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This book is dedicated to
Marketta, Katariina, Marianna and Sonja

ABSTRACT

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Diss.

This review summarises the results of studies on feed intake and growth rate variability in Baltic salmon (*Salmo salar* L.), brown trout (*Salmo trutta* L.) and rainbow trout (*Oncorhynchus mykiss* (Walbaum)) exposed to different temperature and feeding regimes under laboratory conditions. The feed intake and growth of the Baltic salmon increased as the temperature increased from 2°C to the thermal optima and decreased with further increases in temperature. Maximal feed intake and growth were observed at 17.5-18°C and 14.5-15.0°C, respectively. Models for feed intake and growth in relation to temperature are presented. Both Baltic salmon and brown trout were able forage and increase their weight and lipid reserves at low temperatures (2-6°C). In rainbow trout restricted foraging conditions led to the formation of dominance hierarchies. This resulted in increased interindividual variability in both food acquisition and growth rate. The feeding hierarchies were rapidly broken down once food availability was increased. Under conditions of constant low temperature and continuous light the rates of feed intake and growth in Baltic salmon and brown trout were not constant but tended to increase with time. Low rates of feed intake and growth tended to be linked to high interindividual variability. These results indicated the importance of feeding and growth heterogeneity on group growth performance.

Key words: Feed intake; growth rate; temperature; dominance hierarchies; restricted feeding; interindividual variation in foraging and growth.

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CONTENTS

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 Koskela, J., Pirhonen, J. & Jobling, M.: The feed intake, growth rate and body composition of juvenile Baltic salmon exposed to different constant temperatures. - Aquaculture International (in press).

II Koskela, J., Pirhonen, J. & Jobling, M.: Effect of low temperature on feed intake, growth rate and body composition of juvenile Baltic salmon. - Aquaculture International (in press).

III Koskela, J., Pirhonen, J. & Jobling, M.: Growth and feeding responses of a hatchery population of brown trout (*Salmo trutta* L.) at low temperatures. - Ecology of Freshwater Fish (in press).

IV 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. - Journal of Fish Biology 49: 658-667.

V Koskela, J., Pirhonen, J. & Jobling, M.: Variations in feed intake and growth of Baltic salmon and brown trout exposed to continuous light at constant low temperature. - Journal of Fish Biology (in press).

1 INTRODUCTION

1.1 Thermal optima and temperature limits for ingestion and growth

Water temperature is one of the most important environmental factors governing metabolic processes in poikilothermic animals, such as fish. As such, temperature has a marked influence on the feed intake and growth of salmonids. The ingestion and growth rates of fish increase with increasing temperature up an optimum and decrease thereafter, as temperature continues to rise towards the upper temperature limits (Brett 1979, Jobling 1994). For aquaculture to be carried out effectively and profitably it is important that the effects of water temperature on the feed intake and growth rates of the culture species are known. In Finland the annual variation in temperature of freshwater lakes and ponds can be large, from a winter minimum of near zero to a summer maximum of over 25°C.

1.1.1 Lower thermal limits

The estimated lower temperature limits for feeding and growth of Atlantic salmon (*Salmo salar* L.) and brown trout (*Salmo trutta* L.) are based on observations of foraging activity in the wild, and upon the results of laboratory studies. Observations made on juvenile wild Atlantic salmon during daylight hours suggest that very few fish forage when the temperature falls below 7°C (Gibson 1978, Cunjak 1988). Only limited growth may be achieved by wild salmon parr during the winter months. These observations on wild fish, together with the results of laboratory experiments, have led to the suggestion that the lower thermal limits for feeding and growth may be as high as 4-7°C (Allen 1969, Gardiner & Geddes 1980, Jensen & Johnsen 1986, Elliott 1991). Wild brown trout have been observed to forage at temperatures close to zero (Cunjak & Power 1987, Forseth et al. 1992, Heggenes et al. 1993), and in the laboratory, brown trout may continue to feed at temperatures of 2-4°C (Elliott 1975a, Jensen & Berg 1993). Despite active foraging at low temperatures, growth of wild brown trout has been reported to be insignificant during winter (Mortensen 1985, Cunjak & Power 1987), and the lower thermal limits for growth may be as high as 4-6°C (Wingfield 1940, Elliott 1975b, Elliott et al. 1995).

