

**CAUSES AND CONSEQUENCES OF SEXUAL DIFFERENCES
IN INDIVIDUAL BROOK TROUT, *Salvelinus fontinalis*,
GROWTH RATE**

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EXTENDED ABSTRACT ONLY - DO NOT CITE

Introduction

The work described here is part of a research programme that addresses the following general question: What is the influence of environmental heterogeneity on life history? For indeterminately growing organisms, individual growth rate is often a reliable metric of environmental variability. From a behavioural perspective, temporal changes to the physical and biological environment can result in directed movement or undirected displacement. From a life history perspective, environmental variability can effect changes to age-specific rates of survival, fecundity, and growth rate, all of which significantly influence fitness.

To study seasonal patterns in growth rate and movement, naturally occurring brook trout, *Salvelinus fontinalis*, were tagged individually, returned to their natal river, and monitored over a 5-year period. The primary objectives of the research were to: 1) describe patterns of individual movement within an unexploited population near equilibrium; 2) determine whether lifetime movement is sex-biassed; and 3) examine whether seasonal growth rate, and possibly costs of reproduction, differ between males and females.

Material and Methods

The field work was conducted on nonanadromous trout inhabiting Freshwater River, Newfoundland, Canada, a population for which considerable data on life history and survival exist (e.g., Hutchings, 1993, 1994, 1996). PIT (Passive Integrated Transponder) tags were inserted into the body cavities of 943 trout (minimum length of 7 cm, the smallest size at maturity recorded in this population) in June, 1995 and June, 1996. The entire 2.2-km length of the river was electrofished twice annually (June, October) until June, 2000.

Results and Discussion

Patterns in lifetime movement

Among the 192 recaptured fish of known sex, fork length at initial marking did not differ between sexes (females: 9.3 cm, males: 9.4 cm). Lifetime movement differed between sexes, males moving 2.5 times further throughout their lives than females. The difference between sexes was most evident during the spawning period. Notwithstanding this sex bias in movement, most trout moved relatively little, with approximately 85% of females and 65% of males having moved less than 100 m throughout their lives. Interestingly, if an individual was recaptured at a location other than that in which it was originally marked, subsequent recaptures of the same individual revealed movement back to its initial location, suggesting that trout are able to recognise a home territory or range and appear to select these areas preferentially after movement to other sections of the river.

Growth rate

There were significant seasonal differences in growth rate between sexes. The proportionate increase in length experienced by individual males during summer (June through September) was almost double that of individual females. However, the proportionate annual increase in length was not sex-biased, indicating that females grew significantly faster than males from autumn through early spring.

The faster growth rate experienced by males during summer can be attributed to the doubling of lipids allocated to gonadal tissue by females relative to that

allocated by males (Hutchings et al., 1999). Similarly, sex differences in energy allocated during the spawning period might account for the slower growth experienced by males during winter.

Hutchings et al. (1999) found that male trout from nearby Watern Cove River lost significantly more lipids between early October and early April (58%) than females (42%). Although females expend energy during nest construction, mate competition among male salmonids (which can lead to death; Hutchings and Myers, 1987) might account for their significantly greater energy losses. One consequence of these greater lipid losses by males appears to be an increased probability of death during winter (Hutchings et al., 1999). A second consequence may be reduced growth rate during the non-summer months. Furthermore, the energy that males require to undertake their significantly greater within-stream movements might also contribute to a post-spawning energy deficit greater than that of females, resulting again in reduced seasonal growth rate.

Summary

A 60-month study of individually-marked brook trout in Freshwater River, Cape Race, Newfoundland, has revealed sexual differences in seasonal patterns of individual growth rate and movement. Although annual growth rate did not differ between sexes, males grew significantly faster during summer while females grew significantly faster during the remainder of the year. These seasonal differences can be attributed to sexual differences in both allocation of energy to gonads (greater among females) and energetic costs of reproduction (greater among males). Sex-biased patterns of movement, manifested by a 2.5-fold increase in distance moved by males, may also contribute to the seasonal constancy in male growth rate observed during autumn and winter.

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**SOURCES OF GROWTH RATE VARIATION
IN INDIVIDUAL ATLANTIC SALMON PARR**

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Growth rate is a highly plastic trait in Atlantic salmon (*Salmo salar*). Smolt ages can range from one to six among rivers (Metcalf and Thorpe, 1990) and depending on dominance interactions, life history tactic and possibly genetics, growth rate can also vary substantially within a river. Because interactions among fish are often size dependent (Miller et al. 1988), and smolt age in salmonids is related to growth rate (Thorpe, 1986; Duston and Saunders, 1997) understanding the relative importance of factors governing growth rates should lead to increased understanding of individual survival and ultimately population dynamics. Our aim is to describe sources of variation in juvenile Atlantic salmon growth rates based on three years of data on individually-tagged fish from a stream in Massachusetts, USA. We describe variation in growth due to the year, season, life history tactic and present preliminary data on growth rate variation of fish from different families (single mother-father pair).

Our study site was a 1-km stretch of the West Brook, in Whately, MA, a second order stream with an average width of 4.8 m. The study site was divided into 47 contiguous 20-m sections that we sampled in a downstream to upstream direction 22 times from May 1997 to March 2000. In total, we have tagged 3629 fish from three stocking years. Fish greater than 60-mm were tagged intraperitoneally with a 12-mm PIT tag. In a little over one-half of these samples, we sampled fish using electroshocking (500 V unpulsed DC) and we

used night-seining in the remaining samples. In the spring of each year, we constructed a smolt-sampling weir approximately 4-km downstream of our study site. There is no natural reproduction in the West Brook and fry are stocked (50-100 m⁻²) each spring.

Upon capture, we recorded the location of each fish (± 2.5 m). Untagged fish were tagged with PIT tags and sampled for scales after anesthetizing with MS-222; all fish were measured for length, wet mass, maturity status (milt expression), a digital photograph was taken and anal fin clips for fish from the 1999 stocking year were taken for family identification. Upon recovery, each fish was returned to its approximate sampling location. A fish's family was identified by comparing its multilocus genotype (microsatellites) to those of the candidate parents at the hatchery (standard allele matching parentage assignment). All fish stocked into the study section in 1999 were from one of six families.

Seasonal growth variation was substantial. Growth rates were highest during the spring and lowest in the summer. This growth pattern was consistent across years, although growth was slightly slower in 1999 than in 1998. For age-1 and age-2 fish, growth was low to negative in the summer, increased somewhat through the fall and winter and was very rapid in the spring. Among years, average spring growth (\log_{10} instantaneous growth $\cdot 100$) of individual fish caught on consecutive samples ranged from 0.7 to 0.9 for age-1 fish and ranged from 0.3 to 0.6 for age-2 fish. Spring growth was rapid for both age-2 smolts and age-2 residents. Over two years of life in the stream, age-2 smolts amassed 72% of their total 2-year weight gain during just 13% of year (two springs).

Most age-based growth rate variation appeared allometric, with larger fish growing proportionately more slowly, but age-0 fish in 1998 had positive growth rates (~ 0.2), while the age-1 and age-2 fish in the stream were losing mass.

Male parr maturation rates were very high ($\sim 100\%$) for age-1 fish and appeared to significantly influence growth rate variation. For the 1996 and 1997 stocking years, masses of age-1 fish that matured began to diverge from immature fish in the late summer. By the subsequent spring, mature fish (age-2) were about 10-g lighter than immature fish (1996, 33 v. 22 g; 1997 27 v. 18 g). This difference disappeared during the rapid growth spring period; previously mature smolts (40% of the smolts) were only several grams lighter than immature smolts and resident fish (virtually all previously mature) were approximately the same size

as smolts two weeks following smolting. These results did not depend on a size-selective sampling artifact; we obtained similar results comparing individual growth rates of mature and immature fish. A large part of the 10-g difference between mature and immature fish in the spring could be explained by differences in mass between mature fish that would become smolts and immature fish that would become smolts. In March, mature pre-smolts weighed 25 g and immature pre-smolts weighed 27 g. In contrast, mature future resident fish weighed only 18 g. Based on captures of fish caught in the smolt trap, mature smolts were slightly lighter (33 g) than immature smolts (36 g). Mature smolts were heavier than mature residents (31 g).

Patterns of mass difference among fish with different life histories were not limited to smolts, pre-smolts and residents. As early as their first fall, fish that would eventually mature and smolt were significantly heavier (logistic regression, $P < 0.05$) than eventual mature residents. This pattern was continued through to smolting, although mass differences among life histories were not significant during early summer. Eventual immature smolts displayed an intermediate pattern. Masses of immature smolts were similar to mature residents until the middle of their second summer (age-1), when they switched trajectories to match and then surpass masses of mature smolts during late fall and their second winter. These results suggest significant size structuring relating to life history tactic.

Based on data from the 1999 stocking year class, masses also appear to vary among fish from different families. Of the fish sampled from the study section, 81% were assigned to one of the six stocked families. The remaining 19% represented fish with unknown parents stocked outside the section. Over the course of four samples (August 1999 to March 2000), masses of fish from one family (number 5) were consistently 33% greater than masses of fish from the other five families. Masses of fish from family five were also consistently heavier for fish raised in the hatchery, suggesting a genetic component to the greater masses of family five fish. Length at stocking was greatest for family five, but they were not the heaviest. Numbers of fish from the heaviest family were consistently 1.5 to two-fold more dominant during the four samples than numbers of the other families.

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**INDIVIDUAL VARIATION IN GROWTH AND HABITAT USE
BY BROWN TROUT DURING WINTER**

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EXTENDED ABSTRACT ONLY – DO NOT CITE

Our knowledge about the ecology of brown trout (*Salmo trutta*) in streams is largely based on non-winter conditions. And yet winter has been recognized as potentially limiting brown trout and other species of salmonids living at high latitudes and altitudes (Heggenes et al., 1993). The data at hand suggest that brown trout adopt a cost-minimizing strategy in winter. The purpose of this study was to measure activity, habitat use, growth, survival and social status of brown trout on an individual basis in the field to evaluate what strategies the fish were employing.

The study was conducted in eight semi-natural enclosed areas of a stream, each of which consisted of two habitats, a fine substrate habitat and a slightly shallower, coarse substrate habitat. Eight 0+ trout were stocked into each enclosure in late October 1997, and the surviving fish were retrieved in late February/early March 1998. Passive Integrated Transponder (PIT) antennae were placed on the stream bottom between the habitats to be able to continually monitor habitat use of individually PIT-tagged trout (system described in Greenberg and Giller, 2000). Over 420,000 individual movement records from week-long periods in December, January and late February/early March were analyzed.

During early winter most trout (72%) were habitat specialists, defined as spending more than 85% of their time in one habitat. As winter progressed the percentage of specialists decreased to 48% (Table 1). Trout changed habitat

more frequently at night than during the day, with peaks at twilight, and the frequency of habitat changes was directly related to water temperature and body size.

Table 1. Percentage of fish that followed a particular pattern of habitat use during daytime and nighttime in each of the months sampled and over the whole study period. A specialist spent > 85% of its time in either the coarse or the fine substrate habitat, whereas a generalist spent < 85% of its time in any one habitat during daytime, nighttime or both. N = number of fish.

Day/Night	Dec.	Jan.	Feb./March	Total
Coarse/Coarse	50.0%	40.8%	25.0%	25.4%
Coarse/Fine	1.8%	6.1%	4.5%	0%
Fine/Fine	22.2%	16.3%	22.8%	7.3%
Fine/Coarse	5.6%	0%	0%	0%
Generalist	20.4%	36.7%	47.7%	67.3%
N	54	49	44	55

Use of the fine substrate habitats was inversely related to water temperature. The distribution of specific growth rates was unimodal, with most individuals having positive, albeit low, growth rates. Growth rate was not related to habitat use, but was positively related to number of trout surviving in the different enclosures in late winter. Social status was directly related to body size, but had only a weak effect on specific growth rate of trout in early winter. Curiously, individuals of low social status spent more time in the vicinity of the PIT antennae than fish of higher status. Nineteen of the trout died during the study, and the distribution of their deaths was not concentrated to any one period of the winter. Mortality was not related to water temperature, habitat use, nor condition of the fish. However, mortality was related to consistency of habitat use, where mortality was higher for those individuals that only used one of the two habitats (i. e. >85% of the time) than for those individuals that used both habitats (i. e. habitat generalists; Table 2).

Table 2. Number (and percentage) of dead and surviving fish in relation to daytime and nighttime habitat use. Fish using a habitat < 85% of the time during daytime or nighttime were classified as habitat generalists. Only individuals for which habitat use was known for at least three days and three nights were used. Note that 8 fish are excluded from this analysis as 6 fish had died in November before habitat use was measured and 2 fish died from electrofishing.

Day/Night	Dead fish	Survivors
Coarse/Coarse	5 (55.6%)	8 (17.4%)
Fine/Fine	2 (22.2%)	2 (4.4%)
Coarse/Generalist	2 (22.2%)	4 (8.7%)
Fine/Generalist	0 (0%)	1 (2.2%)
Generalist/Fine	0 (0%)	6 (13.0%)
Generalist/Coarse	0 (0%)	8(17.4%)
Generalist/Generalist	1 (11.1%)	17 (37.0%)

Analyses of body fat reserves and fish diets are currently being conducted. Consequently, we await these results before drawing any final conclusions.

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**SEASONAL VARIATION IN PATTERNS OF COMPENSATORY
GROWTH IN ATLANTIC SALMON**

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This talk examines how evolution has shaped the interaction between animals and their food supply, so affecting their strategies of feeding, growth and resource allocation. In contrast to the resource allocation trade-off between reproductive and somatic tissues, that between growth and reserves has received little attention. In particular we address the problem faced by animals in a highly seasonal environment, where the food supply varies predictably over the course of the year as well as unpredictably from day to day. Here resources may have to be gathered at one time of year, to be used when conditions get more extreme. We consider how the allocation of those resources should vary both seasonally and when periods of reduced resource availability simultaneously cause depletion of reserves and a set-back in growth. The optimal strategy in this situation may be to exhibit seasonal variation in both the effort put into foraging (since intensive foraging in winter may be both risky and energetically expensive) and the relative allocation between reserve tissues and skeletal growth.

These principles are illustrated using juvenile Atlantic salmon *Salmo salar*, which have the added interest of having highly flexible feeding and growth patterns that are linked to alternative life history strategies (Metcalf 1998). An experimental approach was adopted, in which the food supply to the fish was temporarily manipulated in both summer and winter, and their subsequent growth pattern recorded. Food deprivation experiments carried out in a single season have shown that juvenile salmon show a hyperphagic response such that they can at least partially compensate for a prior shortfall (Nicieza and Metcalfe 1997; Bull and Metcalfe 1997). However, in the present experiments the same nutritional deficit (as measured by the lipid content of the fish at the end of the food manipulation period) caused marked variation in response between seasons. In winter, fish primarily allocated new resources into restoring lost lipid reserves (so that skeletal growth was negligible), whereas in summer resources were divided between growth and lipid restoration. Moreover, this skeletal growth was faster than in control fish (i.e. a food shortage subsequently causes accelerated or compensatory growth in summer but not winter). Conventional growth or allocation models cannot explain this seasonal variation in response, since they would predict a single outcome for a given nutritional state and food supply.

We therefore developed a dynamic state variable model that takes account of the long-term fitness consequences of different acquisition and allocation strategies. Therefore it incorporates seasonal variation in expected food supply (so that prudent salmon 'look ahead' to anticipate periods of food shortage in the coming winter), and adjusts the risk of predation according to the intensity of feeding, since foraging exposes the animals to greater risk. It also balances the risk of predation against the risk of future starvation. This is an extension of a model that has previously been shown to be successful in predicting the pattern of overwinter fat regulation in juvenile salmon, where fish adjust their foraging to match long- rather than short-term energy requirements (Bull et al. 1996). The new model is parameterised for juvenile salmon, although it provides a more general framework for predicting allocation strategies for any growing organisms living in seasonal environments. The results reveal a close match between the experimental results and model predictions. This suggests that salmon are capable of altering their feeding and resource allocation rules in a manner that maximises their long-term (rather than immediate) survival: their appetite, time of day (or night) at which they feed, and relative allocation of resources to body reserves *versus* skeletal growth are all found to be flexible, and vary in an adaptive manner according to their current state, the time of year and the expected environmental conditions in the future.

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**HABITAT SUITABILITY ASSESSED BY A MODEL
OF THE GROWTH OF SALMON (*SALMO SALAR*) PARR**

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EXTENDED ABSTRACT ONLY – DO NOT CITE

Abstract

A model for compensatory growth of trout was adapted to model body growth of Atlantic salmon by including a behavioural response to temperatures between 0°C and 6°C. Growth responses at higher temperatures (to 22.5°C) were incorporated from a published salmon model. The new, hybrid, model was parameterised to represent growth in ideal conditions, with data from other sites and experiments. Using a detailed temperature record from the Gironck Burn, Scotland, the new model was tested against 18 years of independent data on four age-groups of salmon parr and performed better than the salmon model from which it was derived. A site-quality parameter was introduced to explain the difference between ideal growth given the temperature record and the observed, lower, growth rates. The site quality parameter varied between years in a manner that was robust to uncertainties in the model's parameters. The potential of the model for managing salmonid populations and habitats is discussed, including the need to model the smolting process and density-dependent growth.

The study site

The Gironck Burn flows for 9.4 km to join the River Dee at 57° 3' N, 3° 6' W, some 80 km from the estuary at Aberdeen. Electro-fishing surveys of parr were conducted annually between 1969 and 1986. Fished sections represented the dominant habitat types and totalled 1,260 m². Fork-lengths were measured, and

Length to Weight relationships described from a representative sample by {a,b} in {Weight = a*Length^b}.

Water temperatures were recorded at hourly intervals near the stream's confluence with the River Dee over the period of study: the model uses daily means of the hourly values. Weight loss at low food ingestion rates over winter were estimated using data from Catamaran Brook, New Brunswick (Cunjak, pers. comm). Other parameters were estimated from data in the literature.

Applying existing models to the Girnock data

Given the Girnock temperature record the model of Elliott and Hurley (1997) (E&H) did not predict observed growth either well (Table 1), or realistically, mainly because the weight losses predicted over winter were too high (winter temperatures in the Girnock fell below the parameterisation level of the E&H model for prolonged periods).

We therefore adapted a physiological model (Broekhuizen *et al.*, 1994). This model firstly allows fish of the same weight, W, to be in different conditions, as described by both their structural weight, S (tissues that cannot be catabolised to provide energy) and a reserve weight, R (tissues can be catabolised), such that $W=R+S$. Further, the fish can alter their behaviour, and hence maintenance energy needs, when low temperatures constrain assimilation and growth. The new model combined the behaviour and physiology of Broekhuizen *et al.* (1994) with the temperature response functions of Elliott and Hurley (1997); new parameters were estimated from the literature and Catamaran Brook data.

Testing and development

The new 'hybrid' model was initially run with parameters from the literature that represented growth in ideal conditions (food not limiting) and driven by the Girnock temperatures. Its winter growth trajectories were now plausible, but weights were generally over-predicted, probably because fish in the wild were food-limited: the fit was improved, but not good (Table 1). The model was next amended to estimate the degree of reduced assimilation, ϕ , that best fitted the fish growth data (assuming wild fish fed less well than those in E&H's experiments). The best estimate of a single value of ϕ (=0.90), which was constant across all years, improved the fit only slightly (Table 1), but estimating

a set of ϕ values (one for each year, having similar effects on all age classes) improved the fit appreciably, especially within age-classes (Table 1).

Boot-strap re-sampling procedures demonstrate that the annual estimates of ϕ are robust to both the variation in the fish caught and to likely uncertainties in the model's other parameter estimates (Fig 1).

The poorer fit to the data for 3+ fish can probably be improved by incorporating the smolting process into the model, such that the larger 2+ fish leave as smolts and only the smaller 2+ remain to be measured again, as 3+ parr.

Given minimal electro-fishing data (once annual) and a temperature record, the present model appears to provide a robust way whereby fisheries managers can assess if their stocks are 'growing near maximal potential' ($\phi=1.0$) given the temperatures at any site. Analysis of ϕ over years would indicate the scope for 'habitat' improvement.

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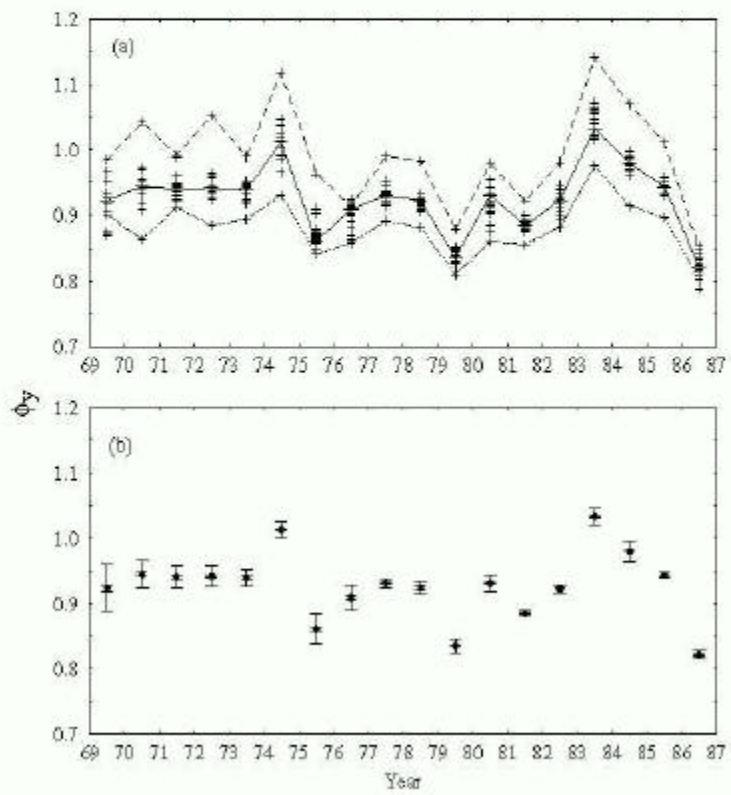
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Table 1. Percent variances of the Girnock data explained by the different models, both across ages and when the fits are compared within age-classes.								
	Across Ages	Within Ages				Model significance.		
Model Fitted		0+	1+	2+	3+	d.f.	F	F sig.
EH	42	13	10	11	0.6	0	~	~
CGME: Max	83	17	0.1	0.5	12	0	~	~
single ϕ	85	15	0.1	0.6	12	1	156.4	<<0.001
annual ϕ	92	51	24	73	23	18	1.8	0.052
Data Points	57	13	14	15	15	~	~	~

Figure 1. Sensitivity analyses of the CGME when predicting ϕ .

