salmon during development. *Aquaculture* 45: 380-381.
- Jobling, M. 1982. Some observations on the effects of feeding frequency on the food intake and growth of plaice, *Pleuronectes platessa* L. *J. Fish Biol.* 20: 431-444
- Jobling, M. 1993. Bioenergetics: feed intake and energy partitioning. In: Rankin, J.C. & Jensen, F.B. (eds), *Fish Ecophysiology*: 1-44. Chapman and Hall, London.
- Jobling, M. & Koskela, J. 1996. Interindividual variations in feeding and growth in rainbow trout during restricted feeding and in a subsequent period of compensatory growth. *J. Fish Biol* 49: 658-667.
- Jobling, M., Christiansen, J.S., Jørgensen, E.H. & Arnesen, A.M. 1993a. The application of X-radiography in feeding and growth studies with fish: A summary of experiments conducted on Arctic charr. *Rew. Fish. Sci.* 1: 223-237.
- Jobling, M., Jørgesen, E.H. & Siikavuopio, S.I., 1993b. The influence of previous feeding regime on the compensatory response of maturing and immature Arctic charr, *Salvelinus alpinus*. *J. Fish Biol.* 43: 409-419.
- Jobling, M., Koskela, J. & Pirhonen, J. 1998. Feeding time, feed intake and growth of Baltic salmon, *Salmo salar*, and brown trout, *Salmo trutta*, reared in monoculture and duoculture at constant low temperature. *Aquaculture* (in press).
- Jonsson, B. 1982. Diadromous and resident trout *Salmo trutta*: is their difference due to genetics? *Oikos* 38: 297-300
- Jonsson, B. 1985. Life history patterns of freshwater resident and sea-run migrant brown trout in Norway. *Trans Am. Fish. Soc.* 114: 182-194.
- Jonsson, B. 1989. Life history and habitat use of Norwegian brown trout (*Salmo trutta*). *Freshw. Biol.* 21: 71-86.

- Jonsson, B. & Jonsson, N. 1993. Partial migration: niche shift versus sexual maturation in fishes. *Rew. Fish Biol. Fish.* 3: 348-365.
- Jonsson, B. & Ruud-Hansen, J. 1985. Water temperature as the primary influence on timing of seaward migrations of Atlantic salmon (*Salmo salar*) smolts. *Can. J. Fish. Aquat. Sci.* 42: 593-595.
- Jørgensen, E.H. & Jobling, M. 1992. Feeding behaviour and effect of feeding regime on growth of Atlantic salmon, *Salmo salar*. *Aquaculture* 101: 135-146.
- Koljonen, M-L. 1989. Uudenmaan maritaimenkantojen geneettinen tutkimus. *Suomen Kalastuslehti* 96(3): 128-131.
- Langdon, J.S. 1985. Smoltification physiology in the culture of salmonids. In: J.F. Muir & R.J. Roberts (eds), *Recent advances in aquaculture*: 79-118. Croom Helm Ltd., London.
- Langdon, J.S. & Thorpe, J.E. 1985. The ontogeny of smoltification: developmental patterns of gill Na^+/K^+ -ATPase, SDH, and chloride cells in juvenile Atlantic salmon, *Salmo salar* L. *Aquaculture* 45: 83-95.
- Leonko, A.A & Chernitskiy A.G. 1986. Comparative analysis of smolt migration of Atlantic salmon, *Salmo salar*, and sea trout, *Salmo trutta*. *J. Ichtyol.* 26: 113-120.
- Mason, J.C. 1975. Seaward movements of juvenile fishes, including lunar periodicity in the movements of coho salmon (*Oncorhynchus kisutch*) fry. *J. Fish. Res. Bd. Can.* 32: 2542-2547.
- McCarthy, I.D., Carter, C.G. & Houlihan, D.F. 1992. The effect of feeding hierarchy in individual variability in daily feeding of rainbow trout, *Oncorhynchus mykiss* (Walbaum). *J. Fish Biol.* 41: 257-263.
- McCleave, J.D. 1978. Rhythmic aspects of estuarine migration of hatchery reared Atlantic salmon (*Salmo salar*) smolts. *J. Fish Biol.* 12: 559-570.
- McCormick, S.D. & Saunders, R.L. 1987. Preparatory physiological adaptations for marine life of salmonids: osmoregulation, growth, and metabolism. *Am. Fish. Soc. Symp.* 1: 211-229.
- McCormick, S.D. & Saunders, R.L. 1990. Influence of ration level and salinity on circulating thyroid hormones in juvenile Atlantic salmon (*Salmo salar*). *Gen. Comp. Endocr.* 78: 224-230.
- McCormick, S.D., Saunders, R.L., Henderson, E.B. & Harmon, P.R. 1987. Photoperiod control of parr-smolt transformation in Atlantic salmon (*Salmo salar*): changes in salinity tolerance, gill Na^+/K^+ -ATPase activity, and plasma thyroid hormones. *Can. J. Fish. Aquat. Sci.* 44: 1462-1468.
- Metcalf, N.B. 1989. Differential response to a competitor by Atlantic salmon adopting alternative life-history strategies. *Proc. R. Soc. Lond. B* 236: 21-27.
- Metcalf, N.B. 1991. Competitive ability influences seaward migration age in Atlantic salmon. *Can. J. Zool.* 69: 815-817.
- Metcalf, N.B., 1993. Behavioural causes and consequences of life history variation in fish. *Mar. Behav. Physiol.* 23: 205-217.