1.1.2 Optimum temperatures and upper thermal limits

The thermal requirements of Atlantic salmon have been little studied (Saunders 1986), although the temperatures at which ingestion and growth rate reach their respective maxima have been reported to be between 16-17°C and 16-19°C for salmon of various sizes (Farmer et al. 1983, Austreng et al. 1987, Dwyer & Piper 1987, Peterson & Martin-Robichaud 1989, Siemien & Carline 1991). Although charts describing the feeding and growth of Atlantic salmon have been published there is little information available about the appetite and growth of salmon at the extremes of their temperature tolerance range (Elliott 1991, Grande & Andersen 1991).

In general, the thermal optima of brown trout seem to be somewhat lower than those of Atlantic salmon since the temperature for maximum feed intake has been reported to be 16-18°C, and the thermal optimum for growth is within the range 12.8-16°C (Elliott 1975b, Elliott 1991, Forseth & Jonsson 1994, Elliott et al. 1995).

1.2 Interindividual variability in feeding and growth of fish as a result of social interactions

For effective aquaculture production it is important that the feed intake and growth amongst the fish making up the rearing group are both high and uniform. The cultivation of territorial salmonids in groups can lead to competition among individuals, and the formation of dominance hierarchies. This can result in marked interindividual differences in feeding activity and food acquisition, with the consequence that the growth of subordinate individuals may be inhibited. Interindividual variation in growth is increased and biomass gain reduced.

During recent years a substantial amount of evidence has accumulated that the patterns of feed intake and growth of salmonids may be markedly influenced by factors that affect the social environment within the fish group (Davis & Olla 1987, McCarthy et al. 1992, Thorpe & Huntingford 1992, Brännäs & Alanärä 1993, Jobling & Baardvik 1994, Jobling 1995a, b). This has led to increased interest in the study of the potential influences of the social behaviour of fish on aquaculture production (Thorpe & Huntingford 1992, Metcalfe 1994, Jobling 1995b, Juell 1995). For example, manipulation of factors such as food supply (Davis & Olla 1987, McCarthy et al. 1992), water flows and stocking density (Brown et al. 1992, Jobling & Baardvik 1994, Adams et al. 1995, Jobling 1995b) has been found to influence the formation of dominance hierarchies in salmonids.

1.3 Questions asked

Environmental temperature and the social position of a fish within a population both have strong influences on feed intake and growth. The optimal rearing practice for a given species will depend upon how well individuals adapt to different holding conditions. There is only limited information about the feed intake and growth of Baltic salmon and brown trout held at low and high temperatures, and almost nothing is known about growth variability amongst fish held at temperatures approaching the extremes of their thermal range. Experiments were, therefore, conducted to examine

- the thermal limits of ingestion and growth of Baltic salmon and brown trout (Papers I-III).

- inter-individual variations in ingestion and growth of rainbow trout under different foraging conditions, with the aim of describing basic relationships between intra-group variability and group performance (Paper IV).

- inter-individual variations of feeding and growth in Baltic salmon and brown trout under low temperatures, with the aim of describing the effects of feeding and growth heterogeneity on group performance (Paper V).

2 MATERIALS AND METHODS

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

All of the experiments were carried out at the Laukaa Research Station of the Finnish Game and Fisheries Research Institute (62°30'N, 26°E) using hatchery-reared juvenile salmonids derived from broodstock held at the research station:

- age 1+ and 2+ Baltic salmon (*Salmo salar* L.) of the river Neva strain (Papers I, II and V)
- age 1+ brown trout (*Salmo trutta* L.) of Rautalampi strain (Paper III)
- age 1+ rainbow trout (*Oncorhynchus mykiss* (Walbaum)) (Paper IV)

All the experiments were carried out using triplicate groups of fish in which a certain proportion were individually tagged by injecting a PIT tag (Destron/IDI) into the body cavity. This enables individuals to be identified and followed throughout the course of a study, and detailed data sets can, therefore, be collected for each fish.

Feed intake was measured using an X-radiographic technique (Talbot & Higgins 1983, Jobling et al. 1993) with X-ray dense ballotini as the marker (Jencons Ltd Leighton Buzzard, UK.). Feed intake measurements were made by providing the marked feed as the daily ration, followed immediately by anaesthetisation of the fish (MS-222), X-raying (Siemens Nanodor X-ray machine; Agfa Structurix D7 film), weighing and identification of individuals by reading the PIT tag. The amounts of feed consumed by the individual fish were then estimated from the numbers of ballotinis present in the gastrointestinal tract.