- 1.a** The solid line joins predictions of ϕ using the observed temperature data, while the dotted and dashed lines join similar predictions of ϕ assuming the temperatures were consistently +1 and -1 °C different from observed, respectively. The + signs, in columns for each year, show the range of values of ϕ predicted when several model parameters, that are imprecisely known, were varied by amounts commensurate with their uncertainty (see list in Appendix 3).
- 1.b** Variations in ϕ induced by 50 bootstrap re-samples of the fish size data. Dots show ϕ estimates with the actual data and the outer bars are one standard deviation of the bootstrap error distribution (inner bars are one standard error). Note that $0.8 < \phi < 1.0$ in 16/18 years and ϕ is never significantly greater than 1.0.



**ACROSS YEAR VARIABILITY IN PATTERNS
OF DENSITY, SURVIVAL, SIZE, AND GROWTH
OF JUVENILE ATLANTIC SALMON
IN THE CONNECTICUT RIVER:
INSIGHTS FOR RESTORATION**

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EXTENDED ABSTRACT ONLY - DO NOT CITE

The Connecticut River drainage extends over 400 miles through the states of Connecticut, Massachusetts, New Hampshire, Vermont, and into southern Canada. Historically, a self-sustaining population of Atlantic salmon, *Salmo salar*, flourished within the Connecticut River watershed but deforestation, pollution, and construction of the first mainstem dam caused the extirpation of the population by the early 1800's. The present Connecticut River Atlantic Salmon Restoration Program, initiated in 1967, seeks to restore a self-sustaining salmon population to the watershed. Since, 1987, the emphasis has been on the annual stocking of fry into all available juvenile rearing habitat. Currently, 27 basins and more than 125 tributaries are stocked with over 9 million fry. This

fry stocking is coupled with an annual evaluation of age-specific juvenile survival, density, total length, growth at 298 index sites throughout the basin. This extensive database can provide insights into spatial patterns and temporal trends in juvenile salmon performance that may help guide restoration strategies.

Herein we examine three questions related to across year variability:

- (1) Do mean trends reflect patterns and relationships observed in individual years?
- (2) Is there a consistent, predictable trend of patterns and relationships across years? If so, why?
- (3) What are the management / conservation / restoration implications of these across-year patterns?

In looking at general trends and relationships, researchers and managers often examine across-year means. Although we know that ecological responses differ from year to year and that some years are "abnormal" or "exceptional," we assume that, in general, across-year means depict useful and consistent trends. For effective management, we need to know if this is a reasonable assumption. Previous results from this juvenile Atlantic salmon database using means from 1990-1996 indicate that juvenile salmon do not perform equally across index sites. Some sites showed exceptionally good performance and others showed exceptionally poor performance. In addition, mean performance within sites differed by basin, scale, and juvenile variable examined. Furthermore, based on 6-year means, some sites were better suited for high densities or large individuals but not both. To understand these patterns of good and poor performance based on mean values, we first examined the effect of density, stream order, temperature, drainage area, gradient, and elevation on survival, density, length, and growth. Based on mean trends, density adversely impacted survival and length. Stream order showed a relationship to density/survival and length/growth at both the within-basin- and watershed-scales. Drainage area was related to survival, density, length, and growth primarily at the smaller, within-basin-scale. Temperature consistently inhibited survival and density within the Farmington basin, yet affected length at the larger, watershed-scale. Similarly, gradient impacted survival and density within the Farmington basin and across the watershed, while influencing length at the larger, watershed-scale only. The relationships with survival and density were consistently opposite to those with length and growth. In fact, stream order, temperature, and drainage area all negatively influenced survival and density, yet positively influenced length and growth at both scales. Not surprisingly, when these patterns based on

across year means were compared to patterns based on data from individual years, in many years, when trends were pronounced, general patterns mirrored the mean trends. For example, relative to 1st year and 2nd year survival and density, in 1993, 1994, 1995, 1996, the same sites had exceptionally high and low performance as seen using average values from 1990-1996. Yet important variations existed across years. Thus, examining the magnitude of coherence and sources of variation can provide additional insights into mechanisms for high and low survival, density, size and growth

Relative to temporal trends, performance varied across basins and across years. Years of high and low performance were not the same for all basins. For examples, numbers of 0+ salmon in the southernmost Farmington were the most variable of any basin with highest values in 1990 and 1996. Whereas in the northern West, densities at the end of the first summer were more constant with the highest numbers observed in 1992, 1993, and 1995. For 1+ density, the opposite trend was observed, with the Farmington being less variable across years than the West. Length was less variable across years although high and low values differed across years. For example, 0+ salmon were largest in 1990 in the White, 1996 in the Deerfield and Westfield, 1991 in the Farmington, and 1992 in the Salmon. Again, the southernmost Farmington and Salmon were more variable than the northern West and White. At the site level, clear patterns of increasing variation were associated with higher mean values. However, when these patterns were examined at the basin level, relationships between mean and variance were less clear.

Thus, describing patterns of responses across years may also be useful as a first step in helping us understand why fish survive and grow better under some conditions. Specifically, we may be able to identify good and bad years overall, good and bad years for certain life stages or response variables, or good and bad years for specific basins. By relating physical and biological conditions in these good or bad years to juvenile salmon performance, we could increase our understanding of which conditions favor high and low survival, density, size, and growth.

**SELF-THINNING IN BROWN TROUT:
LINKING GROWTH
AND POPULATION DYNAMICS**

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EXTENDED ABSTRACT ONLY – DO NOT CITE

Self-thinning is the reduction in density of a cohort of growing organisms that is close to the system's carrying capacity due to competition for limiting resources as the size of each individual member of the cohort and its demand for those resources increase concomitantly. Thus, self-thinning can potentially link those factors affecting growth to population abundance. The phenomenon is common in plants and sessile animals and, following the initial observation of Begon et al. (1986) has been reported for mobile animals as well. Most evidence for self-thinning in mobile organisms (all for wild populations) comes from stream-dwelling salmonid fishes (Grant 1993, Elliott 1993, Bohlin et al. 1994). However, it is not yet clear if limitations in either food or space (mediated through territorial behavior) generally cause self-thinning in stream salmonids. Ideally, they might be distinguished because the slope of the relationship between log body-weight and log density would be the negative of the allometric coefficients of either energetic requirements or territory size (provided the availability of the resource remains constant relative to body weight). However, those coefficients can be similar enough that the errors associated with parameter estimates from field data preclude its distinction.

Moreover, a recent reanalysis of previous evidence has found proof of significantly non-linear thinning trajectories, which has been related to the capacity of mobile animals to respond with niche shifts to resource shortages (Armstrong 1997).

We have examined the density vs. body size relationships for 42 brown trout, *Salmo trutta*, cohorts (11 year-classes, four different sites) in a stream in northern Spain. They displayed two distinct phases with different slopes whose transition occurred at trout lengths of 14-15 cm (Figure 1). Split-lines fitted the trajectories significantly better than single straight lines in 32 of 42 cases and, explained a total of 87.2% of the variation in trout abundance. When a single split-line was fitted to the pooled 42 cohorts, weight accounted for 53.2 % of density variance. This suggested that spatio-temporal variation in thinning trajectories was substantial.

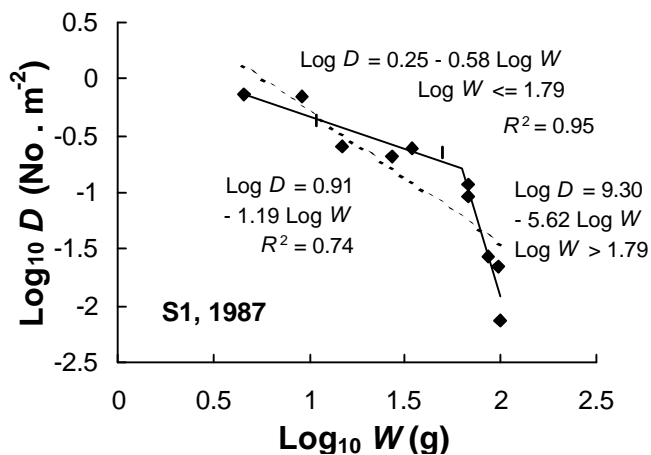


Figure 1. Example of straight and split lines fitted to the thinning trajectory of the 1987 brown trout year-class in site 1 with their corresponding equations and coefficients of determination (r^2).

The slopes of the first phase of the thinning trajectories were typically shallower than those predicted by either energetic or territorial allometry, whereas those of the second phase were steeper. Both, but particularly the first one, were quite

variable among sites and year-classes. In contrast, estimates of the breakpoint were remarkably similar (Table 1).

Table 1. Variability (coefficient of variation) in the estimates of the slopes of the first (b_1) and second phase (b_2) and of the breakpoint (c) of the split-lines describing the relationship between log-transformed mean weight and abundance of brown trout year-classes at each of the four study sites.

Site	b_1	b_2	c
S1	504.6 %	73.9 %	18.9 %
S2	138.7 %	26.4 %	8.2 %
S3	78.1 %	22.3 %	8.4 %
S4	866.5 %	33.1 %	16.3 %
All	206.6 %	67.1%	13.0 %

Percent Habitat Saturation (PHS), defined as: $PHS = 100 D T$, where D is density (inds.m⁻²) and T is individual territory size (m²), is an estimate of the proportion of total habitat that the members of a cohort actually occupy. It has been empirically shown that density-dependent responses in growth or mortality rates of stream salmonids are more likely when PHS values reach over 27. At our sites PHS first increased with body size up to the point where the break occurred, when it was close to 27, and then decreased with size (rather than remaining fluctuating around a value of 27). Together with the thinning trajectories, this pattern indicated that in our study sites cohorts were not initially self-thinning, but that resources (probably pool habitat) became progressively limiting once trout grew over 14-15 cm.

Our findings reflect how size affects resource use differently in sessile and mobile organisms. A larger size may allow mobile animals to exploit previously inaccessible resources, but may also impose new resource quality requirements to add to those of resource quantity. Thus, resource availability is not independent of size. It may increase with it at times, but, even when it decreases, it may do so at rates dependent on local conditions and not directly predictable from simple allometry of food or space needs.

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**ASSESSING THE ANADROMY OF SALMONIDS
USING ANALYSIS OF SCALE MICROCHEMISTRY
AND GROWTH PATTERNS**

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EXTENDED ABSTRACT ONLY - DO NOT CITE

Introduction

Documentation of periods of anadromy often relies on expensive and difficult tracking or marking studies. An alternative non-lethal technique, the analysis of strontium (Sr) content in the scales of these fish, allowed us to successfully determine the age at first movement to sea, timing of migration between fresh- and saltwater environments and the presence of facultative anadromy in some wild and stocked populations of Atlantic salmon (*Salmo salar*) and brook charr (*Salvelinus fontinalis*), at a fraction of the costs involved with other methods.

As the scale develops in concentric ridges, trace elements (eg. Strontium) are incorporated in its calcified matrix in proportion to their ambient level (Bagenal, 1973; Yamada, 1982). Since water strontium (Sr) concentration is directly proportional to salinity, a high Sr/Ca ratio in some circuli would indicate periods of life spent in saltwater. The analysis of Sr was done in this study using a wavelength dispersive X-ray electron microprobe (WD-EM).

We focused on landlocked Atlantic salmon from the Magaguadavic River (New Brunswick, Canada), stocked prior to 1995. Some of these individuals moved below a 20m waterfall and were recaptured between 1996 and 1999 after considerable growth, in a fish ladder at the head of tide, between 1996 and 1999. They were suspected to have moved into saltwater, but it is also possible that they moved downstream but remained in the lower river.

Methods

We analyzed 34 salmon scales (13 from 1996, 2 from 1997, 12 from 1998, and 7 from 1999). The scales were embedded in an epoxy (Epofix) and a transverse cut was made along the long axis of the scale, through the focus, using a steel blade microtome. The smooth surface necessary with the use of WD-EM was attained with a finishing cut using a glass-knife ultramicrotome and the finished blocks were carbon coated.

Analysis was conducted using the electron microprobe on a X-ray Wavelength Dispersive Scanning Electron Microscope (JEOL733). Each sampling point was determined optically and centered on the circuli (ridges). Since calcium (Ca) composes most of the matrix and is less affected than trace elements by the exact position and angle of the beam, we used the Sr/Ca ratio as our measure.

We analyzed the first 5 contiguous circuli and 15 additional points were sampled at every other circulus, when possible, covering a region corresponding to approximately the 35 last-laid circuli. Since between eight and twelve circuli are formed each year in the case of the Atlantic salmon (Summerfelt and Hall 1987), we then investigated the past 3 or 4 years of these fish, at a one or two months time resolution.

Results

Five different patterns were distinguished: true landlocked (n=3), frequent contact with saltwater (n=12), one summer spent in seawater (n=3 early, n=8 late), and multiple migrations to the sea (n=8 - Fig. 1, next page). Fast growth was associated with high Sr contents. Only one fish seems to have spent the majority of its life in saltwater.

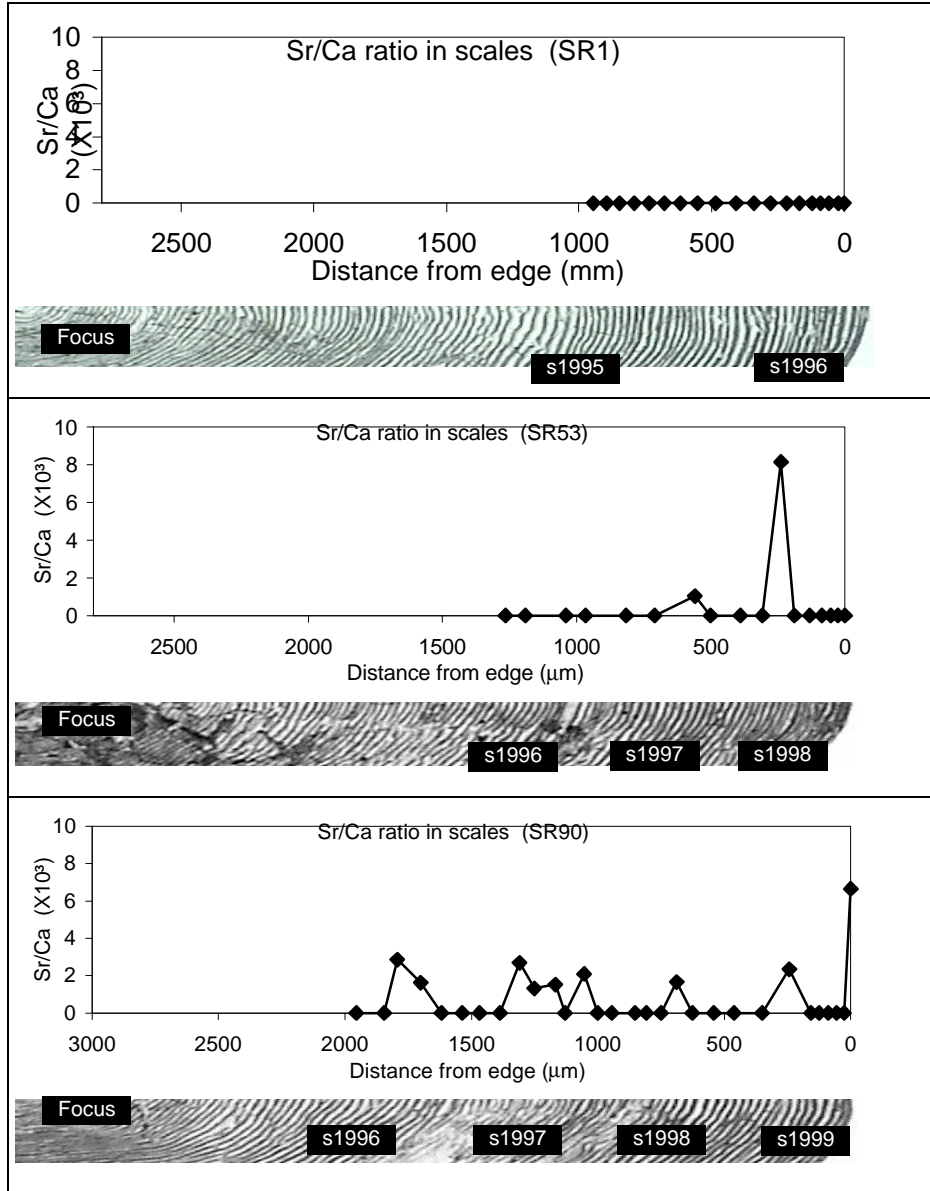


Fig. 1. Sr/Ca analysis showing true landlocked (SR1), saltwater residency in the past summer only (SR53), and frequent use of the saltwater (SR90).

Discussion

These preliminary results may have major management implications. It appears possible that some “landlocked” Atlantic salmon use the saltwater environment. Thus rivers that have lost their wild anadromous runs, but still have landlocked salmon in the system, could regenerate sea-run populations.

Also, in this particular case, individuals that moved into the Bay of Fundy could contact diseases like ISA (Infectious Salmon Anemia), and then move back into the rivers.

The analysis of scale microchemistry coupled with the analysis of growth patterns seems to be an efficient method to assess saltwater residency over many years of a large number of fish, and can be useful for management purposes.

Acknowledgements

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**DRIFTERS VERSUS RESIDENTS: ASSESSING SIZE AND AGE
DIFFERENCES OF ATLANTIC SALMON FRY**

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EXTENDED ABSTRACT ONLY - DO NOT CITE

Introduction

It is well known that some young-of-the-year (0+) Atlantic salmon have a tendency to drift soon after emergence from the gravel while others, so-called resident fry, set up and defend territories. This divergent behaviour can greatly influence survival within a population since very small behavioural and physiological differences between individuals can have major repercussions for subsequent life-history patterns, and therefore on recruitment and population production. According to Northcote (1978), this period is important in determining individual viability because mortality and growth rates are high during this phase of the life cycle. The goal of this project was to distinguish these two groups of fry on the basis of biometric characteristics.

Methods

Atlantic salmon fry were collected in Western Brook and its tributary, Stag Brook, Gros Morne National Park, Newfoundland (Canada). Resident fry were caught by electrofishing, and the drifting fry with drift samplers, simultaneously and in the same habitat. Sampling commenced at the start of the drift period within each brook. We sampled every three days, for each site, until the end of the drift period to determine if there was temporal variation. For each site,

approximately 20 fry of each group were kept for measurements (length, weight) and frozen. Condition factor ($K = \text{weight} / \text{length}^3$) was also calculated.

are currently ageing these fish using the otolith reading technique. Atlantic salmon fry, as many other teleosts, produce daily increment on their sagittae that are visible under light microscopy (Wright et al., 1991). Under natural photoperiod, salmon fry also produce a check ring on the sagittae at first feeding, that can serve as a set-point to establish age (days) since emergence.

Results

Resident salmon fry from both populations were significantly longer and heavier than drifters (Fig. 1, a, b, d, e). Condition factor was significantly higher for residents from Western Brook, but no such difference was measurable for fry from Stag Brook (Fig. 1, c, f).

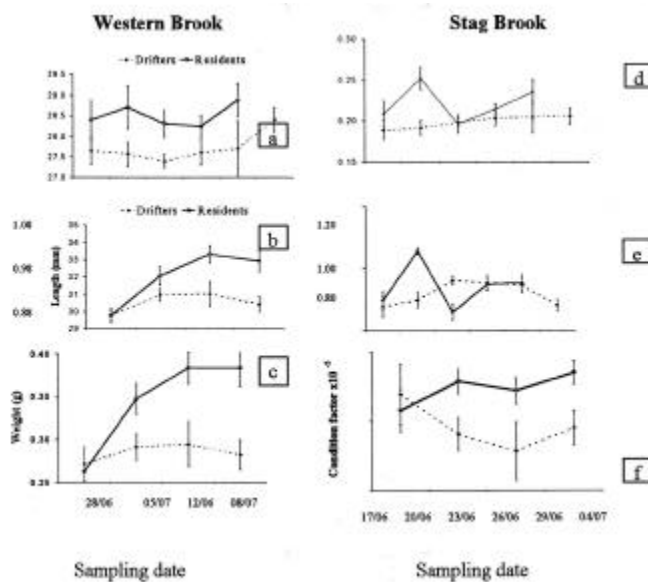


Fig. 1. Comparison between drifting and resident Atlantic salmon fry for length (mm), weight (g), and condition factor sampled during the summer of 1999 in Western Brook and Stag Brook.

Discussion

We found that resident fry are heavier and longer than the drifters for the entire period of drifting movement. These differences were present within the two different brooks and at different periods of the year. Moreover, as seen in Western Brook, the condition of the resident fish improved with time, while the drifters condition worsened.

