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Food availability in spring affects smolting in brown trout (*Salmo trutta*).

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Draft

1 Abstract

2 Prior to out-migration, salmonid fish typically undergo physiological and morphological
3 changes - a process known as smolting. This study indicates that smolting in brown trout
4 (*Salmo trutta*) is affected by feeding conditions in spring immediately prior to out-migration.
5 This conclusion was reached after experimentally testing the effect of seasonal variation in
6 food availability on smolt status in the spring. A migratory strain of trout was administered
7 either high (H) or low (L) food rations in the autumn, winter or spring prior to release in the
8 spring. Whilst fish growth or condition could be affected in any season, it was spring
9 rationing that reduced growth and growth-related variables and which caused increased
10 smolting. Our result supports the idea that smoltification and the decision to migrate is
11 affected by spring food availability regardless of conditions in the previous autumn or winter.

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14 Key words: food rationing, smolt, migration, growth

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24 Introduction

25 Salmonid migrations are some of the best described and understood in the animal kingdom.
26 An initial out-migration from where an individual is spawned is accompanied by a return
27 migration to the place of origin for subsequent spawning. From an evolutionary perspective,
28 migration in salmonids occurs when the cost is less than the benefit of migrating (Gross et al.
29 1988, Bohlin et al. 2001). The cost is related to energy expenditure and mortality, and the
30 benefit is measured in reproductive fitness and growth (Jonsson and Jonsson 1993). A
31 “conditional strategy” has been proposed to operate in salmonid migratory decision making
32 (Metcalf et al. 1988, Wysujack et al. 2009, Morita et al. 2014). According to the conditional
33 strategy, the threshold switch-point or liability for migration is related to growth or some
34 variable correlated with growth. Another way to view migration is to describe it as a
35 probabilistic reaction norm (Heino et al. 2002, Kuparinen et al. 2008).

36 Other indices of fish state related to growth and implicated in migratory decision making are
37 size, metabolic rate, condition factor, lipid content and energetic state of the fish (Jonsson and
38 Jonsson 1993, Forseth et al. 1999, Morgan et al. 2002, Boel et al. 2014). These traits are
39 influenced by biotic (i.e. food) and abiotic (temperature) environmental factors (Elliott 1994,
40 Railsback and Rose 1999), which determine if migration will be undertaken. A compelling
41 biotic environmental factor linked to migratory decision making in salmonids is food
42 availability, where the number of migrants can be increased by reducing the amount of food
43 fish receive (Keeley 2001, Wysujack et al. 2009, Vainikka et al. 2012).

44 Many studies exploring the link between food and migration in salmonids have used brown
45 trout (*Salmo trutta*), which is plastic in its life history tactics, exhibiting the full range of
46 migratory behaviours described for salmonids (Klemetsen et al. 2003). Moreover, the
47 decision to migrate in brown trout has been shown to be influenced by environmental
48 conditions (Olsson et al. 2006). In studies using brown trout, reducing the amount of food has

49 been shown to increase the number of migratory fish (Wysujack et al. 2009, Bergman et al.
50 2013). Most studies have only examined the effect of constant starvation or satiation on
51 migration (see for example Wilzbach 1985, Keeley 2001, Imre et al. 2004, Wysujack et al.
52 2009) over a fixed period of time. An exception to this is the study of Pirhonen and Forsman
53 (1998) in which fish were given different food rations from May – November and then full
54 rations until spring when smolting behaviour was assessed. Studies involving starvation
55 usually show that starvation affects migration, but cannot identify if starvation has different
56 effects on the fish's migratory response, dependent on when and how long the starvation
57 occurs. The closely related Atlantic salmon (*Salmo salar*) migrate in spring, based on their
58 state ~ 9 months before the migratory event (Metcalf et al. 1986, 1988). If a predetermined
59 “threshold” state is reached soon after midsummer, then salmon migrate the following spring.
60 If not, they delay migratory decision making for another year. More recently, Vainikka et al.
61 (2012) have presented other results, showing that winter and spring rationing prior to
62 outmigration can increase smoltification and migration tendency in Atlantic salmon. It is
63 unclear when brown trout decide whether or not to migrate.