At the beginning and at the end of some experiments (Papers I, II, III and V) samples of fish were taken for the analysis of proximate body composition (energy, moisture, protein, lipid and ash) by standard methods.

3 RESULTS AND DISCUSSION

3.1 Feed intake and growth as influenced by temperature

3.1.1 Thermal limits and the temperature optimum for feeding and growth in Baltic salmon

The feed intake and growth of the Baltic salmon increased as the temperature increased from 2°C to 6°C (Paper II), continued to increase until the thermal optima were reached and then decreased with further increases in temperature (Paper I). Both studies covered only part of the complete thermal range, so an attempt was made to construct models to describe feeding and growth over a wider range of temperatures. The fish sizes differed between studies (Paper I - 40-80g & 190-260g; Paper II -140-170g), and it is well known that, when expressed in relative terms, both feed intake and growth rates will decrease with increasing fish size. In salmonids the weight exponent describing the relationship between relative feed intake and body weight has usually been found to fall within the range -0.20 - -0.40 (Jobling 1994), and the exponent for the relationship between body weight and growth rate has been reported to be -0.30 - -0.45 (Brett 1979, Jobling 1994). Consequently it was necessary to include a weight term in the models used to describe the effects of temperature on feed intake and growth.

Various expressions have been used to describe rate-temperature curves (Hewett & Johnson 1992, Koskela & Eskelinen 1992, Binkowski & Rudstam 1994), and Hogendoorn et al. (1983) suggested that Hoerls function could be used to describe rate-temperature relationships. Hoerls function was adopted as the basis for constructing the models describing the rate-temperature relationships for feed intake and growth in Baltic salmon.

The relationship between feed intake (FI in kJ.kg^{-1}.d^{-1}), water temperature (T°C) and fish weight (W g) was described by the equation:

$$FI = (4.974 + 0.007(T + 7.065)^{13.3888} e^{-0.421(T + 14.136)}) (8.627 \times 10^{-6} T^{-2.159}) W^{-0.293}$$

$N = 27$; $R^2 = 0.983$

and the plot of measured and predicted values is shown in Fig. 1. The model provides an excellent fit to the data within the temperature range 2-23°C , and gives an estimate of 17.5-18°C as the temperature at which feed intake is at a maximum.

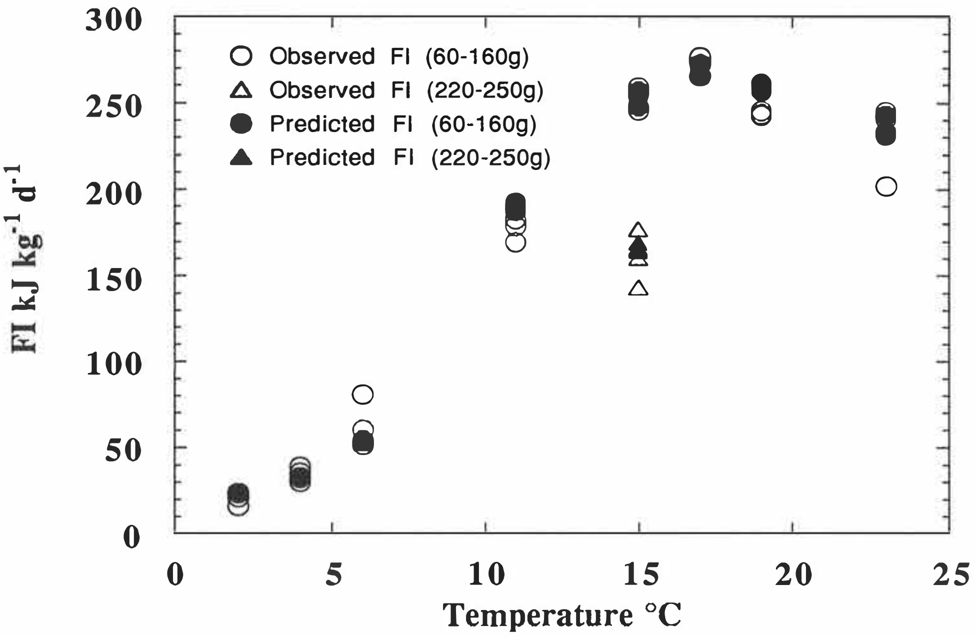

FIGURE 1 Influence of water temperature on the feed intake of Baltic salmon of different body weights (60-250 g). Observed values are taken from Papers I and II, and the predicted values are derived from the model described in the text.