The possible reasons for these differences are that a hierarchy may develop, between the two groups, at a certain time after the emergence from the gravel and that the drifting individuals are driven away from the habitat by the aggressive behaviour of resident fry. Salmon fry could establish a size-related dominance, through aggressive interactions, with dominant fish holding the positions that offer "maximum potential profit" (Titus, 1990). Subordinates may often be excluded from the best feeding areas, or may suffer a reduced foraging efficiency through the loss of food items (Metcalf et al., 1986) which would explain the size difference between the two sub-population.

It is also possible that the differences can be explained by the fact that early emergers gain a competitive advantage over subsequently arriving rivals by having first choice of favourable stream positions, and because of the size advantage they are able to gain. By looking at the otolith, we will be able to determine the timing, in days, of the drifting movement because of the emergence check-mark and then determine if there is an age difference between the groups.

In conclusion, resident fry are in better condition than drifters and that can have major repercussion on their individual future. Dominant fish usually retain and increase their size advantage. Usually, the same fish remains dominant in the wild for months and even years and the resulting differential allocation of resources according to status can produce great variability in the growth and fitness across the population. According to Metcalfe (1993), a major driving force behind life-history variation in fish is variability in growth rates. It has long been recognized that faster growing individuals tend to mature and migrate at an earlier age. Considerable enhanced fitness can result from a minimal increase in growth performance and so might be worth the cost involved in aggressively defending the resources for the resident fry.

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**LINKING DIFFERENCES IN CONSUMPTION RATES
AND GROWTH EFFICIENCIES
TO INTRINSIC ENERGY DEMANDS
OF MIGRANT AND RESIDENT
BROOK TROUT (*SALVELINUS FONTINALIS*)**

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Introduction

In some salmonids such as Atlantic salmon (*Salmo salar*), brown trout (*Salmo trutta*) and brook trout (*Salvelinus fontinalis*), individuals within a given population can be observed to segregate into morphs of varying life history strategies. The differences in life history strategies may be linked to differences in energy budgets, or in energy allocation strategies (Tucker and Rasmussen, 1999; Forseth *et al.*, 1999). In populations of brook trout where the sea is relatively accessible, anadromy has evolved. However, only a partial migration (Jonsson and Jonsson 1993) is observed, resulting in populations composed of both migrants and residents. In such populations, a growth dichotomy is observed; when individual migrants (after migration) and residents of the same age class are compared, the former are much larger in size.

We investigated the possible mechanisms of partial migration using a bioenergetic approach. Estimating the energy intake and coupling this to growth

allows for an analysis of the energetic performance of fish with different life history strategies. We tested the hypothesis that migrant trout have higher annual consumption rates, but lower growth efficiencies than resident brook trout. Given that migrants and residents have different energy demands, reflected by total metabolic costs, the key to identifying the processes governing partial migration may lie in the possible variations of intrinsic standard metabolic rates (SMR) and/or activity rates (swimming and foraging costs, or 'swimmaging'). It is thus hypothesised that migrants have higher SMR and/or swimmaging costs compared to residents. There are some indirect indications that a link could exist between metabolic rates and life-history strategies in Atlantic salmon (Metcalf *et al.*, 1995; Metcalf *et al.*, 1992). Attempting to identify a link directly in the field may allow for new approaches in studying the partial migratory behaviour in fish populations.

Methods

Our study was conducted in the Ste. Marguerite River system (48°20'N, 70°00'W) in the Saguenay region of Quebec, Canada during the summer of 1998 and 1999. Both migrant and resident trout are relatively abundant in this system. Anadromous brook trout have been observed to migrate as young as 1+ (pers. obs.). In 1998, migrants were defined as those captured moving downstream in Alaskan traps installed on three secondary streams (Morin, Allaire and Epinette) of the Ste. Marguerite River as they moved downstream. In 1999, fish captured in the trap were tagged and released approximately 30m upstream. Only fish captured twice in the trap were deemed true migrants. Resident brook trout were captured by electrofishing immediately after the end of the migration period.

Both consumption rates estimated using the ¹³⁷Cs mass balance model (Rowan and Rasmussen, 1996), and growth efficiencies (ratio of growth to consumption) were determined for individual migrant and resident brook trout. Individual ages and growth rates were determined using otoliths (V. Theriault, unpub. data).

In an attempt to elucidate the possible metabolic differences between migrants and residents, both cytochrome-c-oxidase (CCO) and lactate dehydrogenase (LDH) activity were measured as surrogates of SMR and swimmaging costs, respectively. Both of these analyses were performed *in situ* on fish captured during the summer of 1999. Fish were kept alive until dissections were

performed. Liver tissues (for CCO analysis) were immediately frozen in liquid nitrogen and muscle tissues (for LDH analysis) were frozen in a -80°C freezer.

Results and Conclusions

Preliminary results suggest that, as predicted, 1+ Morin migrants have higher consumption rates, but lower growth efficiencies than 1+ Morin residents. Furthermore, the differences in energy intakes were associated with distinct energy demands; that is, migrants had higher SMR than residents at the time of migration. Similarly, regarding the effect of swimming costs, we expected to see a difference between migrants and residents, whereby migrants would have higher swimming costs than residents. However, at the time of migration, higher LDH activity is observed in the residents as compared with migrants. It is thus not certain whether the enzymatic differences observed were due to the process of migration (ie. smoltification) or whether these differences should always be expected. The link between energy strategies and life history patterns may not be so clear.

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ANADROMY AND RESIDENCY

IN BROOK CHARR (*SALVELINUS FONTINALIS*):

THE IMPORTANCE OF GROWTH DURING

THE EARLY LIFE HISTORY STAGES

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EXTENDED ABSTRACT ONLY – DO NOT CITE

Introduction

Partial migration occurs in many anadromous salmonids species, where only a fraction of the population migrates to sea. The remainder stay in freshwater for their entire life-cycle. In Atlantic salmon (*Salmo salar*), a portion of male parr stay in freshwater. In others, such as arctic charr (*Salvelinus alpinus*), brown trout (*Salmo trutta*) and brook charr, some individuals of both sexes reside solely in freshwater while others migrate to sea. The advantage associated with residency is probably a low mortality rate compared to anadromous fishes of the same species, but this benefit is counter-balanced by a significant decrease in fecundity due to limited growth in freshwater relative to growth in the marine environment. Some efforts have been made to find genetic differences between these two forms, but it is generally believed that when no geographical barriers are present, the two forms are genetically identical (Northcote, 1992). Partial migration can then be viewed as a conditional strategy, where the tactic adopted (residency or anadromy) depends on the state or status of the individual (Gross, 1996). This state is often a result of growth, where individuals experiencing

good growth conditions mature in freshwater (Nordeng, 1983). Nevertheless, due to higher mortality associated with smaller size at migration (Bohlin *et al.*, 1993), fast-growing fish tend to migrate first.

This study attempts to examine a conditional strategy based on growth in brook charr, *Salvelinus fontinalis*. We hypothesised that growth rate among young brook charr would be different for resident and migrant fish, thus influencing their decision to migrate or not.

Methods

Fish were collected from Morin creek (average 5.6m wide, 0.3m deep), a small tributary of the Sainte-Marguerite River, (48°20'N, 70°00'W), Québec, Canada. Migrants were captured in traps in 1998 and 1999 during the downstream migration in early spring. Traps were built in such a way that the whole width of the stream was blocked, except in 1998 when a small opening allowed fishes to move upstream, which was needed for other experiments. Fish caught in the traps were marked with T-bar tags (Floy) and capture-mark-recapture experiments confirmed that these fishes were real migrants. Residents were captured by electrofishing during the summers of 1998 and 1999, once the downstream migrations were over. All fish caught were measured to the nearest mm.

Of the 211 and 425 migrant fishes caught in 1998 and 1999, respectively, 44 and 82 were randomly sacrificed for analysis. A further 40 and 82 resident fishes were also sacrificed in 1998 and 1999 respectively. Sagittal otoliths were removed and subsequently ground with fine sand paper. Age was then read and the lengths at emergence and at the end of each growing season were backcalculated using the biological intercept method (BI) (Campana, 1990) using an image analyser system (Scion/SXM). These backcalculated lengths and growth rates were then compared between migrants and residents with a Komolgorov-Smirnov test.

Results and conclusions

Migrant brook charr left the stream at ages 1+ and 2+ during a short period of time in spring for both years studied. Preliminary results for 1999 show no differences in backcalculated lengths at the end of the first growing season

between 1+ migrant and resident fishes (fig.1a, KS, $p=0.12$) but differences were found in backcalculated lengths at the end of the second growing season for 2+ fishes : residents were bigger than migrants (fig 1b, KS, $p<0.0001$). Size distribution of both 1+ and 2+ migrant fish are close (modal size of 87 and 98 mm respectively) suggesting that they may be a critical threshold level beyond

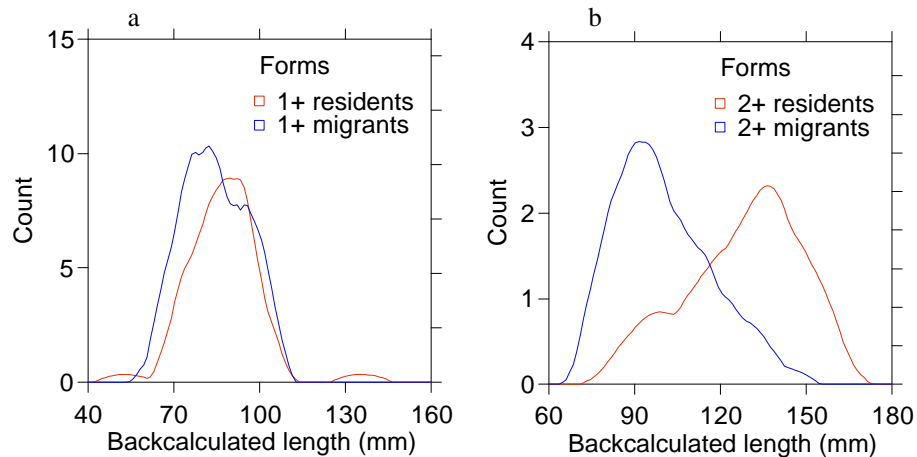


Figure 1. Backcalculated length for migrants and residents at the end of a) the first growing season for 1+ fish (N=68 and 53 respectively) and b) the second growing season for 2+ fish (N=24 and 29 respectively).

which residency is the favored tactic. Furthermore, when backcalculated length at the end of the first growing season is compared between 1999 2+ migrant fishes and 1998 1+ resident fish (fig.2), the former are smaller. This observation suggest that there may be a minimal body size needed for migration such that the smallest 1+ fish delay their decision to migrate or not until the following year.

Two alternative scenarios may explain these observations.

- (a) There is a true conditional strategy based on growth, where a threshold size is needed for migration. Individuals aged 1+ that are smaller than this threshold size delay the decision to migrate until the following year. Individuals that are larger than this threshold may stay as resident fish for their entire life-cycle. This should result in a bimodal distribution of 1+ fish

within the residents (fish smaller than the threshold size for migration that delay their decision and the largest fish that remain in freshwater), which is not observed (fig.1a). One reason for this may be the small sample size of 1+ resident fish. This scenario indicates that once the threshold size for migration is reached, those fish experiencing slower growth rates migrate to sea whereas those fish experiencing the fastest growth rates remain as freshwater residents.

- (b) anadromy and residency may represent two strategies such that migration occurs at 1+ or 2+ depending on growth only for the progeny of anadromous fish. The respective merits of these alternative scenarios will be discussed during the oral presentation.

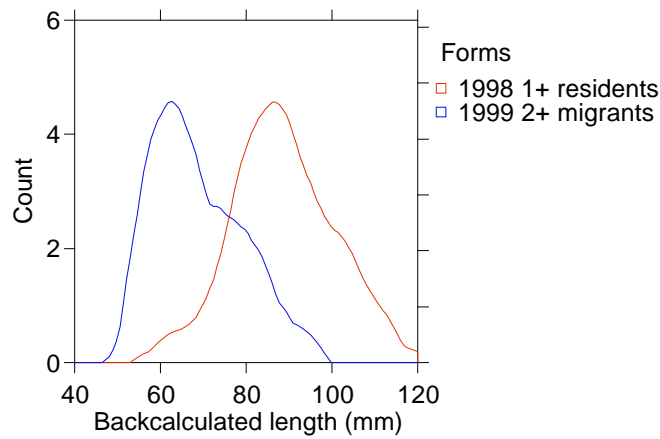


Figure 2. Backcalculated length at the end of the first growing season for 2+ migrant fish caught in the trap in 1999 (N=24) and 1+ resident from 1998 (N=26). The comparison thus represents the same cohort of fish followed over two years.

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Acknowledgements

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FRESHWATER RESIDENCE OR MIGRATION
IN BROOK CHARR, *SALVELINUS FONTINALIS* :
INFLUENCE ON GROWTH AND ASSOCIATED AGE AT MATURITY
AND AGE-SPECIFIC FECUNDITY

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EXTENDED ABSTRACT ONLY – DO NOT CITE

Introduction

Differences in growth rate may be associated with differences in some reproductive traits influencing fitness, such as age at maturity and fecundity (Roff, 1984). Partially migratory fish species, which can present high variations in growth rate within the same population, provide an opportunity to study interactions between growth and life history (Dodson, 1997). In numerous rivers opening into estuaries, brook charr (*Salvelinus fontinalis*) can be found as freshwater residents that mature sexually without any seaward migration and migrants that move between freshwater and saltwater before maturing. As with most charrs, anadromous and freshwater resident forms of *S. fontinalis* are thought to belong to the same gene pool, with different life-history patterns reflecting adaptive phenotypic plasticity in the face of prevailing environmental conditions (Jonsson et Jonnson, 1993). Anadromous brook charr exhibit enhanced growth rates, causing residents to be significantly smaller than their migratory counterparts (Power, 1980).

The objectives of this study were to compare juvenile growth of resident and anadromous charr originating from the same river, as well as to examine associated age at maturity and age-specific fecundity.

Methods

We studied resident and anadromous brook charr from the Sainte-Marguerite River (48°20'N, 70°00'W), in Saguenay, Québec, Canada. In 1998, 2757 anadromous charr were caught in spring during their migration downstream (Alaskan trap) or during their first summer of growth in the Saguenay Fjord (seine). Fish were measured to the nearest mm. 299 charr were sacrificed for laboratory analyses, including sex, reproductive stage and age determination (the latter was determined using sagittal otoliths). 500 fish were individually tagged with T-bar tags (Floy) and released. 4810 more anadromous charr were caught during the spring and summer of 1999. 300 were sacrificed during their downstream migration and 4510 were tagged with T-bar tags. 11% of tagged fish were recaptured by anglers, mostly in September and October 1999. Those recaptures were measured again. Sex, reproductive stage and age were determined. Moreover, 500 fish caught by anglers during 1998 and 1999 were sampled, in order to evaluate size and age at first reproduction. Eggs from ripe females were counted to estimate the relationship between size and fecundity.

Juvenile growth rate, size and age at sexual maturity of freshwater residents were evaluated by collecting 30 fish in two different streams of the Sainte-Marguerite River system in September 1998 and 1999. Six ripe females were collected in one of these streams and were used to estimate a preliminary relationship between size and fecundity in resident charr.

Results

Anadromous charr leave the Sainte-Marguerite River at age 1 or 2 and grow at an accelerated rate, reaching about twice the size of freshwater residents of the same age at the end of their first summer in salt water. At the end of their third summer, migrants that left the river at age 1 still exhibit a greater body size than migrants that left the river at age 2 (in September 1999, respective mean fork lengths \pm SD were 29.9 ± 2.5 cm and 23.0 ± 3.1 cm).

We found a strong relationship between body size and fecundity in anadromous and resident charr (Figure 1) and this relationship did not differ significantly

between the two forms (ANCOVA, slope : $p=0.95$ and elevation : $p=0.09$). Thus, anadromous charr, which grow bigger, exhibit a higher age-specific fecundity than resident charr. Variation in age at sexual maturity between the three groups (residents, migrants that left at age 1 and migrants that left at age 2) will be discussed during the oral presentation.

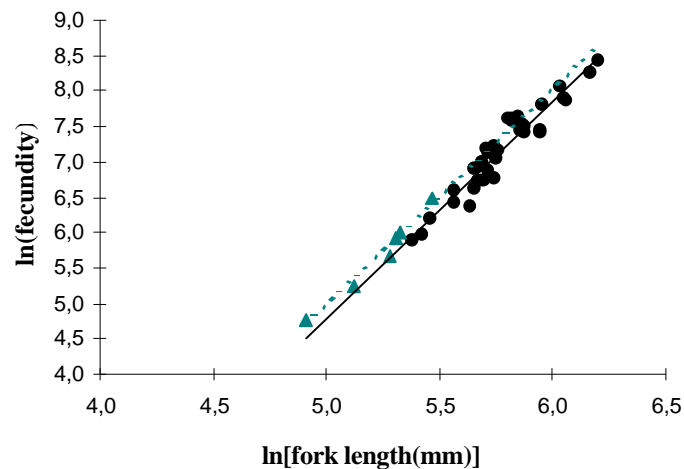


Figure 1. Relationships between fork length and fecundity in anadromous and resident (Morin creek) brook charr collected in 1998 and 1999 (filled triangles : resident brook charr from Morin creek; filled circles : anadromous brook charr). Regression lines in anadromous (solid line) : $\ln(\text{fecundity})=3.0884 \ln(\text{fork length})-10.672$, $r=0.92$, $n= 36$; residents (broken line) : $\ln(\text{fecundity})=3.0952 \ln(\text{fork length})-10.528$, $r=0.98$, $n=6$).

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GROWTH OF STREAM-DWELLING BROWN TROUT
IN CENTRAL SPAIN:
LINKING LIFE-HISTORY AND MANAGEMENT

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EXTENDED ABSTRACT ONLY - DO NOT CITE

Introduction

Nowadays, water temperature, body size and food intake are considered to be the main factors affecting brown trout (*Salmo trutta* L.) growth (Elliott 1994). Variance in growth rate seems to be a key factor for explaining the observed variability in life-history traits among populations (Näslund et al. 1998). The purpose of this work was to analyse growth dynamics of stream-dwelling brown trout among seven contrasting rivers, situated within the most meridional part (40-41°N) of the native distribution of this species (Kottelat 1997). Better opportunities for growth were expected in those rivers with mild temperature regimes and high water productivity, which may ultimately determine the abundance of food for trout. Likewise, reproductive parameters were expected to be affected by differential growth.

Material and Methods

The study was carried out in seven streams from central Spain; five were tributaries to the River Tagus (Hoz Seca, Cabrillas, Gallo, Dulce and Jarama) and two to the River Douro (Cega and Eresma). The selected populations occupy a wide environmental gradient, especially regarding

water temperature, water fertility and abundance of invertebrates (Table 1).

Table 1. Chemical and biological characteristics of rivers studied.

	H. Seca	Cabrillas	Gallo	Dulce	Jarama	Cegama	Eresma
Annual T(°C) (min-max)	10.2 (8-12)	10.2 (5-16)	12.0 (5-18)	13.1 (8-19)	7.4 (0-15)	6.3 (0-13)	6.5 (0-13)
CaCO₃ (mg l⁻¹)	366.7	412.5	388.4	309.7	18.1	20.7	29.6
Ca²⁺ (mg l⁻¹)	84.4	101.3	85.0	56.6	1.2	2.8	3.1
Mg²⁺ (mg l⁻¹)	25.7	33.4	26.4	22.0	1.3	0.9	0.9
Benthos (g m⁻²) (s.d.)	1.8 (0.66)	1.7 (0.42)	6.2 (1.31)	2.8 (1.16)	0.5 (0.03)	0.6 (0.05)	0.5 (0.13)

Fish were sampled every third month from January 1996 to December 1998 at 18 sites by electrofishing. Growth rates were calculated as $G = (\log_{10} S_{\text{final}} - \log_{10} S_{\text{initial}})/t$, where W_{initial} and W_{final} were the mean body size in weight or length of each year class at the beginning and the end of t days, respectively. In 1998 trout were captured monthly in each river to study reproductive features.

Results and Conclusions

Age distribution of trout did not differ significantly among rivers, showing a dominance of 0+ to 2+ groups and a longevity of four to five years. Mean body size at the end of the growing season varied significantly among populations. Differences were attributed to the thermal conditions, which directly affect emergence dates, and to mean egg size in each river, rather than food availability.

During growing season specific growth rates were not significantly smaller in the less productive rivers. Furthermore, significant differences in the annual growth rate among populations in the interval 0+-1+ were not found (Table 1).

During the interval 1+-2+, significant differences were observed among populations, but subsequent comparisons of means only revealed significant differences between R. Hoz Seca and rivers Gallo and Dulce. The annual increment of body size was not significantly correlated with either benthos biomass or mean water temperature during growing season. The balance between the energy devoted to somatic growth and to basal metabolism may probably be different in each river, depending on water temperature and food intake during the growing season. Therefore, trout grow at a similar rate under varied environmental conditions.

Table 2. Mean annual growth in weight ($\text{year}^{-1} \pm \text{s.d.}$) and mean weight ($\text{g} \pm \text{s.d.}$) at the end of each growing season of brown trout in the seven populations studied from 1996 to 1998 (R. Hoz Seca= HS, R. Cabrillas= CA, R. Gallo= GA, R. Dulce= DU, R. Jarama= JA, R. Cega= CE and R. Eresma= ER).