- Metcalfe, N.B. 1994. The role of behaviour in determining salmon growth and development. *Aquaculture and Fish. Manag.* 25: 67-76.
- Metcalfe, N.B., Huntingford, F.A. & Thorpe, J.E. 1986. Seasonal changes in feeding motivation of juvenile Atlantic salmon (*Salmo salar*). *Can. J. Zool.* 64: 2439-2446.
- Metcalfe, N.B., Huntingford, F.A. & Thorpe, J.E. 1992. Social effects on appetite and development in Atlantic salmon. In: Thorpe, J.E. & Huntingford, F.A. (eds), *The importance of feeding behaviour for the efficient culture of salmonid fishes*: 29-40. World aquaculture workshops, number 2. The world aquaculture society, Baton Rouge, Louisiana.
- Milinski, M. 1993. Predation risk and feeding behaviour. In: Pitcher, T.J. (ed.), *Behaviour of teleost fishes*: 285-305. Chapman & Hall, London.
- Mills, D.H. 1964. The ecology of the young stages of the Atlantic salmon in the river Bran, Ross-shire. *Dept. Ag. Fish. Scot., Salmon Freshwater Res.* 32.
- Moore, A., & Potter, E.C.E. 1994. The movement of wild sea trout, *Salmo trutta* L., smolts through a river estuary. *Fish. Manag. Ecol.* 1: 1-14.
- Muona, M & Soivio, A. 1982. Changes in plasma lysozyme and blood leucocyte levels of hatchery-reared Atlantic salmon (*Salmo salar* L.) and sea trout (*Salmo trutta* L.) during parr-smolt transformation. *Aquaculture* 106: 75-87.
- Müller, K. 1969a. Die Tages- und Jahresperiodik der Bachforelle (*Salmo trutta* L.) am Polarkreis. *Aquilo, Ser. Zool.* 8: 50-62.
- Müller, K. 1969b. Jahreszeitliche Wechsel der 24 h-Periodik bei der Bachforelle (*Salmo trutta* L.) am Polarkreis. *Oikos* 20: 166-170.
- Österdahl, L. 1969. The smolt run of a small Swedish river. In: Northcote, G. (ed.), *Symposium on Salmon and Trout in Streams*: 205-215. H.R. Macmillan Lectures in Fisheries, University of British Columbia, Vancouver, B.C.
- Patino, R., Schreck, C.B., Banks, J.L. & Zaugg, W.S. 1986. Effects of rearing conditions on the development of coho salmon (*Oncorhynchus kisutch*) during smoltification. *Trans. Am. Fish. Soc.* 115: 828-837.
- Pickering, A.D. 1989. Environmental stress and the survival of brown trout, *Salmo trutta*. *Freshw. Biol.* 21: 47-55.
- Pickering, A.D. 1990. Stress and the suppression of somatic growth in teleost fish. In: Eppler, A., Scanes, C.G. & Stetson, M.H. (eds), *Progress in comparative endocrinology*: 473-479. Wiley-Liss, New York.
- Pickering, A.D. & Pottinger, T.G. 1987. Crowding causes prolonged leucopenia in salmonid fish despite interrenal acclimation. *J. Fish. Biol.* 30: 701-712.
- Pickering, A.D. & Stewart, A. 1984. Acclimation of the interrenal tissue of the brown trout, *Salmo trutta* L., to chronic crowding stress. *J. Fish Biol.* 24: 731-740.
- Piggins, D.J. & Mills, C.P.R. 1985. Comparative aspects of the biology of naturally produced and hatchery-reared Atlantic salmon smolts (*Salmo salar* L.). *Aquaculture* 45: 321-333.