The relationship between growth rate (SGR %.d^{-1}), water temperature (T°C) and fish weight (W g) was described by the equation:

$$SGR = (-4.275 + 0.065(T + 2.399)^{17.418} e^{-0.528(T + 3.967)}) (1.979 \times 10^{-7} T^{-7.205}) W^{-0.400}$$

$N = 27$; $R^2 = 0.924$

and the plot of measured and predicted values is shown in Fig. 2. The model provides an excellent fit to the data within the temperature range 2-20°C, and gives an estimated temperature optimum for growth of 14.5-15°C. Thus, the optimum temperature for growth is slightly lower than that at which ingestion is at a maximum. The generality of these findings is demonstrated by the results obtained in a number of growth studies conducted on fish species (summarised by Jobling 1995c)

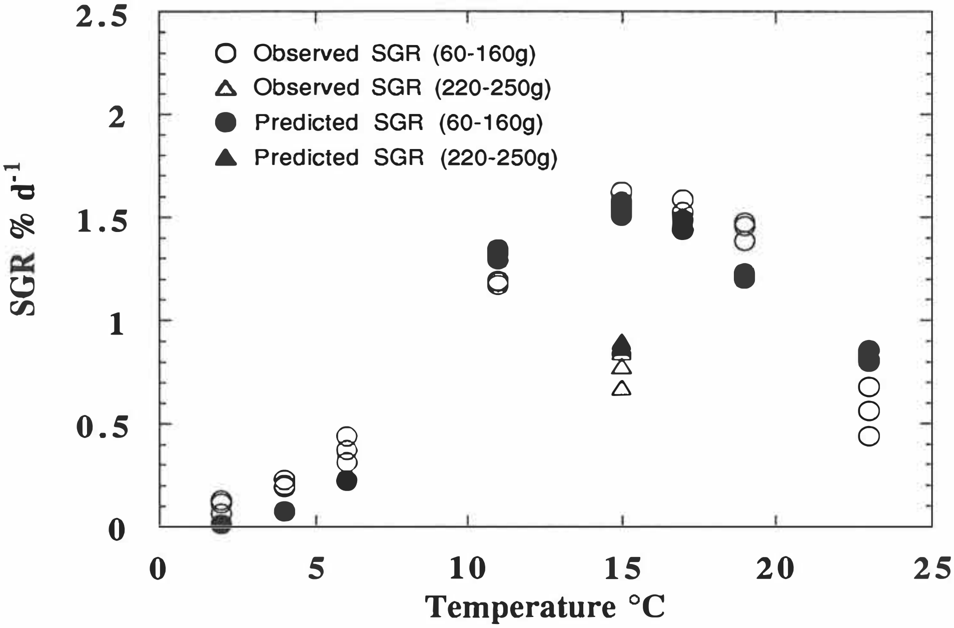

FIGURE 2 Influence of water temperature on growth rates of Baltic salmon of different body weights (60-250 g). Observed values are taken from Papers I and II, and the predicted values are derived from the model described in the text.

Although some workers have suggested that the lower thermal limits for feeding and growth of salmon may be as high as 4-7°C (Allen 1969, Gardiner & Geddes 1980, Jensen & Johnsen 1986, Elliott 1991), the results of both the present work (Paper II), and other laboratory studies on feeding provide clear evidence that feeding and growth is maintained at temperatures under 4°C (Higgins & Talbot 1985, Jørgensen & Jobling 1992).

3.1.2 Lower thermal limits for feeding and growth of brown trout

The brown trout continued to feed at 2°C and it was estimated that feeding would be maintained as temperatures approached zero (Paper III). In the wild, brown trout forage at low temperature, and they may continue to feed throughout the winter months (Cunjak & Power 1987, Heggenes et al. 1993). In the low-temperature (2-6°C) studies described in Paper III, the trout in all groups consumed sufficient feed to grow, and the lower threshold for growth was estimated to be approximately 0-0.6°C. This differs from the results of earlier studies, in which the lower thermal limits for growth have been reported to be 3.6-6°C (Wingfield 1940, Elliott 1975b, Elliott et al. 1995). Also the growth rates observed were appreciably higher at 4 and 6°C than those reported for brown trout by Elliott and co-workers (Elliott 1975b, Elliott et al.