River	Growth		Weight ($\text{g} \pm \text{s.d.}$)		
	0+-1+	1+-2+	0+	1+	2+
HS	1.77 \pm 0.222	1.17 \pm 0.110	5.6 \pm 2.11	29.7 \pm 9.86	81.9 \pm 26.68
CA	1.66 \pm 0.115	0.91 \pm 0.098	7.0 \pm 2.88	35.4 \pm 10.12	83.9 \pm 17.97
GA	1.36 \pm 0.331	0.74 \pm 0.012	11.8 \pm 4.98	46.3 \pm 12.55	95.6 \pm 21.10
DU	1.83 \pm 0.139	0.72 \pm 0.106	10.5 \pm 4.17	65.8 \pm 20.87	138.5 \pm 35.51
JA	1.64 \pm 0.229	0.98 \pm 0.091	5.1 \pm 3.14	26.1 \pm 11.48	58.0 \pm 23.66
CE	1.88 \pm 0.323	0.97 \pm 0.073	3.7 \pm 1.41	19.0 \pm 8.11	45.8 \pm 13.80
ER	1.51 \pm 0.299	0.95 \pm 0.058	3.3 \pm 1.49	15.5 \pm 5.17	40.3 \pm 10.28

The seven populations displayed a similar reproductive performance (Nicola & Almodóvar, submitted). There were no differences found in age at maturity among populations. Females matured as 2+ years and males as 1+ and 2+. Despite the worse environmental conditions, trout from rivers Jarama, Cega and Eresma managed to mature at a size similar or even smaller than trout from the rest of the rivers analysed. Once matured, reproduction seems to take priority over growth, since the annual increment of body mass declined with age of trout, with an average reduction in growth from first to second year of 44%. The populations studied presumably maximise their reproductive potential with an early maturity in order to compensate for the short life span. Finally, life-history data were used to evaluate the effect of current harvest management on the populations studied.

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**WHEN POPULATION AND PHYSIOLOGICAL ECOLOGY MEET:
CHINOOK SALMON SPAWNING
AND THE FATE OF THEIR PROGENY**

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EXTENDED ABSTRACT ONLY - DO NOT CITE

We explore the developmental dynamics of pre-emergent chinook salmon in their natural environment (Methow River, Washington, USA). Using models of developmental processes and daily temperature changes, the emergent properties of two allopatric chinook salmon stocks are explored using data on the timing and location of spawning, characteristics of spawned smolts, life-history patterns; and annual cycles of water temperature and flooding.

Development is modeled with coupled differential equations (Beer and Anderson 1997) with temperature dependent terms for anabolism, catabolism and water absorption. Embryo growth and yolk absorption depend on the daily temperature pattern which ultimately defines the development rate and mass of the fish at emergence. Emergence is defined at a physiological point, either maximum alevin mass or button up, both of which are easily identified (Fig 1). The model can be run on the internet at www.cbr.washington.edu/egg_growth

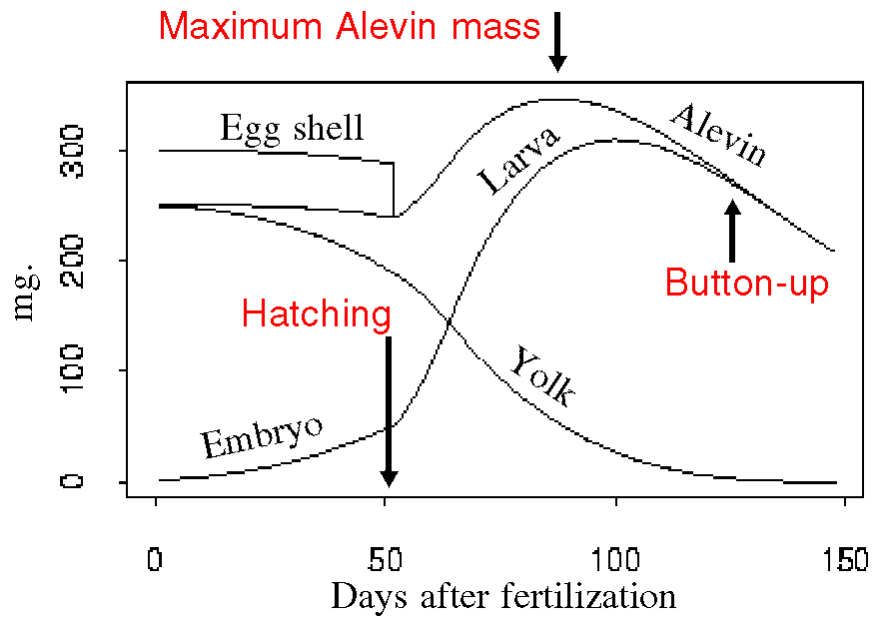


Fig.1 Example growth trajectories tracked through time by the model

We established a base case for each of the two stocks that spawn in the Methow River. August spawners deposit 218 mg. eggs over a narrow range of elevations near 560 m in a two week range spanning August 31. October spawners deposit 284 mg. eggs over a broad range centered at elevation 444 m in a two week range in mid-October. The mean time and range of times to emergence, and mass at emergence (alevin maximum or button-up) were modeled. Subsequent runs examined the consequences of deviations from the base case on emergence properties:

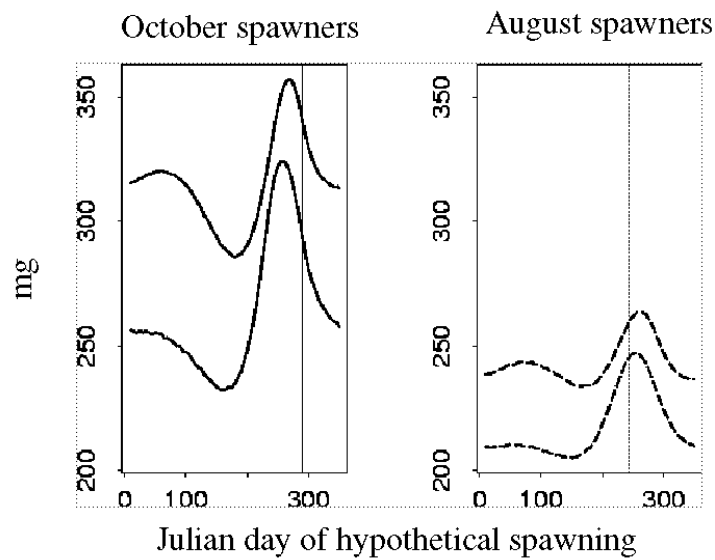
- spawning over the entire year (example in Fig. 2),
- spawning over the entire river,
- variation in egg size.

Considering environmental conditions during the year we conclude that progeny of August spawners are likely to emerge closer to button-up with a wide range in

emergence times. Progeny of October spawners are *forced* to emerge when the alevins reach maximum size but have a narrow emergence timing range (for predator response saturation). A thermal barrier limits first spawning time while the scour risk limits the end of incubation. In general, the further downstream that spawning occurs, the narrower the window of opportunity for successful incubation.

Despite the presence of high quality flow and gravel between their preferred spawning grounds, neither stock can fully exploit this environment although the broad spatial range used by October spawners is predicted from the insensitivity of emergence to elevation given their spawning time.

Fig. 2 Emergence mass at alevin maximum (upper line) or button-up (lower). Vertical lines show actual spawning



Developmental times of embryonic salmon are an important link between the behavior of spawners and fate of their progeny. Other studies measuring intra-specific divergence in developmental rates have had mixed results. We assumed they were identical for both August and October spawners but demonstrate the

importance of egg size, spawning day and spawning location in influencing developmental times.

We conclude that the important differences between emergence qualities of the progeny of August and October spawners are a result of 1) adaptive behaviors on the part of the spawners to optimize the survival of their progeny in different ways, and 2) egg mass which has the effect of altering the observed developmental rate. Efforts to protect and restore salmon runs must consider the spatial distribution of development as a result of temperatures because some habitat may not be usable for reasons related to physiology.

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THE IMPLICATIONS OF MATERNAL DECISIONS
FOR OFFSPRING GROWTH AND SURVIVAL

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Many of the factors determining embryo and early juvenile growth and survival are intimately linked to maternal traits in salmonids. Females choose the spawning sites and times, construct the nests and deposit the nutrient-rich eggs. In Atlantic salmon, female breeding success (i.e., number of her embryos surviving to emergence) shows a strong positive relation to body size due in part to increased fecundity. Increased fecundity, however, is only part of the story, because while female fecundity typically increases at a declining rate with body size, breeding success increases exponentially. Thus large females are producing fewer eggs, but are achieving higher breeding success per unit body size than are small females (Fleming 1998). The female through her effects on nest quality and survival largely determines the probability of embryo survival during incubation.

When the eggs hatch, the small juveniles still have a considerable amount of nutrients and energy stored in the yolk-sac, as a result of maternal provisioning. Once the yolk sac is absorbed, the juveniles emerge from the gravel into the open water. Newly emerged fry are poor swimmers and unlike older fry, are negatively buoyant, rapidly returning to the bottom.

Thus, initially they do not go far from the spawning site. In other words, the female's choice of spawning site and time dictates offspring environment and subsequent growth and survival. A female not able to choose and/or fight for a good site will expose her offspring to potentially harsh environmental conditions and thus poor growth and high mortality immediately after emergence. Loss rates during the first weeks thereafter are very high, with 68-88% mortality during the first 17-28 days (Einum and Fleming 2000a,b). Similar patterns have been observed in brown trout, where about 80% of fry rarely feed after emergence, quickly lose weight and drift down-stream during night and die (Elliott 1994). Incubation and early juvenile life are thus periods of intense selection (Einum and Fleming 2000a,b).

Effects of egg size on early offspring survival and growth

By manipulating egg size and thus controlling for maternal trait interactions, we examined the causal consequences of offspring size in a wild population of Atlantic salmon (Einum and Fleming 2000b). The joint effect of egg size on egg number and offspring survival resulted in stabilizing phenotypic selection for an optimal size. The optimal egg size differed only marginally from the mean value observed in the population, suggesting that it had evolved largely in response to selection on maternal rather than offspring fitness. Maximisation of maternal fitness by sacrificing offspring survival may well be a general phenomenon among highly fecund organisms. Egg size may also influence offspring growth. We found distinct reaction norms in the performance of juveniles from small and large eggs in experiments with brown trout, as growth and survival were similar in high quality environments but became increasingly divergent in poorer environments (Einum and Fleming 1999). The existence of such reaction norms indicates that the optimal egg size varies across gradients of environmental quality, and this has likely shaped the evolution of egg size.

EFFECTS OF SPAWNING TIME ON EARLY OFFSPRING SURVIVAL AND GROWTH

There is indirect evidence that spawning time among females may be affected by competition, with larger, dominant females spawning before smaller, less dominant females (Elliott 1994, Petersson and Järvi 1997).

Such differences can directly influence hatching and emergence time, which may have important consequences for offspring performance (e.g., Metcalfe and Thorpe 1992). To quantify the extent to which timing of breeding may ultimately affect fitness, we undertook laboratory and field experiments with Atlantic salmon (Einum and Fleming 2000a). To control for confounding effects caused by correlated traits, manipulations of the timing of fertilization combined with intraclutch comparisons were used. Mortality was intense and selective during the initial period following emergence from the gravel resulting in a significant phenotypic shift toward an earlier date of emergence. Moreover, timing of emergence had additional consequences for juvenile body size, with late-emerging juveniles being smaller than early-emerging ones at subsequent samplings, both in the wild and in parallel experiments conducted in semi-natural stream channels. This may affect success at subsequent size-selective episodes, such as winter mortality and reproduction. However, further evolution towards earlier emergence is most likely countered by the probability of experiencing unfavourable environmental conditions early in the spring.

The causality of maternal effects (e.g., egg size and spawning time) in our studies indicate that selection on juvenile traits plays an important role in the evolution of maternal traits in natural salmonid populations. Moreover, they indicate that the reproductive potential of females is dictated by much more than simply their fecundity.

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**INFLUENCE OF MALE PARENTAL IDENTITY
ON THE GROWTH AND SURVIVAL OF OFFSPRING
IN ATLANTIC SALMON (*SALMO SALAR* L.)**

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EXTENDED ABSTRACT ONLY – DO NOT CITE

Introduction

Atlantic salmon show a great variability in size and age at which individuals reach sexual maturity. In males, two distinct classes are clearly defined: 1) anadromous males are large individuals which fight for access to females, 2) precocious parr are small sexually mature males which sneak fertilizations (reviewed in Fleming, 1996). It is hypothesized that these two phenotypes represent alternative tactics within the conditional strategy theoretical framework (see Gross, 1996). In this framework inheritance of growth rate is proposed to be an important factor contributing to the development of precocity. However, it is known that environmental and behavioral factors present immediately after emergence can influence growth of juvenile fish (Thorpe et al., 1983). Therefore, the main objective of this study was to determine if there is an influence of male reproductive phenotype on the development of offspring in Atlantic salmon. In order to isolate the influence of parental identity from exogenous factors, the growth and survival of Atlantic salmon offspring fathered by precocious and anadromous fish were recorded during the yolk-sac stage prior to emergence. We tested the hypothesis that there is a significant

difference in growth rate and survival during the first early-life history stages between the two groups. We also aimed to determine if the relationship between fish and otolith size is the same between the two groups from hatching to emergence. Specifically, we established for each group: i) the age and size at hatching (from otolith measurements) and ii) the age and size at emergence. We then tested the hypothesis that alevins fathered by precocious males hatch earlier, grow faster, and emerge at larger sizes than do alevins fathered by anadromous males, thus increasing the probability of precocious maturity.

Methods

Fish from the Sainte-Marguerite River (48°20'N, 70°00'W), Québec, Canada, were used in this experiment. Eggs from a single anadromous female salmon were fertilized using sperm from both anadromous and precocious male phenotypes. Crosses were performed as follows: batch #1) sperm from two precocious parr and ¼ of female eggs (approximately 2000 eggs/batch), batch #2) replicate of #1 but with two different precocious males, batch #3) sperm from two anadromous males and ¼ of female eggs and batch #4) replicate of #3 with two different anadromous males. These eggs were then transferred to an egg incubator located on the river. At hatching, 90 eggs of each batch were transferred to individual cages in which they were filmed every two days (two batches - one of each parental identity - per day) until emergence in order to monitor the growth and survival rate of each family. Data from video monitoring were analysed with an image analyser which allowed us to determine length and daily growth rate of each alevin as described in Meekan et al. (1998). As we closely missed the hatching of eggs we used otoliths of these fish to establish their age at hatching. We also used microsatellites loci to discriminate the proportion of progeny fathered by each salmon in each batch. We then used a mixed-model analysis of variance (ANOVA) to detect differences in growth rate, age and size at hatching, age and size at emergence for each group. This test takes into account interdependency of samples since all fry shared the same mother.

Results and Conclusion

Analysis of these data are still in progress at this time. Preliminary results from the analysis of growth and development of precocious parr and anadromous offspring showed that precocious offspring from batch # 1 were significantly bigger than any other groups on the first day of observation. However there were no other significant statistical differences between the two groups as shown in figure 1. Total mortality from hatching to emergence was also higher in anadromous (32.2%) than in precocious (25.0%) alevins, even if this difference was not significant ($P = 0.274$). A more exhaustive analysis concerning the precise date of hatching for each fish will be required in order to clearly compare each “cohort” separately. Also, genetic data will allow us to compare the contribution of each father separately. This will be discussed in more detail during the oral presentation as will the implications of growth variation for our understanding of alternative reproductive tactics.

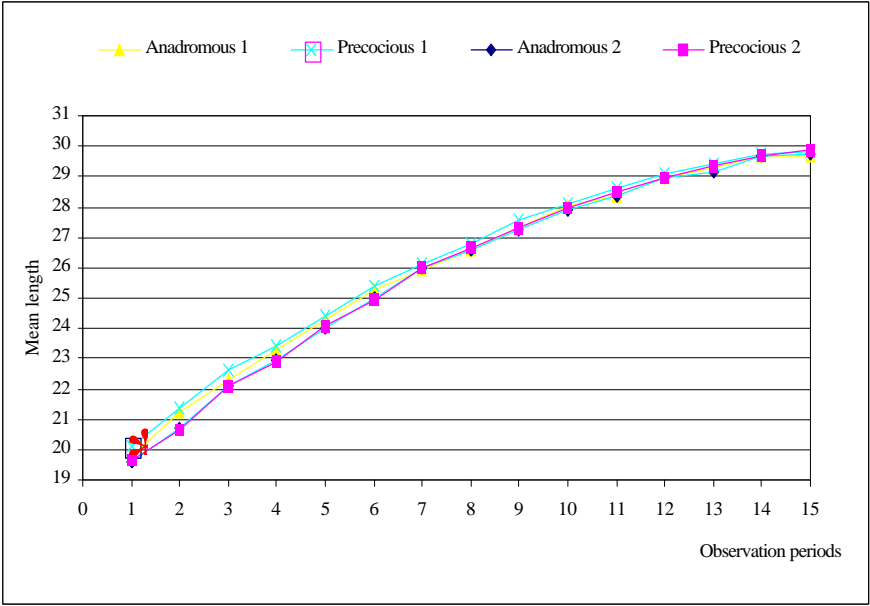


Figure 1. Mean length at each observation period for anadromous and precocious offspring

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**SPATIAL AND TEMPORAL VARIABILITY
OF JUVENILE ATLANTIC SALMON SIZE AND
OF SIZE-SELECTIVE MORTALITY RATE:
INFLUENCE ON THE INCIDENCE
OF PRECOCIOUS SEXUAL MATURITY IN MALE PARR.**

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EXTENDED ABSTRACT ONLY – DO NOT CITE

Introduction

Focus on the freshwater part of juvenile Atlantic salmon (*Salmo salar*) life reveals important differences in growth and reproductive patterns. Variability in juvenile size can be detected between rivers but also between sites within a river and between years for a particular site. One important alternative reproductive tactic that has been recognised is the occurrence of precociously mature male parr, which are capable of reproducing with mature anadromous females while being 1/10th of their size (Hutchings and Myers 1988). It has been suggested that the expression of this alternative reproductive pattern is related in part to size attained by juvenile males at a particular moment in life (Myers et al. 1986, Rowe and Thorpe 1990, Gross 1996). The occurrence of this tactic could therefore be as variable as size reached by individuals. Experiments suggest that size-selective mortality in age 0+ salmon is important and that the direction, i.e. the size class affected, is variable among years (Good 1997). It is not known if

this differential mortality rate among individuals related to size occurs in subsequent years of freshwater life for this species. If this is the case, it could have a major influence on size attained by parr of a given age. Thus, the incidence of precocious parr could not only reflect that a certain number of individuals attained the threshold size for maturity but also that their size class survived. Our objectives were to 1) evaluate the spatio-temporal variability of size-at-age and of the incidence of precocious maturity in age 1+ and 2+ Atlantic salmon parr, 2) estimate if size attained at different moments of life vary significantly between precocious males and immature parr in the wild, 3) evaluate the importance and direction of size selective-mortality and its influence on precocious maturity.

Methods

During the summers of 1996 to 1999, seven sites on the Ste-Marguerite river in Québec, Canada (48°20'N, 70°00'W) were sampled. The sampling schedule involved a visit to each site in June and August. 40 to 50 juvenile salmon of a length expected to correspond to age 1+ or 2+ fish were collected. Length, weight and sexual maturity were recorded. Age was assigned using scales and otoliths. Individual backcalculated size at different moments of life (first-feeding, end of first summer of life, beginning of the second growth season) were obtained for precocious and immature male parr sampled in August by using the microstructure of sagittal otoliths. This analysis was also performed on otoliths of male parr collected in June. We used the relationship between otolith and somatic length validated in another study for age 1+ salmon parr (Aubin-Horth and Dodson, unpublished) and the backcalculating method described in Sirois et al. (1999). It was then possible to compare the mean size and size frequency distribution at different moments of life of male parr depending on their sexual maturity. These data also permitted us to compare the backcalculated size frequency distribution of the population at the beginning of the growth season for individuals taken either at the beginning or the end of summer. This allowed us to evaluate which size-classes that were present at the beginning of the growing season survived until August. If these two distributions differed, it suggests that individuals of a particular size disappeared from the population during the time interval between the two sampling periods. It is therefore possible to estimate the importance and direction of size selective mortality for a definite time period. This method also permits us to distinguish between the effect of individual growth and survival on size attained by an individual.

Results and conclusion

Our data suggest that size attained at a given age is variable at different spatio-temporal scales and that an important proportion of precocious males are present in the Ste-Marguerite river system for each age-class studied. The mean occurrence of precocity for the whole system is relatively stable among years. This mean percentage of males that are precocious is calculated by pooling the data from all the sites sampled for each age class. Nearly half the age 1+ males and more than two-third of the age 2+ parr are precocious for the years studied. The proportion of male parr that are precocious is much more variable among years when it is computed on a site-by-site basis. Furthermore, the spatial variability within the river for a given year is more important than the temporal variability for a given site. The results concerning the relationship between size at different moments of life and the incidence of this conditional strategy as well as the importance of size-selective mortality for the size structure of juvenile cohorts will be discussed during the oral presentation.

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**SPATIAL VARIATION IN THE OPPORTUNITY FOR GROWTH
DURING A POTENTIAL CRITICAL PERIOD:
IS THERE A LINK TO SURVIVAL FOR AGE-0 ATLANTIC SALMON?**

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EXTENDED ABSTRACT ONLY - DO NOT CITE

Introduction

Survival during the first 2-9 weeks after stocking or emergence has been proposed to strongly influence year class strength in stream-dwelling salmonids. Differences in survival (usually estimated via loss rates) within a particular stream have been suggested to result from differences in the ability of streams to provide suitable feeding locations during this critical period (Elliott 1989, Armstrong 1997). Previously, we examined survival and growth for age-0 Atlantic salmon in six Vermont, USA streams. We found that the amount of habitat providing positive growth opportunity for Atlantic salmon fry was significantly more limited in the first six weeks after stocking than later in the summer. In addition, differences in overall spring to summer loss rates among these rearing streams could be predicted by the amount of good early season habitat at each site (Nislow et al., 1999, Nislow et al., 2000). These findings were consistent with predictions for the importance of a critical period for survival.