64

65 In this study we investigate how food rationing during autumn, winter or spring affects brown
66 trout's state (size, condition, lipid content) and migratory readiness (indicated by smolting).
67 Our hypothesis was that a greater proportion of starved fish would smolt than fish fed full
68 rations. More specifically, the number of fish smolting should increase in spring when food
69 was restricted as compared to fish fed full rations - regardless of previous food availability in
70 autumn or winter. This should also be reflected by differences in fish state, with spring-
71 starved fish displaying lower growth, condition and lipid reserves than fish fed to satiation.

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73 **Methods**74 **Ethical statement**

75 The protocol was approved by the Gothenburg Animal Review Board (Permit number 249-
76 2010). The study was conducted in strict accordance with the ethical guidelines stated in the
77 permit. The fish used in the study were hatched and reared at the Gammelkroppa fish
78 hatchery, north of Filipstad, Sweden. Fish were anaesthetized with tricaine mesylate prior to
79 measuring, and animals sacrificed for fat content analysis were euthanised using a high dose
80 of tricaine mesylate.

81 **Study area**

82 The experiment took place from 29 September 2010 – 18 May 2011 at Brattfors fish farm,
83 mid-western Sweden (N 59° 67'; E 14° 02'), using hatchery brown trout raised by
84 Gammelkroppa fish farm. Prior to the experiment, fish were reared at high densities in
85 circular tanks outdoors (50 m squared; water depth 120 cm). Water flow was continuous and
86 supplied by a nearby lake (Yngen). Fish were fed commercial pellet feed (Aller-Aqua,
87 Denmark) at rations designed for maximum growth. The trout originated from a migratory
88 breeding stock from the nearby River Klarälven. The Klarälven trout are landlocked and
89 historically migrated between Lake Vänern (5650 km²) and their spawning grounds, up to
90 400 km upstream. In the 1900s hydropower development blocked migration in all but the
91 lower 25 km of the river (Norrgård 2011). To compensate, the Gammelkroppa fish farm
92 operates an annual restocking programme for brown trout and Atlantic salmon in the River
93 Klarälven. Klarälven trout raised for restocking typically smolt, and are released in their 3rd
94 spring (i.e. aged 2+).

95 A total of 3840 fish, aged 1+, were transferred in oxygenated tanks from the nearby
96 Gammelkroppa fish farm and randomly placed into 24 1.25 x 1.25 m tanks (160 ind. tank⁻¹)
97 on 21 September 2010. An additional 340 replacements for fish that died were split between 2
98 tanks. Water circulation was continuous and supplied by an adjacent stream. The tanks were
99 indoors but windows and skylights meant that fish were reared under ambient photoperiod.

100 **Experimental design and initial measurements**

101 Initial fish fork length and mass were measured for all fish in 4 randomly selected tanks ($n =$
102 640). Condition factor was calculated by regressing weight against length and using the
103 residuals to indicate condition variation. A subsample ($n = 25$, total $n = 500$) from the
104 remaining 20 tanks were measured to ensure no significant differences in length or mass
105 occurred among tanks. The number of precociously mature males recorded during measuring
106 was only ~5%, and we did not exclude them from the experiment because their occurrence
107 was randomly distributed among tanks. Treatments were randomly assigned to the hatchery
108 tanks. Fish were subjected to 1 of 6 different food treatments, each replicated 4 times.
109 Treatments included a high ration control (fish fed high rations for the entire experiment), a
110 low ration control (fish starved for the duration of the experiment) and four other treatments
111 which involved starving fish in autumn, winter or spring (Table 1). The amount of food
112 administered to the fish was adjusted based on water temperature and the biomass of fish in
113 each tank. High food rations were chosen according to hatchery guidelines for achieving
114 maximum fish growth. Low food rations were 30% of high rations (see Table 1 for approx.
115 rations fed to fish). Fish were fed commercial food pellets (Aller-Aqua, Denmark)
116 administered by automated dispensers. Food was dispensed to low ration treatments for 2
117 hours in the morning and 2 hours in the evening. High ration treatments received food for 3
118 hours in the morning and 3 hours in the evening. Temperature was recorded hourly using 4

119 temperature loggers (HOBO) placed in 4 separate tanks. Mean daily temperatures were
120 calculated by averaging all daily readings.