1995). The difference in growth limits and growth rates between studies is obviously related to differences in feed intake. Brown trout in Paper III ate more than did those in previous studies, and, consequently, they had more energy available for anabolic processes and could grow faster at any given temperature.

3.2 Feed intake and growth variations resulting from social interactions

3.2.1 In restricted foraging conditions

Rainbow trout fed full rations consumed more, grew faster and showed lower interindividual variability in consumption and growth than fish held on restricted rations (Paper IV). There were clear decreases in group feed intake and growth and increases in the coefficient of variation of intake (CV_{intake}) and growth (CV_{SGR}) when fish were changed from a full to a restricted ration. Correspondingly, when fish were switched from restricted to full rations there were clear increases in feed intake and growth and decreases in CV_{intake} and CV_{SGR}. The results of restricted feeding on interindividual variations (CV_{intake} and CV_{SGR}) are in agreement with those of several previous studies carried out on salmonids (Davis & Olla 1987, McCarthy et al. 1992, Thorpe & Huntingford 1992, Grant 1993, Jobling 1995b). The findings indicate increased competition among individuals as resources become restricted.

The rainbow trout that had shown low rates of growth during the period of food restriction were able to compensate for the period of growth depensation by increasing feeding and growth when food became available in increased quantities. This result is in agreement with previous findings that rainbow trout display compensatory growth when food supplies are increased following a period of undernutrition (Weatherley & Gill 1981, 1987, Dobson & Holmes 1984, Kindschi 1988, Quinton & Blake 1990), and the results of Paper IV clearly demonstrate that the response is strongest amongst those individuals that suffer the greatest growth depensation during the period of feed restriction. Further, the fact that the previously-suppressed fish were able to display compensatory growth provides clear evidence that the feeding hierarchies established during the period of restricted feeding were not persistent, but broke down rapidly once food availability was increased.

3.2.2 In conditions of constant low temperature and continuous light

Given a liberal food supply the rates of feed intake and growth of fish could be expected to be uniformly high and variability small. However, in Baltic salmon and, in particular, in brown trout held under conditions of constant temperature and continuous light (Paper V) rates of feed intake and growth tended to increase during the course of the experiment. At the same time interindividual variation decreased. This could have been a reflection of a temporal rhythmicity in feeding and growth (cf. Saether et al. 1996), with the changes in CV with time being indicative of considerable asynchrony among individuals.

The growth of salmon and brown trout is closely related to either changes in day length or to the length of the photoperiod, growth being accelerated in conditions of extended day-length. This photostimulation of growth is probably connected to the photoperiod-induced changes in plasma growth hormone levels (Brown 1946, Swift 1955, Komourdjian 1976, Saunders et al. 1985, Komourdjian et al. 1989, Saunders et al. 1989, Stefansson et al. 1990). Such a photostimulation can not, however, be used as an explanation of the increased growth of the Baltic salmon and brown trout seen in the experiment described in Paper V because a continuous light regime was used. Further, extended day-lengths have been found to accelerate growth at high temperatures (8-15°C) but in a study at low temperature (3°C) no photostimulation of growth was observed (Saunders et al. 1989). In addition, recent studies provide evidence that Atlantic salmon and brown trout tend to forage at night when exposed to low water temperatures (Fraser et al. 1993, 1995, Heggenes et al. 1993). It is therefore unlikely that an extended light regime would have a stimulating effect on feed intake and growth of juvenile salmonids at low temperatures.

Low values of feed intake and growth tended to be linked to high levels of interindividual variability amongst fish within a group. High levels of interindividual variation in feed intake (CV_{FI}) and growth (CV_{SGR}) have been linked to competition or aggressive behaviour among individuals, whereas high rates of feed intake and low CV_{FI}s and CV_{SGR}s are thought to reflect good feeding conditions (Davis & Olla 1987, McCarthy et al. 1992, Thorpe & Huntingford 1992, Jobling & Baardvik 1994, Jobling 1995a, b). Thus, it is possible that the increases in rates of foraging and growth with time might have been associated with the breakdown of feeding hierarchies established during the initial period of the experiment.