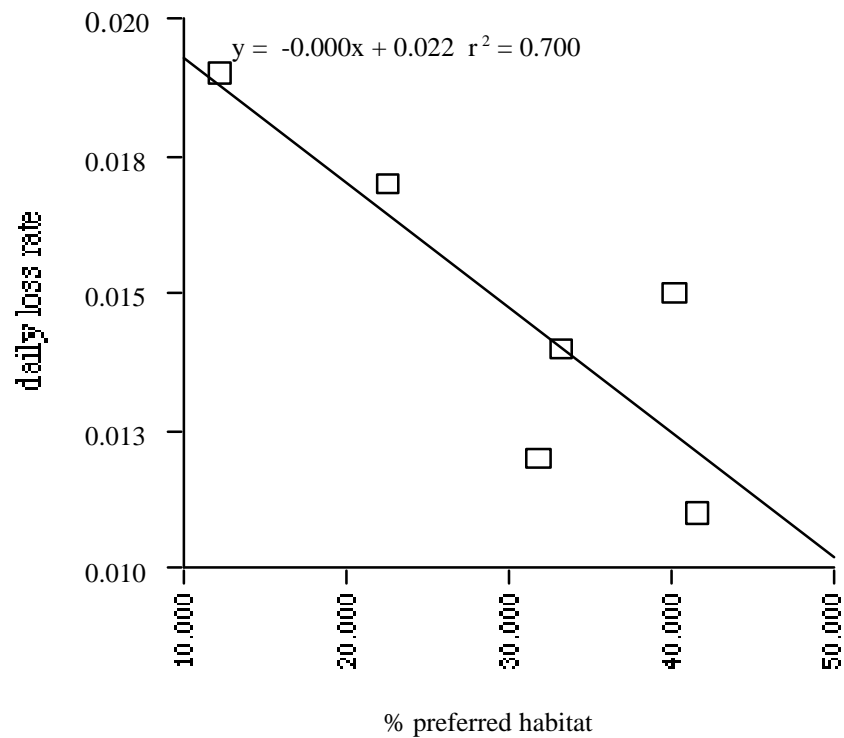
If this hypothesis is true, we would expect to see that sites that have high overall loss rates, and low amounts of high quality early season habitat, would also have high early season loss rates. However, few studies have actually measured loss-rates during this proposed critical period (Elliott, 1985; Bley and Moring, 1988). Furthermore, none have tested the relationship between growth opportunity and loss-rates during a potential critical period. Our objectives were to test these hypotheses by measuring early season habitat and loss rates, in rearing tributaries with known differences in total spring-summer survival. Our goal was to strengthen the link between habitat and performance in juvenile Atlantic salmon.

We collected field data on microhabitat use and availability from six 3rd- 4th-order streams in the White and West River drainages, two major tributaries of the Connecticut River in central and southern Vermont. We hand stocked unfed age-0 Atlantic salmon fry, obtained from the White River National Fish Hatchery in Bethel, VT, into 100m-long sections of the six study sites at various dates between May 3 and June 3 1997. These sections were stocked on the same dates and at the same densities (30 - 50)/ 100m²) that the rest of the stream was stocked by management personnel. We then conducted censuses, using 3-pass electrofishing removals, in 40m sections located within the 100m study sections in all six streams, during the early season, which we categorize as 7-8 weeks after stocking. Fish population size for all species, and, for salmonids, separately for each age class, was estimated using a modified Zippin removal method (McMenemy, 1995). We used correlation analysis to test whether 1) streams with a greater proportion of microhabitats preferred by age-0 salmon had higher early season retention rates, 2) early season loss rates were correlated with total spring-summer loss-rates.

Results and Discussion

Habitat conditions in all six tributaries exhibited the normal seasonal pattern of change characteristic of salmon rearing streams in central and southern Vermont - decreased current speed, depth and stream width over the course of the season, as discharge declines to summer low flows. White River basin sites tended to have higher discharges, particularly in the early season. Estimates of the proportion of habitats suitable for early season fish in the six index sites ranged from <13% in the Tweed River site to >40% in the Marlboro Branch site. Index sites with the highest proportion of suitable early season habitat had the lowest daily loss rates of age-0 salmon (n=6 $r^2 = 0.7$, $p < 0.05$ (Fig. 1).

Fig. 1 Daily loss rates of age-0 Atlantic salmon vs. % preferred habitat (predicted by a habitat suitability model). The relationship is significant ($p < 0.05$)



Index sites in streams with consistently high total spring-summer survival had low early season loss rates in our study sections. In conclusion, supporting our original hypothesis, age-0 salmon loss rates within the first 8 weeks after stocking were negatively correlated with the availability of favorable foraging locations, and these early loss rates accurately predicted overall, long-term differences in age-0 performance between sites. To our knowledge this is the first study to explicitly link early life history conditions and salmon early season

site-specific survival or site-specific retention, reinforcing a potentially important mechanism underlying growth and survival.

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**EFFECTS OF GROWTH MANIPULATION
ON GROWTH, SPACE USE AND DOMINANCE
OF JUVENILE ATLANTIC SALMON IN THE WILD**

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EXTENDED ABSTRACT ONLY – DO NOT CITE

Introduction

Growth rates of organisms under natural conditions are considered to be the results of complex sets of trade-offs involving foraging, energy expenditure, risk of predation and competition (Stearns 1992). Growth manipulations can have a major effect on the social interactions and patterns of resource use of individual animals (Nicieza & Metcalfe, 1999). Our aim in these experiments was to examine the effects of manipulation of natural growth rates on patterns of space use and social dominance in wild, juvenile Atlantic salmon.

Methods

Experiments were conducted in a flow-regulated, semi-natural stream channel adjacent to the Girnock Burn, Scotland in which an array of Passive Integrated Transponder (PIT) tag detector plates was set. The areas between the PIT tag

detectors were landscaped with gravel, cobbles and boulders to resemble natural riffle habitat.

Groups of eight size-matched wild fish (n=3 in 1998, n=4 in 1999) were caught, anaesthetised, measured and implanted with a PIT tag in the peritoneal cavity. Fish were given a dominance rank from 1 to 8 after testing using a serial removal procedure adapted from Metcalfe et al. (1990) in an in-stream flume.

After dominance testing, fish were all placed together into the middle of the experimental section of stream and left undisturbed for 14 d. All movements of fish over detectors were logged with a computer system. At the end of this period they were caught, re-measured and the four fish with the lowest dominance ranks were implanted with a slow-release growth hormone (gh) pellet while the four fish with the highest dominance ranks were given a placebo. They were left undisturbed for a further 14 d after which they were caught, re-measured and dominance tested a second time.

Specific growth rates (SGR) were calculated and used as the response variable in ANOVAs. PIT tag data were used to calculate rates of fish movement. Parametric and non-parametric correlations were performed between crossing rate, SGR and dominance rank. Change in dominance rank following GH implantation was analysed non-parametrically using Mann-Whitney U tests.

Results

Month, treatment and three 2-way interactions (table 1) significantly affected growth rate. Gh significantly increased sgr but this effect was only apparent during trials in June and July (significant month x gh interaction). Patterns of change in sgr were different between sexes across trials (significant month x sex interaction). Implantation of gh during August and September had no effect on sgr.

TABLE 1. SIGNIFICANT RESULTS ONLY OF 4-WAY ANOVA FOR SGR POST-GH IMPLANTATION

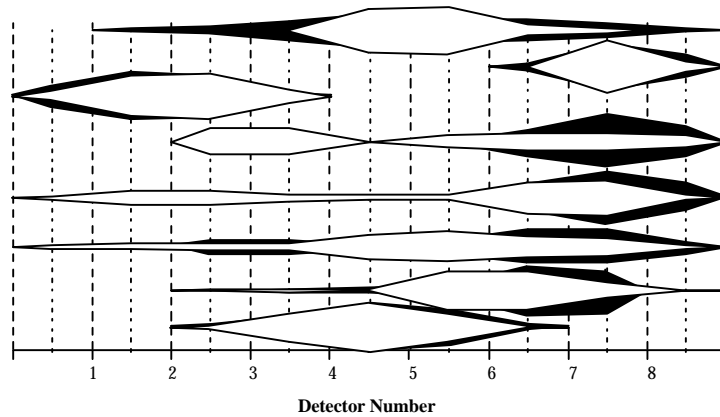
SOURCE	DF	F-VALUE	P-VALUE
CORRECTED MODEL	26	4.38	<0.001
INTERCEPT	1	44.58	<0.001
MONTH	3	14.64	<0.001
GH	1	9.96	0.005
YEAR X MONTH	2	4.08	0.033
MONTH X SEX	3	5.51	0.006
MONTH X GH	3	3.78	0.027
ERROR	20		
TOTAL	47		

Post-implantation dominance rank showed no significant correlation with sgr but there were significant increases in the dominance ranks of fish receiving gh. Sixteen of 22 fish implanted with gh showed an increase in dominance rank (11 or which were greater than or equal to +3) while only four of 19 fish implanted with placebo showed increase in dominance rank (all of which were +1).

Since males and females did not show significantly different relationships between crossing rate and sgr in the pre-implantation period, data for both sexes post-implantation were pooled and analysed by gh treatment. There significant linear relationships between crossing rate and sgr for both placebo and gh fish and the regression lines were significantly different (ancova $f_{1,44}=4.73$, $p=0.035$).

Patterns of space use following implantation were almost exactly the same as before implantation (figure 1).

Figure 1. Patterns of space use exhibited by fish from trial 4 pre- and post-implantation. Fish are ranked in order of increasing dominance from top to bottom and width of polygon at any point is proportional to the time spent there. Post-implantation space use has been superimposed (in white) over the top of pre-implantation space use (in black).



Conclusions

We have demonstrated that growth rates can be experimentally increased in the wild, but only at certain times of year. We speculate that this is the result of decreasing food availability and increasing fish weight through the year. Furthermore, we have shown consequences of manipulated growth rate on social status. However, the lack of any relationships between social status, space use and growth rate suggests that these factors may be less important in the wild than exploratory movements in determining growth. We hypothesise that this is a result of high levels of spatio-temporal variation in food abundance.

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**DOES ASSOCIATING WITH KIN AFFECT GROWTH
OF JUVENILE ATLANTIC SALMON IN THE WILD?**

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EXTENDED ABSTRACT ONLY – DO NOT CITE

Introduction

The factors that determine growth of individual fish have been extensively studied, but the influence of social structure on growth is poorly understood. Laboratory experiments have shown that juvenile salmon use the water-borne chemical cues of conspecifics (hereafter termed 'odours') to recognise their relatives, and are less aggressive when they associate with kin. The implication of these results is that growth should be faster for individuals in groups where fish are closely related because kin use less energy for aggressive territory defence. Data collected in a recirculating laboratory stream tank confirmed this prediction (Brown & Brown 1993). However, rivers differ markedly in character from laboratory aquaria because there is little recirculation of water. Here we first test whether water recirculation influences kin-biased territorial interactions, and second, we describe a field study designed to test directly whether growth of wild fish in the wild is influenced by kinship.

Methodology

1. Does recirculation influence aggression?

We tested pairs of fish from two categories: those that were reared apart and were related to one another and those that were reared apart but were unrelated to one another. Each category of fish was tested under recirculating water-flow conditions, where fish were continuously exposed to water that had passed them many times before, and under through-flow conditions, where water ran to waste after having passed through the aquarium only once.

2. Does kinship affect growth of salmon in the wild?

Juvenile salmon were released in early summer into c. 50m² sections of a tributary of the River Conon in North Scotland, UK, either in single family groups (n = 8), or in mixed relatedness groups of eight families (n = 8). The fish were resampled four months later using quantitative electric-fishing techniques.

Results

1. Does recirculation influence aggression?

Levels of aggression were similar between pairs of kin and pairs of non-kin when there was negligible recirculation of water. However, when water was recirculated, pairs of nonkin were on average 1.56 times more aggressive than pairs of kin (Griffiths & Armstrong 2000, Fig. 1).

2. Does kinship affect growth of salmon in the wild?

Growth rates were similar between kin and mixed groups (Fig. 2).

Discussion

The results of the first experiment suggest that concentration of odours influences aggressive behaviour of juvenile Atlantic salmon. Differences in

growth between groups of kin and mixed relatedness salmon observed in laboratory stream-tanks may therefore be much greater than expected for fish in the wild. The results of the second experiment confirm this prediction. It seems that in natural riffle conditions where there is little recirculation of water, growth rates of juvenile Atlantic salmon do not differ between groups of mixed relatedness and full siblings (kin).

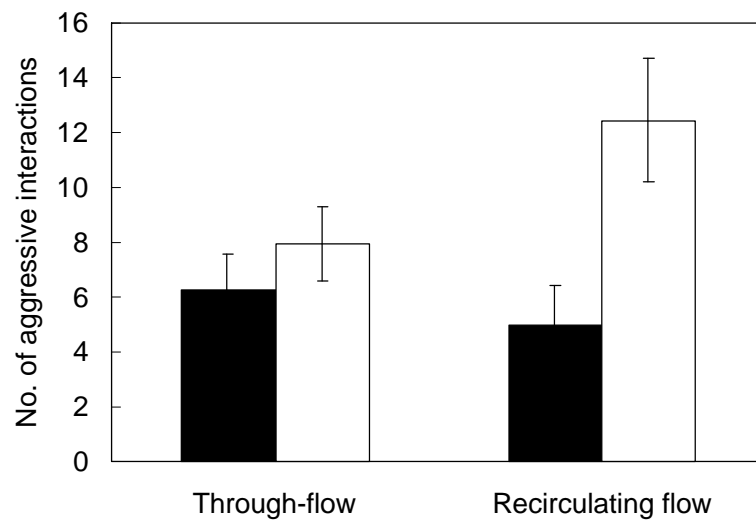


Figure 1. The total number of aggressive interactions of wild juvenile Atlantic salmon when paired with kin (■) or non kin (□) . Water flowed continuously either in a through-flow ($N=5$ kin, $N=6$ non kin) or in a recirculating flow ($N=5$ kin, $N=6$ non kin). In all cases means \pm S.E. per 10min are given.

Figure 2. The percent weight increase per day of groups of kin (■) and mixed relatedness (●) Atlantic salmon. In all cases means ($n=8$) \pm S.E. are given.

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EXPERIMENTAL INVESTIGATIONS
OF THE RELATIONSHIPS BETWEEN GROWTH AND DENSITY
OF JUVENILE ATLANTIC SALMON IN THE WILD

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EXTENDED ABSTRACT ONLY – DO NOT CITE

Introduction

Recent models of the factors that influence growth, weight and densities of wild juvenile *Salmo* spp. have raised a paradox (Armstrong, 1997). There is evidence that salmon self-thin, which indicates strong density-dependence of growth and/or mortality. However, the most influential models suggest that growth and mortality are largely independent of density. The purpose of our work was to examine experimentally first, whether growth does vary with local density, and second, whether populations of stocked juvenile Atlantic salmon fully utilise the carrying capacity of their habitat as they develop (which would be expected if they self-thin).

Methodology

Experimental procedure

The experimental site was the Cochill Burn, Perthshire, Scotland (03°48'W, 56°32'N), which is isolated from populations of naturally-spawned salmon in the main River Tay system by a waterfall. Twenty-four sites (eight groups of three) of 20 m length were marked, separated by at least 100 m of stream between the upstream end of one site and the downstream end of the next. Sites were chosen subjectively to be as homogeneous as possible with respect to substrate and cover and to be similar to each other. Within each group of three, sites were randomly allocated to one of three treatments: unfed fry only (UF), fed fry only (F) and unfed & fed fry together (UF+F).

Fry for stocking were obtained from eggs from wild fish caught in the River Braan (1998) or River Almond (1999) which were held, stripped and reared at the FRS Almondbank hatchery. Fish for the unfed treatment were stocked when the majority of the yolk sac had been absorbed. Each stocking group consisted of a mixture of three or four crosses of different parentage. Unfed fry were at a density of approximately 10 m⁻². Fork length (FL) and weight (Wt) of 20 randomly selected individuals were recorded prior to stocking. One third of each stocking group were retained and fed on commercial salmon food for approximately 12 weeks.

One week before stocking, all of these fed fry were anaesthetised with benzocaine solution and their adipose fins removed. Two or three days before stocking, sites to receive fed fry only were electrofished and any unfed fry found were removed. FL and Wt of the first 20 individuals (or all if less than 20 were caught) were recorded. Fed fry were stocked at a density of approximately 5 m⁻². FL and Wt were recorded for 20 randomly selected individuals on each occasion.

All sites were electrofished for remaining fry between 25 Aug and 17 Sep 1998 and 30 Aug and 6 Sep 1999. Only the middle 10 m of each site was fished to control for edge effects. A minimum of three electrofishing passes was performed; if more than five fry were caught on the third pass, an additional pass was undertaken. The identity and FL of all fish caught were recorded and Wt of the first 20 unfed or fed (fin-clipped) fry were also recorded. Water temperatures were logged every hour automatically.

Data analyses

Data on the number of fish of each species/life stage of interest (0+ salmon, older salmon, brown trout) caught in each pass were used to generate maximum likelihood estimates of total numbers and confidence intervals. Numbers were converted to densities (nos. m⁻²) using site dimensions. Numbers and FL/Wt were compared between experimental treatments using multivariate analysis of variance (MANOVA).

Linked experiments

Separate complementary experiments (not detailed here) were conducted to assess dispersion and affects of stocking density on growth.

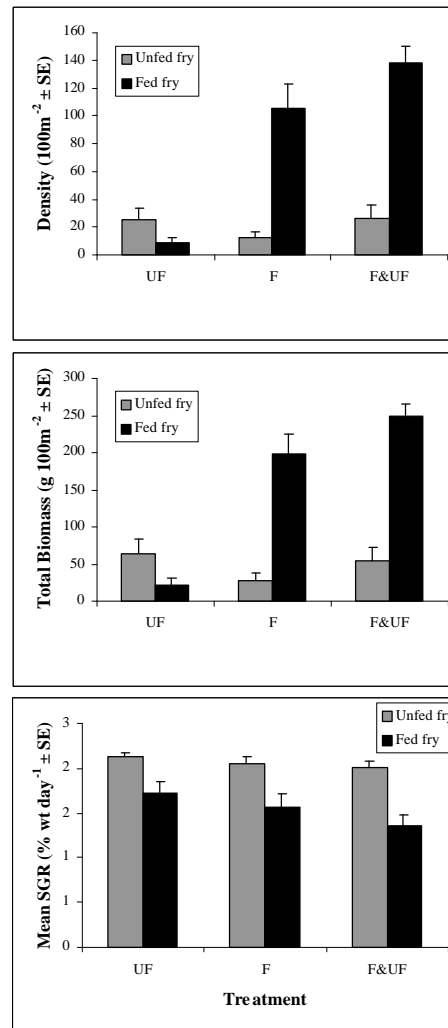
Results

Growth rates of unfed fry in 1998 were density dependent (plot of residuals from the Elliott & Hurley (1997) model, $r^2 = 0.366$, $F_{1,10} = 5.6$, $p=0.037$). When resampled, densities of unfed fry were similar between areas with and without stocking of fed fry (Fig. 1a). However, the total biomass of salmon was five-fold higher in sites that had been overstocked with fed fry (Fig. 1b). Growth rates were not significantly different between treatments (Fig. 1c) but were consistently higher among unfed fry compared with fed fry. Similar patterns resulted from the experiments conducted in 1999.

Discussion

Growth of salmon fry was density dependent, consistent with self-thinning. However, when the sections were overstocked, biomass could be increased by five-fold. The overstocked fish were smaller than those salmon stocked as unfed fry. Moreover, the unfed fry would have enjoyed the advantage of having prior residence. These factors explain why the density and growth of unfed fry were similar between overstocked and control sections. The data indicate that although the unfry were stocked at high densities and their growth was constrained, four weeks later there was substantial capacity for increasing production higher than the standing stock. The experiments are consistent with the concept that the populations of unfed fry self-thinned during an early critical period but were then well below the carrying capacity of the stream.

Fig. 1. Comparisons of (a) density, (b) biomass and (c) growth of salmon parr stocked as unfed (UF), fed-on (F) and both fed and unfed (F&UF) fry in 1998. Bars show the means and standard errors.



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**DO SALMON HATCHERIES SELECT FOR HIGH
METABOLIC RATE? A MODEL AND EVIDENCE
FROM OTOLITH MICROSTRUCTURE**

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EXTENDED ABSTRACT ONLY- DO NOT CITE

I propose that domesticated behaviour in salmonids (National Research Council, 1996) is caused by selection for elevated metabolic rates in the hatchery environment. I hypothesize that fish with an innate tendency for a higher metabolic rate (MR) are favoured in hatcheries because they develop faster (Metcalfe et al., 1995) start exogenous feeding earlier, and are more aggressive competitors for food (Metcalfe et al., 1995). Thus they may grow faster than low-metabolic rate fish and have higher fitness because of advantages to a larger body size (Fig 1). In the more complex natural environment, several counteracting forces, such as optimal emergence time, elevated predation risk for more active fish and higher maintenance energy demands of high MR fish will stabilize the tendency for metabolic rate at a lower optimum than in the hatchery.