- Rimmer, D.M. & Paim, U. 1990. Effects of temperature, photoperiod and season on the photobehaviour of juvenile Atlantic salmon (*Salmo salar*). *Can. J. Zool.* 68: 1098-1103.
- Rimmer, D.M., Paim, U. & Saunders, R.L. 1983. Autumnal shift of juvenile Atlantic salmon (*Salmo salar*) in a small river. *Can. J. Fish. Aquat. Sci.* 40: 671-680.
- Ruohonen, K. & Grove, D.J. 1996. Gastrointestinal responses of rainbow trout to dry pellet and low-fat herring diets. *J. Fish Biol.* 49: 501-513.
- Schreck, C.B. 1981. Stress and compensation in teleostean fishes: response to social and physical factors. In: Pickering, A.D. (ed.), *Stress and fish*: 295-321. Academic Press, London.
- Schreck, C.B. 1982. Stress and rearing of salmonids. *Aquaculture* 28: 241-249.
- Schreck, C.B., Patino, R., Pring, C.K., Winton, J.R. & Holway, J.E. 1985. Effects of rearing density on indices of smoltification and performance of coho salmon, *Oncorhynchus kisutch*. *Aquaculture* 45: 345-358.
- Schrock, R.M., Beeman, J.W., Rondorf, D.W. & Haner, P.V. 1994. A microassay for gill sodium, potassium-activated ATPase in juvenile Pacific salmonids. *Trans. Am. Fish. Soc.* 123: 223-229.
- Smith, L.S. 1982. Decreased swimming performance as a necessary component of smolt migration in salmon in the Columbia River. *Aquaculture* 28: 153-161.
- Soivio, A. & Virtanen, E. 1980. Methods for physiological experiments on fish. *Ekotoxikologiska metoder för akvatisk miljö*. Nordforsk, Helsinki, Report no. 16: 1-15.
- Soivio, A. & Virtanen, E. 1985. The quality and condition of reared *Salmo salar* smolts in relation to their adult recapture rate. *Aquaculture* 45: 335-343.
- Soivio, A., Muona, M. & Virtanen, E. 1989a. Temperature and daylength as regulators of smolting in cultured Baltic salmon, *Salmo salar* L. *Aquaculture* 82: 137-145.
- Soivio, A., Muona, M. & Virtanen, E. 1989b. Smolting two populations of *Salmo trutta*. *Aquaculture* 82: 147-153.
- Sokal, R.R. & Rohlf, F.J. 1981. *Biometry*. 859 p., W.H. Freeman and company, San Francisco
- Solomon, D.J. 1978. Migration of smolts of Atlantic salmon (*Salmo salar* L.) and sea trout (*S. trutta* L.) in a chalkstream. *Env. Biol. Fish.* 3: 223-229.
- Solomon, D.J. 1982. Smolt migration in Atlantic salmon (*Salmo salar* L.) and sea trout (*Salmo trutta* L.). In: Brannon, E.L. & Salo, E.O. (eds), *Proceedings of the salmon and trout migratory behavior symposium*: 196-203. School of Fisheries, Univ. of Washington, Seattle.
- Talbot, C. & Higgins, P.J. 1983. A radiographic method for feeding studies of fish using metallic iron powder as a marker. *J. Fish. Biol.* 23: 211-220.
- Thorarensen, H., Clarke, W.C. & Farrell, A.P. 1989. Effect of photoperiod and various intensities of night illumination on growth and seawater adaptability of juvenile coho salmon. *Aquaculture* 82: 39-49.