Alternatively, the changes could be interpreted as providing evidence that the fish were poorly acclimatized to the test conditions when the experiment was started, even though an acclimatization period of three weeks was allowed prior to first sampling. Thus, the fish may have required several weeks to become fully acclimatized to the new rearing environment. Heterogeneity tended to be greatest within the groups of fish held at the lowest temperature, possibly suggesting that acclimatization occurred more rapidly at higher temperature. Further, the temporal changes were less pronounced, and CV_{FI} and CV_{SGR} were generally lower, amongst the groups of trout than salmon, perhaps indicating that the trout acclimatized more rapidly and more uniformly to the new rearing conditions than did the salmon.

4 CONCLUSIONS

The results of the studies described in the five papers clearly indicate that feed intake and growth rates in salmonids are not only temperature dependent but are also markedly affected by the social environment within the fish group.

Feed intake and growth of Baltic salmon and brown trout were influenced by temperature, results that are in accord with many other feeding and growth studies on salmonids. In contrast to some of the previous studies the feed intake and growth of the two species did not cease at low temperature, but both species were able to forage and maintain positive rates of growth at temperatures of 2-6°C. Further, Baltic salmon maintained feeding and growth at higher temperatures than reported to inhibit growth of Atlantic salmon.

Restricted feeding conditions led to formation of dominance hierarchies within groups of rainbow trout. However, the feeding hierarchies were rapidly broken down once food availability was increased, and the previously-suppressed fish were able to display compensatory growth.

In the three salmonids, rainbow trout, Baltic salmon and brown trout low values of feed intake and growth tended to be linked to high levels of interindividual variability. This may be indicative of competition or aggressive behaviour among individual fish within a group. The results suggest that the social environment may have important influences on the feeding and growth performance of a fish group.

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YHTEENVETO

Veden lämpötilan ja sosiaalisen hierarkian vaikutus lohikalojen ravinnon kulutukseen ja kasvuun

Kalojen tuotantobiologiatutkimuksen yksi keskeinen päämäärä on selvittää ne olosuhteet, joissa yksilöiden kasvu voi olla mahdollisimman nopeaa ja tasasuuruista. Lohikalojen ravinnon kulutus ja kasvu ovat hyvin joustavia ja niihin vaikuttavat kalan fysiologisen tila ohella monet ympäristötekijät, joista erityisesti veden lämpötilalla on suuri merkitys. Vaikkakin veden lämpötila asettaa rajat kalan ravinnon kulutukselle ja kasvupotentiaalille, niin niiden toteutumiseen yksilötasolla vaikuttavat myös kalayksilöiden väliset suhteet parven sisällä. Kalaparvessa voi muodostua yksilöiden välille hierarkia, jossa muutamat dominoivat yksilöt estävät muita parven kaloja ruokailemasta ja kasvamasta sen mukaisesti mitä ympäristön lämpötilan perusteella olisi mahdollista.

Väitöskirjassani olen tutkinut matalien ja korkeiden lämpötilojen vaikutusta lohen ja taimenen ravinnon kulutukseen ja kasvuun ja pyrkinut määrittämään niiden rajalämpötilat sekä olen kuvannut mallin avulla lämpötilan vaikutuksen lohen ravinnon kulutukseen ja kasvuun. Lisäksi tutkin rajoitetun ravinnon tarjonnan ja kylmän veden vaikutuksia kalaparven sisäisen hiearkian muodostumiseen. Oletan, että mikäli rajoitettu ruokinta aiheuttaa parven sisäisen hiearkian syntymisen, se ilmenee parvitason kasvun alenemisen lisäksi myös ravinnon kulutuksen ja kasvun yksilöiden välisen variaation kasvamisena. Kaikissa tutkimuksissa käytin parvessa olevien kalojen yksilöllisen ruokailukäyttäytymisen havainnointiin röntgen-menetelmää, ja yksilöllistä tunnistamista varten merkitsin kalat passiivisilla radiolähettimillä.