As an indirect test for differences in MR between domesticated and wild salmon populations, I compared the otolith dimensions of domesticated with wild masu salmon (*Oncorhynchus masou*) populations. Growth rate of the otolith in larval fish is a function of basal MR rather than somatic growth rate (Wright 1991). In salmon from different populations raised under identical conditions, the otolith size variation should reflect differences in MR at a given life stage life stage. I compared otoliths of swim-up fry from three populations of masu salmon, one wild, one sea-ranched, and one aquaculture (farmed), all fry being raised from eggs in the laboratory.

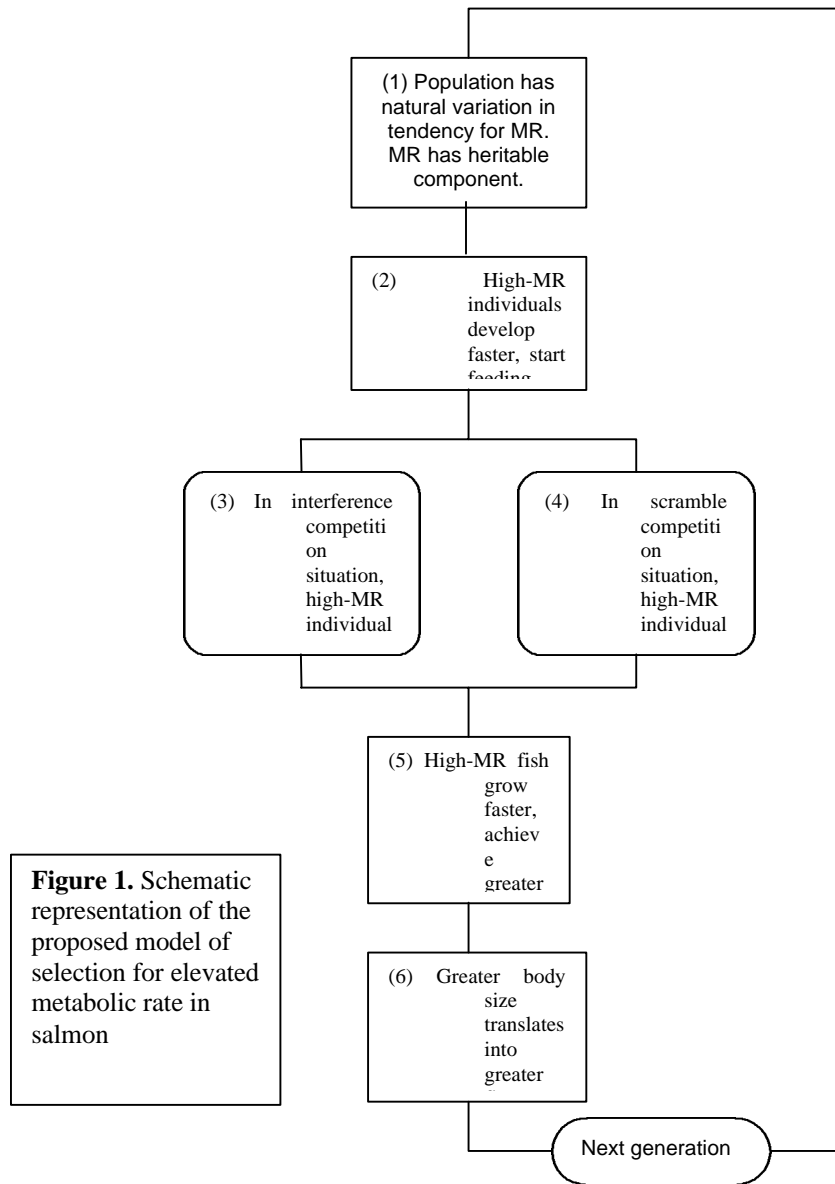
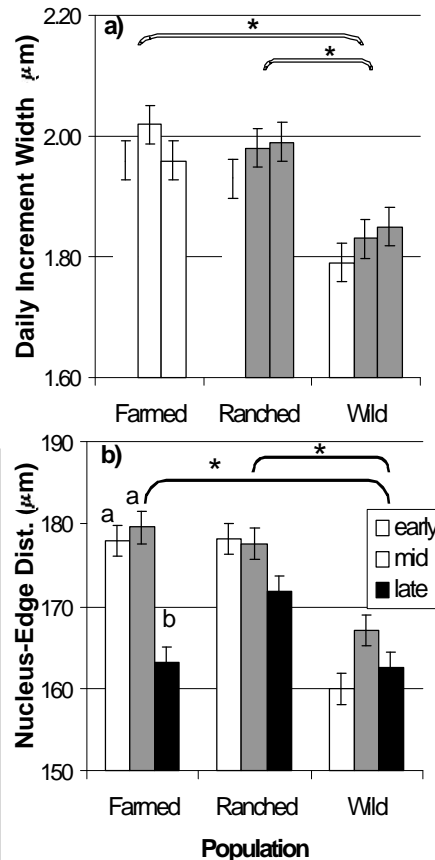


Figure 1. Schematic representation of the proposed model of selection for elevated metabolic rate in salmon

Ninety swim-up fry each (equal numbers from “early”, “mid” and “late” emergers) from the three masu salmon populations were sampled for otolith analysis. Two measurements were done on each sagitta : a) the distance between the nearest nucleus and the posterior edge and b) mean width of daily increments in an area formed in the time between hatching and swim-up.

As predicted, the mean increment width of wild fish was significantly smaller than that of the farmed (by 0.14 μm or 7.8 %) and sea-ranched fish (0.13 μm , 7 %) (Fig. 2 a). The mean swim-up date-adjusted distance between nucleus and posterior edge in wild fish was 9.6 μm (5.8%) smaller than in farmed fish and 12.6 μm (7.7 %) smaller than in ranched fish (Fig. 2 b).

Figure 2. Mean daily otolith increment width (+/- SE) before swim-up (a), and mean age-adjusted distance from the closest nucleus to the posterior otolith edge (+/- SE) at time of fry swim-up (b) in three populations of masu salmon. Shown for each population are values for (from the left to right) early, intermediate (“mid”), and late swim-up fry.



The prediction that early-swim-up fish within a population have relatively bigger otoliths (Metcalfe et al., 1995) was met in farmed fish only (Fig. 2 b). Because wild fish had a lower mean body weight, it was examined whether the smaller otolith dimensions of the wild fish may have been an effect of their smaller body size. Within any of the three populations, neither otolith increment

width nor adjusted nucleus-edge distances were significantly correlated with body weight (all correlations $p > 0.1$).

The results from the otolith examination lend preliminary support to my hypothesis of selection for elevated MR through domestication. As predicted, wild fish had smaller otoliths dimensions than either of the two captively-bred populations. Considering the causal relationship between otolith growth and metabolic rate (Wright, 1991), it is likely that the wild fish in this study had smaller otoliths because of lower metabolic rates during egg and alevin development. The mean daily increment widths differed by about 7.5 % between the wild and domesticated populations, which would have been equivalent to an about 30 % difference in weight-specific oxygen respiration rate of resting fish in a different study (Yamamoto et al., 1998).

Further study using pairs of domesticated salmon and their ancestral wild stock are necessary to give conclusive evidence for the hypothesis of selection for high metabolic rates through domestication. Measuring the MR of hatchery and ancestral wild populations may become a way of judging the magnitude of past domestication selection and the effectiveness of new hatchery designs aimed at avoiding domestication selection.

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DRAMATIC ACCELERATION OF SALMONID GROWTH RATES

USING GENETIC MANIPULATION:

WHY DON'T WILD FISH GROW THIS FAST?

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EXTENDED ABSTRACT ONLY - DO NOT CITE

Introduction

Through genetic manipulation, it is possible to dramatically alter the patterns of growth for both Atlantic (*Salmo salar*) and coho salmon (*Oncorhynchus kisutch*). Using this procedure, manipulated fish can be up to 37 times the size of control fish after one year, and can achieve sexual maturity in half the time (Devlin et al. 1994, 1995a) and have a higher feeding rate (Abrahams & Sutterlin 1999, Devlin et al. 1999). From an ecological perspective, such a manipulation may potentially be advantageous since the rapid growth would reduce the time period these fish would be susceptible to predators, as well as allowing them to more rapidly exploit larger food items within their environment (Werner & Gilliam 1984). Here we address the question of why wild salmon do not possess this apparently beneficial characteristic. Two distinct possibilities exist. Either this genetic manipulation has allowed the production of fish superior to the wild-type, or the ability to grow more rapidly is not selectively beneficial. For our research, we believe that there is no obvious selective impediment that would prevent wild fish from altering their hormone levels over time to achieve this accelerated growth. Indeed, for

juvenile salmon there may be circumstances where high growth rates are disadvantageous (Bull et al. 1996). We therefore assume that the energetic requirements necessary to sustain this growth, or correlated characters such as disruptions in pituitary function (Mori & Devlin 1998), acromegaly (Devlin et al. 1995b, Ostefeld et al. 1998), swimming performance (Farrell et al., 1997) and antipredator behaviour (Abrahams & Sutterlin 1999), will limit the ability of transgenic fish to survive in the wild.

Here, we test the hypothesis that accelerated growth rates of transgenic fish is a function of an artificial hatchery environment, and that with a more natural feeding regime their growth advantage relative to wild-type fish should diminish.

Methods

Sixty transgenic and sixty wild-type fish were used for this experiment. All fish were of approximately equal size at the beginning of the experiment and every individual was identified for the duration of these experiments with an internal PIT tag. For these experiments, these 120 fish were divided between four tanks, with each tank containing a group of 15 transgenic and 15 wild-type fish. All tanks received a feeding ration that was equivalent to 1% of their total body weight per day. Two tanks received this ration via two feedings per day. The other two tanks received that same total amount of food over a four week period, but according to a negative binomial distribution. As a consequence, this feeding regime was unpredictable, including extended periods of food deprivation, with periodic large feedings. Every four weeks, all fish were removed from their tank, identified, and weighed. This experiment continued for 16 weeks.

Results and Discussion

The influence of this temporal manipulation of feeding regime had no measurable effect upon the wild-type fish, but did alter the pattern of growth of the transgenic fish. Surprisingly, average growth rates of transgenic fish were not affected by this manipulation. Instead, providing food in an unpredictable fashion generated two modal groups of transgenic fish. The upper mode had a growth rate greater than transgenic fish on a uniform diet. The lower mode had a growth rate less than that of wild-type fish.

It is possible that dominance interactions between transgenic and control fish at a time when food is available in large quantities may be partially responsible for this result.

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WHY DO SALMONIDS NOT GROW FASTER?

- GROWTH HORMONE AND TROUT PERFORMANCE IN STREAMS

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EXTENDED ABSTRACT ONLY – DO NOT CITE

Introduction

Fish and other animals are capable of catch-up growth after periods of starvation suggesting that growth rates normally are kept below the physiological maximum. This indicates that rapid growth may incur costs such as increased predation risk, reduced tolerance to starvation, reduced developmental stability or reduced immune capacity (Arendt, 1997). Growth hormone (GH) increases tissue growth by stimulating cell growth and cell differentiation. GH-treatment also induces increased competitive ability and reduced anti-predator responses similar to what has been observed in GH-transgenic fish (e.g. Abrahams and Sutterlin, 1999). Exogenous GH treatment is thus an excellent tool to simulate increased growth investment, which can be used to test growth rate trade-off hypotheses in general and to predict the impact of growth-enhanced (i.e. GH-transgenic) fish in the wild. In a series of field experiments we treated brown trout (*Salmo trutta*) either with GH or with sham-injections to study the effects of GH-mediated growth investment on performance in natural or near-natural streams.

Methods

Young brown trout (size range 5-40 g) were measured for weight and length, pit-tagged and simultaneously implanted with a sustained-release GH pellet (exp. I-IV) or a gel-like GH formulation (exp. V-VII). Control fish were sham-implanted. The trout were then released in the stream and recaptured by draining

and netting (exp. I-V), or by electric fishing (exp. VI-VII). Recaptured trout were measured for weight, length and various other parameters reported elsewhere (Johnsson et al., 1999; Johnsson et al., 2000). Experiments I-V were conducted in the experimental stream in Älvkarleby (see Johnsson et al., 1999) and experiments VI –VII were conducted in the Norumsån river.

Results and Conclusions

Mortality rates did not differ significantly between GH-treated and control fish. There was a general trend for increased mortality in GH-treated trout in the experimental stream in Älvkarleby, but not in river Norumsån (Table 1). These results do not strongly support the hypothesis that increased mortality selects against increased utilisation of GH in wild fish. Furthermore, GH-treatment increased weight and length growth rate in all stream experiments under a wide range of environmental conditions (Table 1). GH-treated trout in the experimental stream (exp. I-V) lost more energy reserves than control fish (Johnsson et al., 1999; 2000), but this effect was not significant in river Norumsån.

In summary, our field experiments do not reveal any clear fitness costs associated with increased growth rate and thus can not explain why the endocrine growth regulatory system of wild fish is not set at a higher level to promote faster growth. It is possible, however, that selection against increased GH-secretion is more intense at other life-history stages and/or during certain years with severe climate conditions. Our results also raise the concern that released or escaped growth-enhanced salmonids may compete successfully with resident fish in the wild. Faster growth may confer several size-related advantages such as reduced susceptibility to predation, increased fecundity and increased ability to compete for spawning sites and mates. A recent model by Muir and Howard (1999) suggests that increased mating success of large GH-transgenic males, in conjunction with reduced viability of their offspring, may result in rapid extinction of wild populations. Their results and our empirical findings indicate that the ecological risks associated with release of growth-enhanced fish should not be ignored.

Table 1. Summary of the effect of growth hormone treatment on mean growth rates (SGR) and mortality in control (C) and growth hormone treated (GH) brown trout in seven field experiments. Significant differences (P<0.05) are denoted by *. Mortality rates based on recapture by electro-fishing are denoted by °.

Experiment location	Time span	SGR weight		SGR length		Mortality (%)	
		C	GH	C	GH	C	GH
I Älvkarleby exp. stream	Feb-Mar	-0.11	-0.10	0.01 *	0.02	26	26
II Älvkarleby exp. stream	Mar-May	0.0	0.05	0.08 *	0.11	40	48
III Älvkarleby exp. stream	Jul-Aug	1.37	1.57	0.38	0.45	28	33
IV Älvkarleby exp. stream	Sep-Oct	1.95 *	2.15	0.70 *	0.84	25	30
V Älvkarleby exp. stream	Sep-Mar	0.22 *	0.28	0.05 *	0.08	36	48
VI Norumsån river	Aug-Mar	0.16	0.20	0.07 *	0.09	82°	82°
VII Norumsån river	Aug-Mar	0.20 *	0.25	0.08 *	0.09	83°	77°
Overall mean		0.54 *	0.63	0.20 *	0.24	46	49

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**LONG-TERM GROWTH AND ENERGY COSTS OF REDUCED
FOOD AVAILABILITY IN OVERWINTERING SALMON**

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EXTENDED ABSTRACT ONLY – DO NOT CITE

Delayed migrant Atlantic salmon (those that do *not* migrate to sea after their first year in fresh water) show a period of greatly suppressed appetite and growth during the winter known as the anorexic phase. The fish rely heavily on lipid reserves accumulated during the late summer and autumn as a primary source of winter energy. Bull *et al.* (1996) developed a state variable model to predict the daily foraging effort that would maximize over-winter survival of delayed migrant salmon. The model predicted that anorexia should only occur if sufficient, prior lipid accumulation takes place, and that if this were prevented then the salmon should continue to feed until their lipid reserves were normal for the time of year.

In order to test this prediction, we subjected delayed migrant salmon to a six-week period of reduced (weekly) food availability in Sept./Oct., and compared the food consumption, growth and lipid reserves of the food-deprived fish to daily-fed controls over the subsequent seven months (to April). Food consumption was measured by X-radiography (Morgan *et al.* 2000) and whole body lipid reserves (%) were calculated from a regression equation of lipid weight against body weight and length obtained from a separate, sacrificed, group of salmon ($r^2 = 0.935$, $P < 0.001$). The fish were then held together until August when sex, and the incidence of male maturity were determined.

At the end of the experimental treatment, the food-deprived fish were significantly smaller than the controls (Table 1). They also had significantly lower lipid reserves, but whilst larger fish carry proportionately more lipid, the size difference did not explain the difference in lipid. On the resumption of daily feeding, the food-deprived fish responded to their reduced lipid levels with a dramatic increase in food consumption. This compensatory response was sufficient to restore lipid reserves to control levels within two weeks. However, neither the weight nor length of the food-deprived fish returned to control values by December (Table 1).

Table 1. The effect of a six-week period of food deprivation on size and whole-body lipid reserves in delayed migrant salmon. *Indicates a value for food-deprived fish that is significantly different to that of controls ($P < 0.05$).

Measurement/time†		Controls	Food-deprived
Weight (g)	September	3.20 ± 0.11	2.94 ± 0.08
	October	3.77 ± 0.12	2.89 ± 0.09*
	December	4.05 ± 0.13	3.44 ± 0.11*
	April	7.05 ± 0.29	4.79 ± 0.23*
Lipid (%)	September	6.93 ± 0.09	7.07 ± 0.09
	October	7.03 ± 0.10	5.95 ± 0.14*
	December	6.61 ± 0.11	6.43 ± 0.10
	April	8.84 ± 0.16	7.07 ± 0.21*

† Experiment started September, ended April. October = immediately after food deprivation.

We had anticipated that, once any compensation for the temporary reduction in food availability was completed, the two groups of fish would show similar patterns of growth. However, two months after the experimental treatments, from December onwards, the performance of the two treatments began to diverge. The growth rates of the food-deprived fish fell below those of the

controls, so that the post-treatment size discrepancy between the two groups had increased by April (Table 1). The lipid reserves of food-deprived fish decreased from December to March whereas those of the control fish increased, so that by April, the lipid reserves of the controls were some 25% greater than those of the food-deprived fish (Table 1).

The two treatments had a similar proportion of female fish in August. However, only 48% of food-deprived males achieved maturity compared to 74% of the controls. Male maturation in non-migratory Atlantic salmon may be switched off if lipid reserves are not replenished during spring growth (Rowe *et al.* 1991). Maturation may begin as early as November (Simpson, 1993), but by that time the lipid levels of the food-deprived fish had recovered from the experimental treatment. It is therefore probable that the unexpected lipid deficit in the food-deprived fish was a direct cause of the reduced incidence of male maturation.

In conclusion, this study confirmed the prediction that anorexia in delayed migrant salmon would be delayed by a failure to accumulate sufficient lipid reserves in autumn. This delay would reduce the probability of later starvation (Bull *et al.* 1996) but would increase predation risk and could therefore lead to increased short-term mortality. Moreover, the temporary depletion of lipid reserves appears to have deferred, long-term costs. The suppressed growth of the food-deprived fish may cause migration to be postponed for a further year, while a significant decrease in mature males could reduce the reproductive success and subsequent recruitment in Atlantic salmon populations.

This work was supported by a grant from the Natural Environment Research Council (UK) to N.B. Metcalfe.

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**LOCAL ADAPTATIONS OR PHENOTYPIC PLASTICITY
IN THERMAL PERFORMANCE? EVIDENCE
FROM FIELD STUDIES ON GROWTH IN 63 POPULATIONS
OF BROWN TROUT AND ATLANTIC SALMON**

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New laboratory based growth models for brown trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*) fed on maximum rations (Elliott et al., 1995, Elliott and Hurley, 1997) were used as baselines to explore latitudinal variation in growth among natural populations. The models allowed us to control for differences in ambient temperatures and fish size among populations. Annual growth rates of anadromous brown trout parr from 22 Norwegian populations and Atlantic salmon parr from 19 Norwegian populations at 61 to 70 °N were compared with predictions from the growth models. Published field data for brown trout from one Spanish, 15 British and four Danish populations at 44 to 58 °N and for Atlantic salmon from two British populations at 57 and 58 °N were included in the analyses to increase the latitudinal range.

Among the Norwegian populations of brown trout, the ratio between observed and predicted growth rates were not significantly different from 1.00 in eight rivers, significantly higher in eight, and significantly lower in six. Observed growth was highest, relative to predicted growth, in the coldest rivers. In

Spanish, British and Danish rivers, observed growth did not exceed predicted growth.

The ratio between observed and predicted annual growth rate of brown trout decreased significantly with increasing annual mean temperature (Fig. 1). Observed annual growth was higher than predicted growth only in rivers with an annual mean temperature lower than 5.1 °C, and this indicates that some kind of thermal adaptation may occur in trout populations in the coldest rivers.

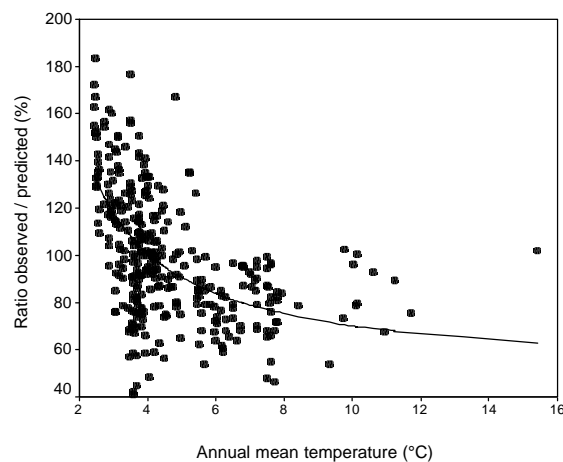


Figure 1. Relationship between the ratio of observed to predicted annual instantaneous growth rate of brown trout (RA %) in one Spanish, 15 British, four Danish and 22 Norwegian populations ($n = 365$) and the annual mean temperature (T_{ANN} °C) in the rivers in the sampling years ($RA = 186 / T_{ANN} + 55.0$, $r^2 = 0.335$, $P < 0.001$).