- Thorpe, J.E. 1977. Bimodal distribution of length of juvenile Atlantic salmon (*Salmo salar* L.) under artificial rearing conditions. *J. Fish Biol.* 11: 175-184.
- Thorpe, J.E. 1982. Migration in salmonids, with special reference to juvenile movements in freshwater. In: Brannon, E.L. & Salo, E.O. (eds), *Proceedings of the salmon and trout migratory behavior symposium*: 86-97. School of Fisheries, Univ. of Washington, Seattle.
- Thorpe, J.E. 1986. Age at first maturity in Atlantic salmon, *Salmo salar*: freshwater period influences and conflicts with smolting. *Can. Spec. Publ. Fish. Aquat. Sci.* 89: 7-14.
- Thorpe, J.E. 1989. Developmental variation in salmonid populations. *J. Fish Biol.* 35(suppl. A): 295-303.
- Thorpe, J.E. 1994. An alternative view of smolting in salmonids. *Aquaculture* 121: 105-113.
- Thorpe, J.E. & Metcalfe, N.B. 1998. Is smolting a positive or a negative developmental decision? *Aquaculture* (in press).
- Thorpe, J.E. & Moore, A. 1997. The migratory behaviour of juvenile Atlantic salmon. In: Ueda, H. & Bern, H.A. (eds), *Proceedings of the international symposium of fish migration*: 39-59. Lake Toya, Hokkaido, Japan.
- Thorpe, J.E. & Morgan, R.I.G. 1978. Periodicity in Atlantic salmon *Salmo salar* L. smolt migration. *J. Fish Biol.* 12: 541-548.
- Thorpe, J.E., Morgan, R.I.G., Pretswell, D. & Higgins, P.J. 1988. Movement rhythms of juvenile Atlantic salmon (*Salmo salar* L.) in experimental flumes. *J. Fish Biol.* 33: 931-940.
- Thorpe, J.E., Adams, C.E., Miles, M.S. & Keay, D.S. 1989. Some influences of photoperiod and temperature on opportunity for growth in juvenile Atlantic salmon, *Salmo salar* L. *Aquaculture* 82, 119-126.
- Thorpe, J.E., Metcalfe, N.B. & Huntingford, F.A. 1992. Behavioural influences on life-history variation in juvenile Atlantic salmon, *Salmo salar*. *Env. Biol. Fishes* 33, 331-340.
- Thorpe, J.E., Metcalfe, N.B. & Fraser, A. 1992. Temperature dependence of switch between nocturnal and diurnal smolt migration in Atlantic salmon. In: Mackinlay, D.D. (ed.), *High Performance Fish*: 83-86. Fish Physiology Association, Vancouver.
- Tytler, P., Thorpe, J.E. & Shearer, W.M. 1978. Ultrasonic tracking of the movements of Atlantic salmon smolts (*Salmo salar* L.) in the estuaries of two Scottish rivers. *J. Fish Biol.* 12: 575-586.
- Valdimarsson, S.K. & Metcalfe, N.B. 1998. Shelter selection in juvenile Atlantic salmon, or why do salmon seek shelter in winter? *J. Fish Biol.* 52: 42-49.
- Virtanen, E. 1988. Smolting and osmoregulation of Baltic salmon *Salmo salar* L., in fresh and brackish water. Ph.D. Thesis, Yliopistopaino, Helsinki.
- Virtanen, E. & Forsman, L. 1987. Physiological responses to continuous swimming in wild salmon (*Salmo salar* L.) parr and smolt. *Fish Physiol. Biochem.* 4: 157-163.