Lämpötilan (2 - 23 astetta) vaikutus lohen ravinnonkulutukseen ja kasvuun noudatti lohikaloille tyypillistä käyräviivaista muotoa. Kasvu nopeutui veden lämpötilan noustessa aina 15-16 asteeseen ja ravinnon kulutus lämpötilan noustessa 17-18 asteeseen. Parhaiten lohi pystyi muuntamaan ravinnon energian kasvuksi 11 asteen lämpötilassa, ja muuntotehokkuus alentui tätä korkeammissa lämpötiloissa. Aineiston perusteella olen laatinut mallin, jonka avulla voidaan ennustaa lämpötilan ja kalan koon vaikutusta lohen ravinnon kulutukseen ja kasvuun. Tulosten perusteella Itämeren lohen lämpötilalokero on laajempi mitä eräissä aikaisemmissa tutkimuksissa on havaittu Atlantin lohella, sillä laji pystyi ruokailemaan ja kasvamaan vielä 2 ja 23 asteen lämpötiloissa.

Kylmän veden olosuhteissa taimen ruokaili ja kasvoi 2 - 6 asteen lämpötiloissa ja aineiston pohjalta extrapoloitu rajalämpötila oli ravinnon kulutukselle ja kalojen kasvulle n. 0-0.6 astetta. Tulosten perusteella taimen on sopeutunut hyvin elämään kylmän veden olosuhteissa.

Ravinnon tarjonnan rajoittaminen johti kirjolohella parven sisäisen hierarkian muodostumiseen, koska tarjottu ravinto ei jakautunut tasan yksilöiden kesken vaan jotkut kalat söivät muita enemmän ja kasvoivat myös muita paremmin. Tämän seurauksena rajoitetun ruokinnan ryhmissä dominoivat yksilöt kasvoivat yhtä hyvin kuin kontrolliryhmän yksilöt. Ravinnon tarjonnan rajoittamisen lopettaminen johti hierarkian purkautumiseen. Parven ruokailun ja kasvun variaatio säilyi kuitenkin suurena, koska kilpailussa aiemmin kasvutappioita kärsineet yksilöt söivät nyt muita enemmän ja kasvoivat myös muita nopeammin. Seurauksena tästä oli, että kalat pystyivät kompensoimaan rajoitetun ruokinnan aikana kilpailutilanteessa kärsimäänsä kasvutappiota.

Vakio-oloissa (tasalämpöinen kylmä vesi ja jatkuva valo) lohen ja taimenen ravinnonkulutuksen ja kasvun voidaan olettaa säilyvän vakiosuuruisina. Seuratessani kalayksilöiden käyttäytymistä parvessa havaitsin, että ravinnon kulutus oli seurannan alkuvaiheessa parvitasolla vähäistä ja kasvu heikkoa ja näiden suureiden yksilöiden välinen variaatio oli suurta. Kalaparven ravinnon kulutus ja kasvu kuitenkin kiihtyivät seurannan edetessä ja samanaikaisesti myöskin alkuvaiheen suuret erot yksilöiden välisessä ravinnon kulutuksessa ja kasvussa pienenivät. Havaittu vaihtelu on voinut johtua alkuvaiheen voimakkaasta parven sisäisestä hierarkiasta, joka purkautui kokeen edetessä. Havaittu vaihtelu voidaan selittää myös yksilöiden erilaisella aklimoitumisella koeolosuhteisiin.

Tämän tutkimuksen perusteella on ilmeistä, että veden lämpötilan ohella kalaparven sisäisellä hierarkialla on suuri merkitys tutkittujen lohikalojen ravinnon kulutukseen ja kasvuun. Eri ympäristötekijöiden merkitys hierarkioiden muodostumisessa ja eri lajien herkkyys muodostaa niitä tunnetaan vielä huonosti, ja on selvää, että tarvitaan lisätutkimuksia ennen kuin voidaan kuvata tarkemmin ne olosuhteet, joissa eri kalalajien hyvä kasvu on mahdollista.

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ORIGINAL PAPERS

I

The feed intake, growth rateand body composition of juvenile Baltic salmon exposed to different constant temperatures

Koskela, Juha, Pirhonen, Juhani & Jobling, Malcolm

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II

Effect of low temperature on feed intake, growth rate and body composition of juvenile Baltic salmon

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III

Growth and feeding responses of a hatchery population of brown trout (*Salmo trutta* L.) at low temperatures

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IV

Interindividual variations in feeding and growth in rainbow trout during restricted feeding and in a subsequent period of compensatory growth

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V

Variations in feed intake and growth of Baltic salmon and brown trout exposed to continuous light at constant low temperature

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