Regression analyses (Table 1) showed that besides the direct effects of temperature and body size predicted by the growth model, annual growth rates of brown trout were significantly related to annual mean temperature, densities of juvenile salmonids, duration of twilight (average for May-August) and latitude. Adding these variables to the original model increased the explanatory power from 73.9 to 80.6%.

Table 1. Multiple regression analysis (stepwise inclusion procedure, $P < 0.05$) of observed annual growth rate of juvenile brown trout (G_{OBS}) in relation to predicted growth rate from the model of Elliott *et al.* (1995) (G_{PRED}), latitude (L) of rivers, inverse of annual mean water temperature ($1/T_{ANN}$), annual amplitude of monthly mean temperatures (T_V), day-length at midsummer (DL), number of bright nights each year (BN), duration of the civil twilight period (TW), density of juvenile brown trout (D_{BT}) and total juvenile salmonid density (D_{TOT}).

Variables	Unstandardised Coefficients (\pm SE)	Adjusted R^2 change	t	P
G_{PRED}	0.866 ± 0.026	0.739	33.538	< 0.001
$1/T_{ANN}$	2.590 ± 0.324	0.045	7.999	< 0.001
D_{TOT}	-0.00292 ± 0.00064	0.009	-4.602	< 0.001
TW	0.00173 ± 0.00042	0.008	4.153	< 0.001
L	-0.0144 ± 0.0049	0.005	-2.954	0.003
T_V			1.948	n.s.
DL			1.253	n.s.
D_{BT}			-0.661	n.s.
BN			0.263	n.s.
(Constant)	0.253 ± 0.271		0.933	n.s.

In the two British as well as eight of the Norwegian Atlantic salmon populations, the observed growth rates were not significantly different from the predicted ones, in six rivers they were significantly higher, and in three rivers they were significantly lower than those predicted from the model. Observed growth was highest, relative to predicted growth, in the coldest rivers.

The ratio between observed and predicted annual growth rate in the 21 Atlantic salmon populations included in the analyses decreased significantly with increasing annual mean temperature. Based on multiple regression analysis, the observed annual growth rate of Atlantic salmon (G_{OBS}) was best described by the following model ($F_{3, 226} = 141.1$, $p < 0.001$):

$$G_{OBS} = 0.987 G_{PRED} + 5.114/T_{ANN} - 0.0565 L + 2.515$$

where G_{PRED} was the annual growth rate predicted from the model of Elliott and Hurley (1997), T_{ANN} was annual mean temperature and L was latitude. The new

model explained 64.7 % of the variation in annual growth, compared to 46.9 % by the original model.

In summary, the present study shows that most of the variation in growth of brown trout and Atlantic salmon in Europe can be related to environmental variables. Most of the observed variability in growth rates and body size for juvenile stages among these fish populations is phenotypic and a product of local conditions. However, even after taking into consideration the effects of temperature predicted from laboratory studies and several biological and environmental factors, a significant relationship existed between growth and temperature. This relationship (explaining ca 5 % of the variance in brown trout) occurred because the laboratory model strongly underestimated growth in some of the coldest rivers. Thus the combined modelling and field approach has successfully narrowed the geographical area and the environmental conditions in which thermal adaptation may occur. In some of the coldest rivers both species may show adaptation to life at low temperatures and/or short growth seasons. To what extent these adaptations are genetically based can be determined by performing experiments in a common environment with a selection of the populations. In contrast to several earlier studies, we found little if any support for the countergradient variation hypotheses for thermal adaptation in ectothermal animals. The general pattern appears to be phenotypic plasticity.

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**ASPECTS OF SIZE AND GROWTH IN THE DIVERGENCE
OF NEW SALMON POPULATIONS**

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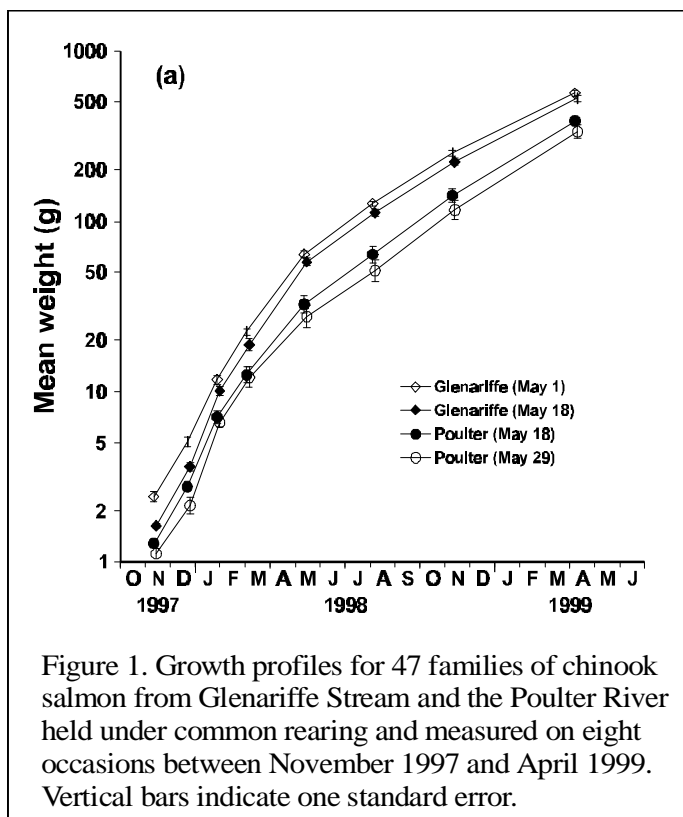
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EXTENDED ABSTRACT ONLY – DO NOT CITE

Studies in the past few decades have demonstrated the potential for life history evolution to occur on contemporary time scales in fishes and other animals (see Hendry and Kinnison 1999 for review), though few studies have documented such divergence under relatively natural conditions of colonization and continued gene flow. We suggest that among the traits initially contributing to divergence are characters, such as growth rate, that are pivotal to early phenotypic divergence through their wide ranging interactions with environment, development and other characters. Here, we demonstrate recent genetic divergence in growth patterns among new populations of salmon and discuss the implications of this evolution to broader divergence in their overall life history patterns.

In order to assess genetic divergence, we compared juvenile growth patterns under common rearing for two New Zealand populations of chinook salmon (*Oncorhynchus tshawytscha*), the Glenariffe Stream and Poulter River populations. These two populations were formed by straying following initial

introduction of the species to another river system in the early 1900s, and other studies indicate that some gene flow persists among rivers (e.g., Quinn et al., 1996). In the wild, peak spawning in the Poulter River occurs 2-3 weeks later than in Glenariffe Stream, and scale patterns indicate that the majority of Poulter salmon migrate to sea after spending a full year in freshwater (i.e., “stream-type”), whereas the majority of Glenariffe fish migrate to sea in their first year (i.e., “ocean-type”). Differences in spawning date and subsequent hatching and emergence times, may have significant implications for subsequent growth opportunities (in the wild or hatchery). Thus, in addition to comparing growth patterns for fish spawned on a common date, we also quantified the influence of



spawning time on growth within populations.

We established four groups of full-sib families of Glenariffe or Poulter origin in May (autumn) 1997. The four groups corresponded to peak spawning in Glenariffe Stream (1 May – 14 families), late spawning in Glenariffe Stream and peak spawning in the Poulter River (18 May – 14 families for each population), and late spawning in the Poulter River (29 May - 7 families). Egg size was recorded for each family and they were in turn incubated, hatched and reared through two years under shared conditions. Over this period we quantified time to hatching, mean family weight on eight dates and the incidence of male maturation at two years of age. Rearing and trait measurements were similar to those of Kinnison et al. (1998a, b).

Neither egg size nor time to hatch differed between the two populations, but substantial differences in mean family weight were apparent 6 months after fertilization, and persisted throughout the study (Figure 1). Differences in growth rates from 12 to 24 months were observed but were relatively small, suggesting that most of the divergence in size and growth occurred during the first six months of life, though a growth rate inversion occurred in the second year resulting in slightly higher growth rates of Poulter fish. We also observed differences in mean weight for the same population spawned 11 to 17 days apart, but these did not persist beyond 7 months.

Slower growth in the population with more post-yearling migrants is consistent with life history patterns for “stream-“ and “ocean-type” chinook populations in their natural range (Taylor, 1990). This pattern also fits with expectations for selection on growth rate when 1) appreciated growth determines whether individuals smolt (Thorpe, 1989), and 2) subsequent survival is size or timing dependent (e.g., salinity tolerance: Kinnison et al., 1998b). For example, in a growth-limited environment genetically fast-growing fish may smolt in their first year but have low fitness due to their relatively small size, thus favoring genetically slower growing fish that smolt later. Divergence in growth likely contributes to other aspects of divergence among populations due to genetic and developmental correlations. Significantly more Glenariffe males matured at age 2 than Poulter males, consistent with higher growth promoting a higher incidence of maturation within and among experimental groups (Figure 2).

Our results provide evidence of evolutionary divergence in growth patterns between partially isolated salmon populations over c. 30 generations since their initial colonization. We contend that these genetic differences are due to the interaction between genetic and environmental influences on growth potential when development and survival are growth dependent. Divergence in growth

also contributes to phenotypic divergence in other characters (e.g., incidence of juvenile migration types and adult maturation in a given season) and may thus represent a pivotal trait in shaping initial, and perhaps long-term, life history patterns among populations.

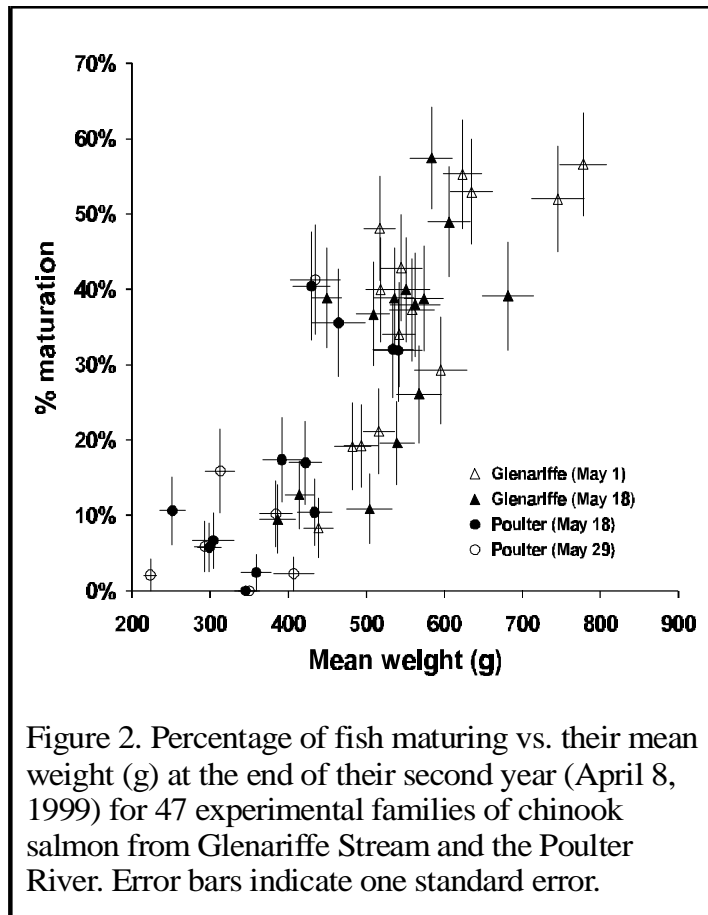


Figure 2. Percentage of fish maturing vs. their mean weight (g) at the end of their second year (April 8, 1999) for 47 experimental families of chinook salmon from Glenariffe Stream and the Poulter River. Error bars indicate one standard error.

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**NATURAL SELECTION ON JUVENILE BODY SIZE
IN AN ATLANTIC SALMON RESTORATION PROJECT**

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EXTENDED ABSTRACT ONLY – DO NOT CITE

Transplants of non-native fish are often used when attempting to reintroduce salmon into river systems from which they have been extirpated. Immediate success in restoration efforts is rarely achieved, in part because introduced fish are not well adapted to the new system. When maladaptation is strong, the introduced population should be subject to strong selection for traits that improve survival in the new environment. Our goal was to quantify the strength and form of natural selection acting on juvenile body length and mass in an Atlantic salmon population recently introduced to the Connecticut River basin, Massachusetts.

Un-fed fry (progeny of wild adults returning to the Connecticut River) were stocked into a 1 km section of the Westbrook, a Connecticut River tributary, in

spring 1996, 1997, and 1998. All fish in the section were collected by electroshocking and night-seining during the summer of their stocking year, measured for length and mass, and PIT-tagged. At monthly (summer) or tri-monthly (winter) intervals thereafter, all fish were recaptured and measured for length and mass. A smolt trap was used to collect fish leaving the section each spring. Additional information on the study is provided by Letcher et al. (this volume).

We analyzed selection on body length and mass over three-month intervals, including two winters and two summers. For each fish captured at the start of each interval, we determined whether it survived to the end of the interval (captured in the ending sample, or any sample thereafter) or died before the end of the interval (not captured in the ending sample, or thereafter). Fish that matured as parr were excluded from analyses.

Body length and mass (cube-root) were standardized (mean = 0 and SD = 1), and relative fitness was calculated by dividing each individual's absolute fitness (survived = 0, died = 1) by average absolute fitness during an interval. Selection was quantified using Lande and Arnold's (1983) linear regression methods and visualized using Schluter's (1988) cubic spline analysis.

Linear selection differentials represent combined effects of direct and indirect (i.e., total) selection acting to increase (when positive) or decrease (when negative) mean trait value. Linear differentials can be interpreted as the change in mean trait value owing to selection. Non-linear (*quadratic*) selection *differentials* represent total selection acting to increase (when positive) or decrease (when negative) trait variance. *Linear selection gradients* represent direct effects of selection acting to increase (when positive) or decrease (when negative) mean trait value. Gradients can be interpreted as the change in relative fitness with a given change in the trait, holding effects of other traits constant. Non-linear (*quadratic*) selection *gradients* represent direct effects of selection acting to increase (when positive) or decrease (when negative) trait variance. Brodie et al. (1995) further describes these measures of selection.

The strength and direction of selection on body length and mass varied between seasons (summer, winter), among cohorts (1996, 1997, 1998), and between age classes (1+, 2+). The only consistent pattern for total effects of selection (i.e., differentials and splines) was that larger individuals did not survive better than smaller individuals during the winter (Table 1; Fig. 1). Some interesting patterns were evident when considering direct effects of selection (i.e.,

gradients, which hold effects of the other trait constant). In most cases, gradients for length and mass were of opposite sign (Table 1), indicating that either longer/lighter or shorter/heavier individuals survived at higher rates. The most striking pattern was that length gradients were positive and mass gradients negative for all four samples of 1+ fish (highly significant during summers). This result indicates that longer/lighter fish survived at higher rates during their second year of life. Stabilizing selection acted on length and mass of 1+ fish during summers (highly significant in 1996). When differentials and gradients were non-significant, it was because of small effect sizes rather than small sample sizes (Table 1).

In the future, we intend to add data for additional stocking years, examine selection on growth rate, and evaluate likely evolutionary responses in the population. Assuming a heritability of juvenile body length of 0.11 and mass of 0.13 with a genetic correlation of 0.98 (Gjedrem, 1983; Jónasson, 1993), and considering only selection during summers (Table 1), evolutionary responses predicted by equation 5.14 in Roff (1997) are slight per-generation decreases in length (0.008 SD) and mass (0.010 SD). Quantifying natural selection and the genetic basis for phenotypic traits allows prediction of evolutionary responses during restoration. This predictive ability may facilitate consideration of alternative restoration strategies, and suggest time frames needed for recovery.

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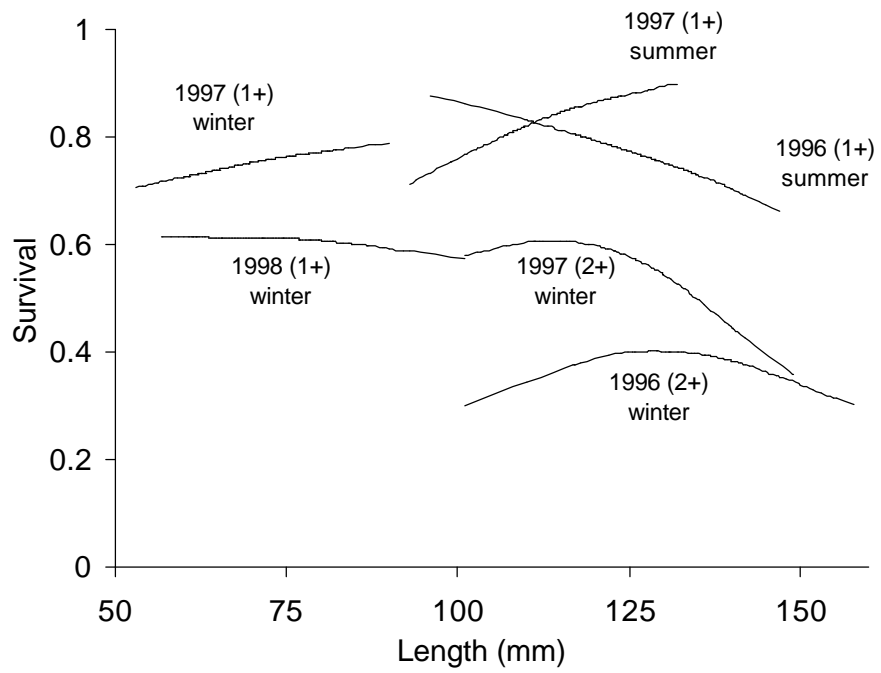
Acknowledgements

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Table 1. Results of tests for selection on body length and mass, including total selection (differentials) and direct selection (gradients), as well as directional selection (linear) and stabilizing or disruptive selection (quadratic). Positive linear differentials and gradients indicate directional selection for larger trait values. Negative quadratic differentials and gradients indicate stabilizing selection (a reduction of trait variance). ^a $P < 0.10$, ^b $P < 0.05$, ^c $P < 0.01$, ^d $P < 0.001$

Stock year	Winter				Summer	
	1997	1998	1996	1997	1996	1997
Fish age	1+	1+	2+	2+	1+	1+
Start day	Dec 10	Dec 01	Dec 10	Dec 01	Jun 17	Jun 22
End day	Mar 17	Mar 16	Mar 17	Mar 16	Sept 23	Sept 10
Starting N	231	748	121	96	139	78
Survival (%)	67.1	61.0	38.8	57.3	64.7	70.5
	<u>Linear selection differentials</u>					
Length	-0.106	-0.010	-0.070	-0.109	-0.023	0.082
Mass	0.046	-0.015	-0.081	-0.109	-0.066	0.025
	<u>Linear selection gradients</u>					
Length	0.331	0.141	-0.931 ^a	0.023	0.835 ^d	1.627 ^d
Mass	-0.327	-0.153	0.907 ^a	-0.133	-0.881 ^d	-1.574 ^d
	<u>Quadratic selection differentials</u>					
Length	-0.015	-0.041	-0.116	-0.177	-0.044	-0.035
Mass	-0.037	-0.043	-0.101	-0.216	-0.013	-0.050
	<u>Quadratic selection gradients</u>					
Length	-0.908	0.348	-0.166	-0.854	-4.894 ^c	-1.576
Mass	-1.760	0.266	0.054 ^b	-2.154	-4.110 ^b	-1.776

Figure 1. Non-parametric cubic splines illustrating the form of total selection acting on body length in juvenile Atlantic salmon.



**THE CONSEQUENCES OF VARIABLE TIME
OF SMOLT MIGRATION OF ATLANTIC SALMON
IN NORTH ICELAND**

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Abstract

In Iceland environmental conditions of salmon smolts vary considerably with respect to geography. In general conditions show greater annual variation in the N and NE than in the S and SW and this has been shown to affect the life history of the fish. During the last decade, studies have been conducted in three index rivers; River Ellidaar in the SW, River Midfjardara in the N and River Vesturdalsa in the NE. The smolt migration in two northern rivers was very variable in time, compared to the smolt run in R. Ellidaar. The migration time in the north ranges from the middle of June to early August.

There was significant correlation between water temperature in June and mean migration time in R. Vesturdalsa. In cold summers smolt migration was delayed. As a consequence of this delay the smolt reached larger size, and some part of the run postponed migration, resulting in a higher mean smolt age the following year. In 1998 the smolt run in R. Vesturdalsa was bimodal, with peaks in early July and in early August. Noticeably, the observed return rate was higher for the August smolts than for the July smolts.

It is hypothesized that these differences in migration time reflect local adaptations to different environments in the south and the north, respectively. The data suggest that salmon stocks in the northern rivers have adapted to annually fluctuating environments by greater flexibility in mechanisms that control smolt migration.

Synopsis

The time of the smolt run was different in the three rivers in the study. The smolt usually migrated a month earlier in the SW-Iceland than in the N and the NE (Figure 1). In River Ellidaar (SW) most of the smolt migrated to sea during the latter part of May and the first days of June. In the northern rivers this was later and more variable from year to year. In River Nupsa (N) the smolt run commenced earliest in 1991 on the 9th of June, but latest in 1989 on the 25th of June (Figure 1). In River Vesturdalsa (NE) the run commenced earliest in 1992 on the 8th of June, but latest in 1995 on the 26th of July.