- Virtanen, E. & Soivio, A. 1985. The patterns of T_3 , T_4 , cortisol and Na^+K^+ -ATPase during smoltification of hatchery-reared *Salmo salar* and comparison with wild smolts. *Aquaculture* 45: 97-109.
- Wallace, J.C., Kolbeinshavn, A. & Aasjord, D. 1988. Observations on the effect of light intensity on the growth of Arctic charr fingerlings (*Salvelinus alpinus*) and salmon fry (*Salmo salar*). *Aquaculture* 72: 81-84.
- Wardle, C.S. 1993. Fish behaviour and fishing gear. In: Pitcher, T.J. (ed.), *Behaviour of teleost fishes*: 609-643. Chapman & Hall, London.
- Wedemeyer, G.A. & McLeay, D.J. 1981. Methods for determining the tolerance of fishes to environmental stressors. In: Pickering, A.D. (ed.), *Stress and fish*: 247-275. Academic Press, London.
- Youngson, A.F. & Simpson, T.H. 1984. Changes in serum thyroxine levels during smolting in captive and wild Atlantic salmon, *Salmo salar* L. *J. Fish Biol.* 24: 29-39.

Responsibilities of Juhani Pirhonen in the articles of this thesis

Paper I. I was responsible in planning, designing and setting up the experimental tank and the data storage system. I was also responsible in running the experiment, measuring and X-raying the fishes. After the experiment I handled the data and wrote the draft of the article.

Paper II. Leena Forsman and I together designed the experiment. We also tested together the new micromethod for the analysis of the enzyme activity and analysed the samples. I was responsible in taking the gill samples, measuring and X-raying the fishes. After the experiment I handled the data and wrote the manuscript.

Paper III. Planning and designing of this experiment was done by the three authors. I was responsible in setting up the system and running the experiment. Physiological samples were taken by Leena Forsman and me. I handled the movement activity data. I took part in writing the article.

Paper IV. Leena Forsman and I together designed the experiment. I was responsible in running the experiment, measuring and X-raying the fishes. Physiological samples were taken by Leena Forsman and me. After the experiment I handled the data and wrote the manuscript.

Paper V. Planning and designing of this experiment was done together by the three authors. Together with Juha Koskela I was responsible in setting up and running the experiment. We also measured and X-rayed the fishes together. All the three authors handled the data and took part in writing the article.

Jyväskylä 1.4.1998,



Juhani Pirhonen

I

Effect of prolonged feed restriction on size variation, feed consumption, body composition, growth and smolting of brown trout

Juhani Pirhonen and Leena Forsman

Aquaculture (in press)

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II

Effect of long term stress on the smolting of two forms of brown trout (*Salmo trutta* L.)

Leena Forsman, Juhani Pirhonen and Antti Soivio

Aquaculture (accepted)

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III

Differences in feeding between 1+ and 2+ hatchery brown trout exposed to low water temperature

Juhani Pirhonen, Juha Koskela and Malcolm Jobling

Journal of Fish Biology 50: 678-681

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IV

Movements of hatchery reared *Salmo trutta* during the smolting period, under experimental conditions

Juhani Pirhonen, Leena Forsman, Antti Soivio and John Thorpe

Aquaculture (accepted)

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**Relationship between Na^+, K^+ -ATP-ase activity and migration
behaviour of brown trout and sea trout (*Salmo trutta* L.) during the
smolting period**

Juhani Pirhonen and Leena Forsman

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