The smolt run began as snowmelt was over and temperatures started to rise in the rivers. Environmental factors that stimulate the smolt run differ between regions. In the SW rain occurs as warm southerly winds are blowing. In River Ellidaar the discharges increase during such weather and the smolt migrate downstream in turbid and relatively warm river water. During southerly winds it is dry and sunny in the north. In such a conditions the river water temperatures increase there and the smolt migrate downstream. In River Vesturdalsa there is a strong ($R^2 = 0.80$), highly significant relationship ($p = 0.0012$) between the river water temperature and the mean time of the smolt run.

In 1998 the smolt run occurred during two time periods, one in early July, the other in early August (Figure 1). The period in between, was cold and the smolt migration was depressed. As it grew warm again in the beginning of August the smolt run started again. Apparently, the smolt did not desmolt during the cold period. In 1993 and 1994 no smolt were caught despite of usual effort. By then it was not believed that smolt would migrate as late as was later observed. It is likely that in those cold years the smolt run was late in the summer.

The consequences of the delayed smolt runs are that the smolt were larger in those years as they grew while waiting for environmental stimuli (higher temperature) to migrate to sea. Some part of the run postponed their migration until next year. This was resulted in older smolt the following year as can clearly be seen in 1995 (Figure 2b). In the colder summers when the smolt run occurs late there are also fewer smolt migrating (Figure 3). These changes were not as pronounced in the south as seen in River Ellidaar (Figure 2b).

Ocean conditions greatly affect the climatic condition in Iceland. The ocean condition in the Iceland sea north of the country is more variable from year to

year than in the sea off the coasts of S and W Iceland. This is reflected in the climate in different regions of the island. The climate is more variable in the north than in the south of Iceland.

The timing of the smolt migration seems to be crucial for the survival of the smolt. The temperature in the northern rivers is the key indicator for the smolts on how oceanic conditions are. The variable and sometimes late migration time of the smolt in north Iceland is presumably a local adaptation to the fluctuating environmental conditions there. An example of this is that the latter group of smolt in River Vesturdalsa in 1998 returned at a higher rate than the earlier group.

Conclusions

- Smolt migration is on the average month earlier in SW- Iceland than in N and NE.
- In SW smolt migration is stimulated by floods but in the N and NE the key stimuli is water temperature.
- Migration time is very variable from year to year in the N and NE and in cold summers the smolt run is delayed even to early August.
- As a consequence of delayed migration the smolt reach larger size, and some part of the run postpone migration, resulting in a higher mean age the following year.
- It is hypothesized that these differences in migration time reflect local adaptations to different environments in the S and N Iceland.

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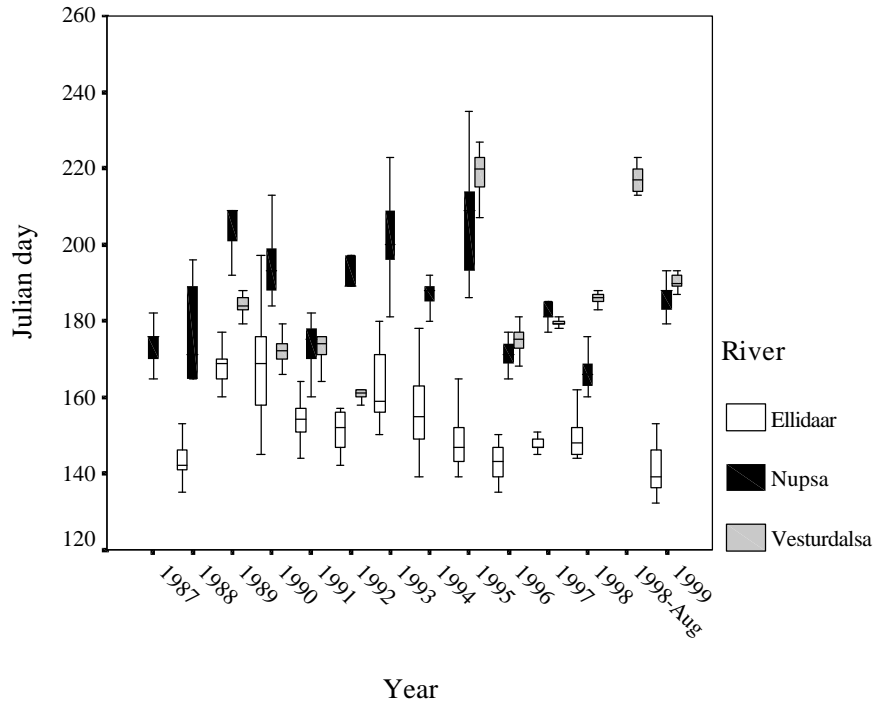


Figure 1. Smolt migration time in each of the three rivers. In River Vesturdalsa the migration was divided in two periods in 1998.

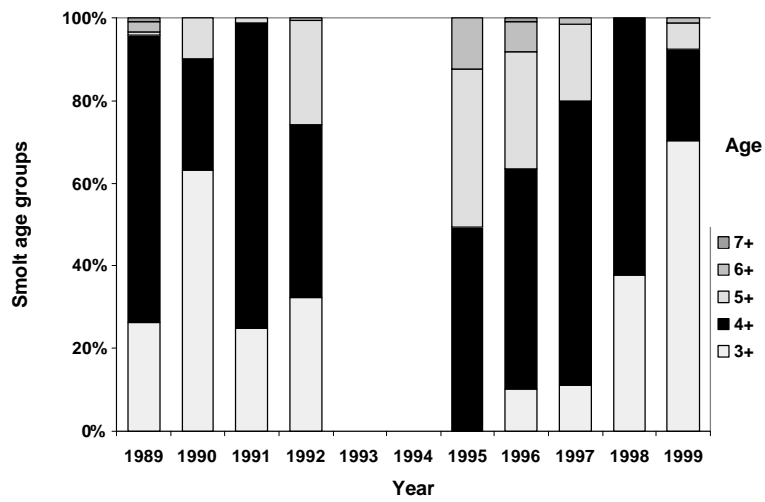


Figure 2a. Smolt age in River Vesturdalsa NE-Iceland.

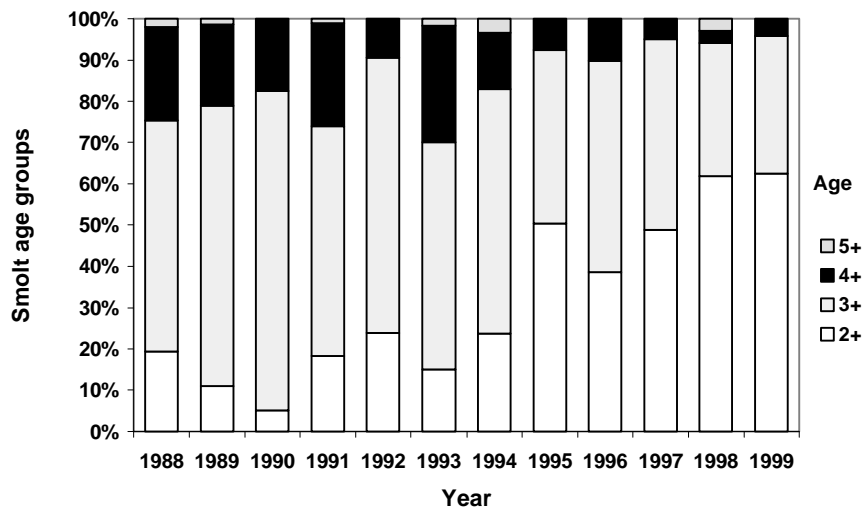


Figure 2b. Smolt age in River Ellidaar in SW-Iceland.

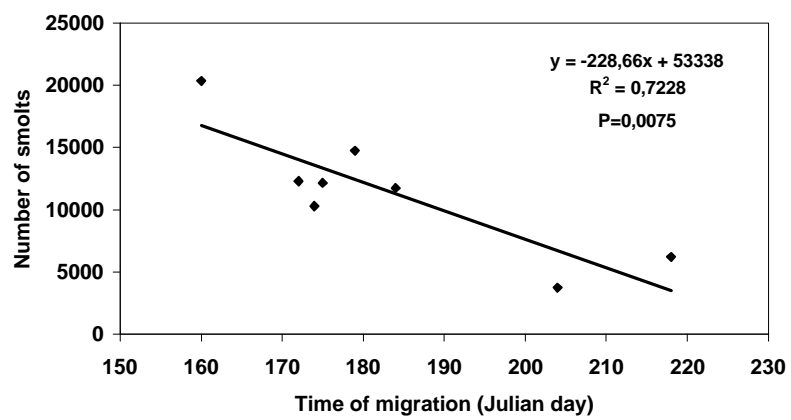


Figure 3. Connection between migration time and number of smolts in River Vesturdalsa.

**AN AGE AND GROWTH COMPARISON
BETWEEN JUVENILE ATLANTIC SALMON (*Salmo salar*)
'MOVERS' AND 'STAYERS'
IN THE PONOI RIVER SYSTEM, NORTHERN RUSSIA**

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EXTENDED ABSTRACT ONLY – DO NOT CITE

Movements of juvenile Atlantic salmon (*Salmo salar*) between mainstem spawning sites and small tributaries, where salmon do not spawn, were monitored in the Ponoï River (67° N, 40° E), Russia from June - September 1998. Atlantic salmon parr have traditionally been viewed as sedentary territory holders (Gerking, 1959), however, it has been well established that a small fraction of a population may become mobile (the 'movers') prior to smolting. Movers have been found to leave their natal sites (the 'stayers') to take up residence in lakes, estuaries and small streams; they also tend to be the older members from parr populations and contribute significantly to annual smolt production (see Bardonnet and Baglinière, 2000). Movers, therefore, leave the natal area, not as a result of intraspecific competition, but because needs are not met, or they are undertaking an ontogenetic niche shift.

In contrast to many rivers where Atlantic salmon are native, the Ponoï is not experiencing the global decline in adult returns. In fact, adult returns have been

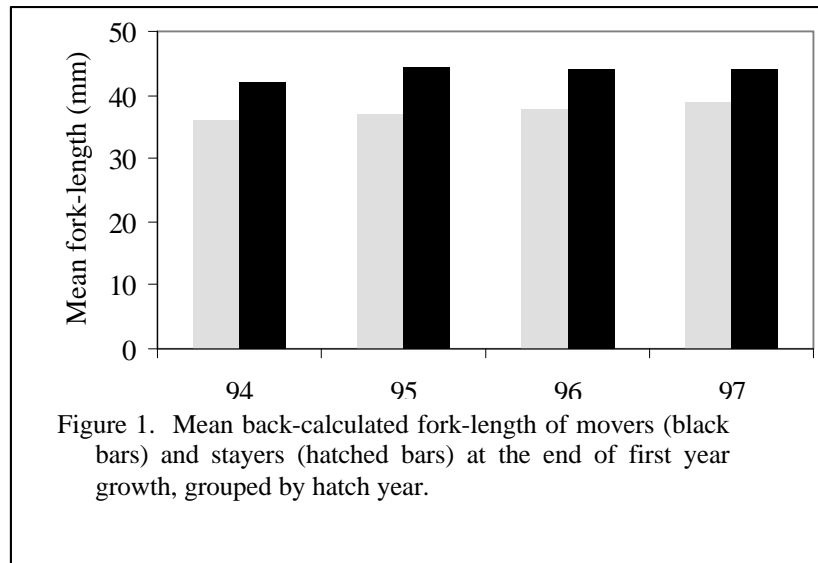
increasing due in part to a conservation effort initiated in 1994. As a result, juvenile salmon densities within natal sites have increased dramatically over a short period of time. The current study was conducted to determine if the ontogenetic niche shift model, as an explanation for juvenile salmon release of holding behaviour, also holds for a river system where parr densities increase rapidly.

Trap-fences were used to monitor parr movements between the mainstem and three small, non-spawning tributaries (< 3 m wide), where no adult salmon spawn, that feed directly to the mainstem. Brown trout (*Salmo trutta*) were the primary residents of these streams and are a known predator of salmon parr. Fences were checked daily and captured salmon parr were measured, movement direction was noted and scale samples were collected. Scale samples from the stayers were obtained during autumn electrofishing surveys. Age and growth information for individual parr was obtained by measuring distance from the scale focus to the first annulus and employing the scale-proportional method of back-calculation to estimate fork-length of movers and stayers at the end of first year growth (Francis, 1990).

Streamward migration occurred sporadically from June through September, but intensified during the last two weeks of July when water temperatures exceeded 10 °C. Upstream movers were predominantly 1+. After leaving the mainstem, movers remained upstream in Falls and Clough Creek and no return to the mainstem occurred, indicating this movement was not random. Parr that moved upstream prior to the 1998 season did leave these two streams. Movers also remained upstream after moving into the Little Ryabaga, but a mass return to the mainstem occurred during the first week of September. 62% of the returnees were 1+ parr that had moved upstream earlier in July. Few older parr and no smolts were among Clough Creek and Little Ryabaga emigrants, while parr leaving Falls Creek were older than those entering. Clough Creek was found to be a spawning site for adult salmon, as young-of-the-year salmon were among its emigrants. When back-calculated end of first year fork-lengths were compared, movers were larger than the stayers, for all hatch years, although both groups spent their first year in the mainstem (Fig. 1). Mean fork-length of 1+ movers at the end of the 1998 growing season was not different from the stayers ($p>0.05$) and movers older than 1+ were smaller compared to mainstem parr ($p>0.05$, Fig. 2), although they were initially larger at the end of their 1st year.

Although parr leaving the mainstem were the largest of their cohort, they were also the youngest from the mainstem population (>80% of Ponoï parr smolt at

3+ and 4+) and their growth decreased once in the tributaries, indicating movement is a result of intraspecific competition within natal sites. Decreased growth of the movers was not expected because the tributaries had suitable substrate, fewer predator species and greater insect drift than the mainstem. Tributary temperatures were cooler than the mainstem, yet remained within the range required for growth. Although Cunjak and Gibson (1986) found little evidence for interspecific competition between salmon parr and brown trout, small stream size may prevent sufficient habitat segregation based the two species' preferences and cause high competition for resources. The ontogenetic niche shift model, therefore, does not universally apply to salmon parr release of holding behaviour; the cause for this behaviour must be determined at a riverine scale.



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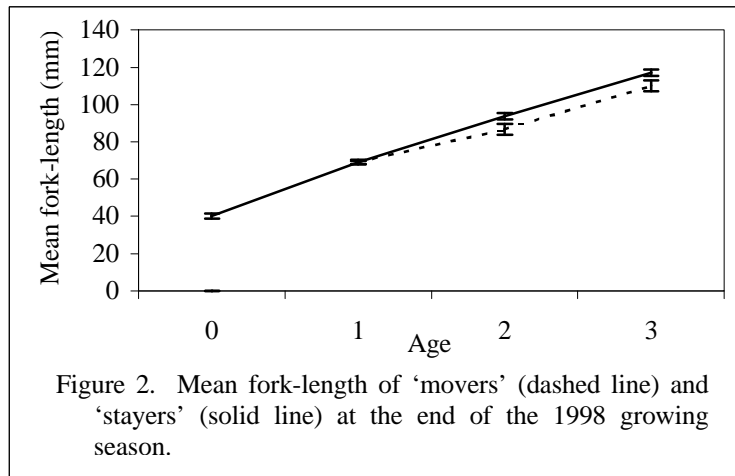
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**EFFECT OF SEAWATER ENTRANCE
ON FEEDING AND GROWTH OF STEELHEAD SMOLTS**

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EXTENDED ABSTRACT ONLY - DO NOT CITE

Anadromous salmonid smolts under cultivation must often be able to tolerate abrupt transfer from fresh water (FW) to seawater (SW) and then continue growth (Clarke et al. 1996). In the present experiment we wanted to test how long a period is needed for steelhead (*Oncorhynchus mykiss*) smolts to fully adjust to SW in terms of feed intake and growth, and whether they can adapt to SW if transferred as pre- or post-smolts. Our previous experiment conducted in 1999 to monitor short term changes in feed intake indicated that steelhead smolts eat significantly less after a 96 h SW exposure than fish in FW, even during the best smolting time.

Steelhead smolts were tested for their SW adaptation in terms of feed intake, growth and osmoregulatory ability. Three separate experiments were carried out at four-week intervals during the spring 2000. Based on the results of the experiment in 1999, the starting dates designated for the three experiments were 12 April, 10 May and 7 June in order to obtain data from pre-smolts, smolts and post-smolts. Three replicated tanks were used for fish in FW as well as in

flowing SW, each containing 50 individuals at the beginning. After the start (i.e. exposure to SW) of each experiment, measurements were made at weeks 1, 2, 4 and 6 for feed intake, growth, plasma sodium and potassium, muscle water and hemoglobin. Fish were also fed a diet containing X-ray dense particles each of the four sampling days; 10 individuals were then collected from each tank and killed with an overdose of MS-222. Food intake was estimated by X-radiography (Jobling, 1993) and individual growth rates for PIT-tagged fish in each experiment were determined. Possible relationships between feed intake and physiological data were evaluated.

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**TESTING THE PREDICTIONS FROM A SPATIALLY-EXPLICIT
BIOENERGETIC MODEL FOR AGE-0 ATLANTIC SALMON
USING FLUXES OF TRACE ELEMENTS**

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EXTENDED ABSTRACT ONLY - DO NOT CITE

Our inability to directly measure the consumption rates of fish in the field generally precludes validation of models that relate foraging opportunity to growth and survival. In spite of this, population models implicate the importance of food and habitat availability in determining growth and survival for many juvenile fish (Elliott 1989, Nislow et al. 1999). Consumption and growth rates of stream-dwelling salmonids are frequently modeled as a function of prey abundance and hydrologic conditions (Hughes and Dill 1990, Hill and Grossman 1993). In the case of juvenile Atlantic salmon, spatially-explicit bioenergetic models implicate the importance of early-season foraging habitat for salmon fry growth and survival (Nislow et al. 2000). However, exactly how these factors interact to determine prey consumption, growth and survival under a range of habitat conditions is often complex and difficult to ascertain without reliable field-based techniques for measuring consumption rates. Building upon earlier models of radiocaesium accumulation in fish (Forseth et al. 1992, Rowan and Rasmussen 1996), the goal of this study was to use the turnover of naturally occurring stable Cs to compare *in situ* consumption rates of stocked Atlantic salmon (*Salmo salar*) fry in tributaries of the Connecticut River. We related these consumption measurements to 1) predictions from a bioenergetics model

over the same time period and 2) growth and survival of age-0 salmon at these sites.

Atlantic salmon were stocked as unfed fry into tributaries of the West and White River Vermont, USA in early May 1991 and 1992. In six sites fish were destructively sampled at approximately two-week intervals during the growing season. To calibrate bioenergetic models, habitat and macroinvertebrate measurements were taken both at salmon feeding locations as well as at random sites along the stream bed. Gut contents were separated for diet analysis. For trace element analysis, fish and insect samples were digested in a microwave under class 100 ultra-clean laboratory conditions. To parameterize the trace metal consumption model, we analyzed fish, common prey taxa and stomach contents for Cs, Rb and K using high-resolution inductively-coupled plasma mass spectrometry.

Field-based estimates for assimilation efficiencies showed no differences among sites, however interspecific differences in the Cs concentrations of common prey taxa emphasize the importance of quantifying fish diet composition before applying this model. Our estimates of early season (2 to 3 weeks) consumption rates using Cs were significantly lower than those of the spatially-explicit bioenergetics model. However, the relative rankings of sites were similar using both methods (Fig.1). In both cases, significant differences in consumption rates across sites during the early season were correlated with underyearling survival. During the late season (10 to 12 weeks) Cs-based consumption rates compared more favorably with model predictions. Consistent with model predictions, late season consumption rates were not correlated with survival. Our results support a hypothesized resource and habitat limitation during the early season. Specifically, high variability in consumption rates and decoupling of growth and consumption when fish are less than 6 weeks old suggests that this a challenging time for fry when habitats are limiting and energetic demands are high.

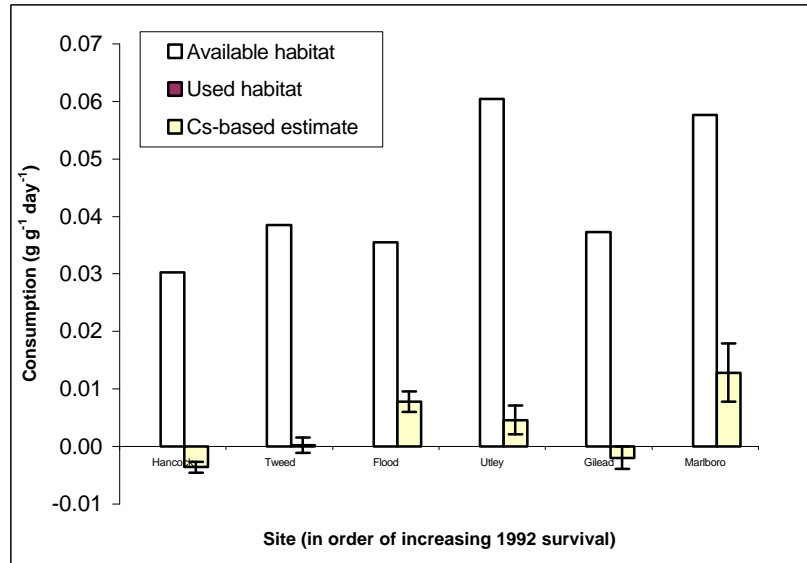


Figure 1. Early season consumption rates (two to three weeks post stocking of Atlantic salmon fry in six tributaries of the Connecticut River estimated by 1) a spatially-explicit bioenergetic model and 2) a technique that employs the passive turnover of trace metal (Cs) turnover in tissues. The bioenergetics model makes separate predictions for available habitat (random sampling points in the stream) and used habitat (actual foraging locations of salmon fry).

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