121 **Sampling regime**

122 Each sampling event occurred prior to a change in feeding regime. As such, fish were
123 measured at the beginning of the experiment (September), at the end of autumn (December),
124 the end of winter (March) and the end of spring (May). At each sampling event the length and
125 mass of 50 haphazardly selected individuals from each tank were measured.

126 Smolt state was recorded for individuals in May (late April through to May is the regular
127 smolting season for trout in Klarälven). Smolt state was judged on a three point scale
128 according to Tanguy et al. (1994). Morphological metrics (silvering, loss of pigment from the
129 fins, loss of parr marks, and prominent lateral line) have been shown to be correlated with,
130 and in some cases more reliable than, physiological measures (such as gill NA^+ and K^+
131 ATPase and saltwater tolerance challenge tests) in predicting migration in trout (Debowski et
132 al. 1999). Furthermore, Atlantic salmon in the Klarälven system are known to change both
133 morphologically and physiologically prior to outmigration (Norrgård et al. 2014a, Norrgård
134 et al. 2014b) and fully-silvered fish migrate faster and have a greater migration success than
135 fish with less developed morphological smolt characteristics (Norrgård et al. 2014b). We
136 assumed fish that showed at least two clear signs of smoltification (two of the following:
137 silvering and loss of parr marks, prominent lateral line, loss of pigment from the fins) were in
138 the process of developing full smoltification (pre-smolt). As such, fish displaying pre-smolt
139 or smolt morphologies (categories 2 and 3) were classified as smolts. Fish displaying parr
140 morphologies (category 1) were classified as residents.

141

142 A subsample of fish was sacrificed for lipid content analysis; we used mid-infrared
143 transmission spectroscopy (Elvingson and Sjaunja 1992) to measure lipid content and

determine how starvation affected the lipid content of fish. This was done at the start ($n = 20$ haphazardly selected individuals) and at the end of each season (2 or 3 individuals sampled haphazardly from each tank; $n = 10$ individuals per treatment per sample event). In addition to lipid content analysis, we recorded fish fork length, mass and sex (after inspection of gonads).

Statistical analysis

All statistical analysis and graphing were carried out using the “ez” (Lawrence 2013), “scales” (Wickham 2014), “lme4” (Bates et al. 2013), “arm” (Gelman and Su 2014), “plotrix” (Lemon 2006), “gplots” (Warnes et al. 2015), “pbkrtest” (Halekoh and Højsgaard 2014) and “stats” packages in R version 3.1.1 (R Core Team 2014).

Growth, condition factor and fat content

To test for an overall effect of food treatment and time on fish length, mass, condition factor and fat content we performed Linear Mixed Effects Models (LMMs) on each response variable and time period, with tank ID as a random factor. Models were validated visually by plotting residuals against fitted values (homogeneity), QQ-plots and histograms of residuals (normality), and plotting residuals against explanatory variables (violating independence).

Proportion of smolts

Smolts were classified as those fish which were not clearly parr (smolts were fish that displayed any sign of smolting, i.e. with scores ≥ 2) and the proportion of smolts was analysed using Generalised Linear Mixed Effects Models (GLMMs). We analysed the proportion data using a logit-link function and binomial error structure. Our explanatory factors were starvation period (autumn, winter, spring), fish length at time of sampling (mm), and interactions between starvation period and fish length; tank nested within treatment were included as a random effects. Length was centred so that intercepts were meaningful

(Schielzeth 2010). Whilst temperature was the same for all treatments, and food availability controlled, we could not control for differences in individual growth rates, and it was for this reason we included length in the GLMM. Mass and condition factor were not included in the models because they are highly dependent on treatment (i.e. food availability). Lipid content was not included in the model because we only measured lipid content for a small subsample of fish ($n = 10$ per treatment for lipids, compared with $n = 200$ per treatment for measures of length). We began with the fullest model including all possible interaction terms. Using the “drop1” function with the chi-square test, we removed explanatory variables sequentially and compared the difference in model deviances to a chi-square distribution with the appropriate degrees of freedom. In all instances we tried to achieve the most parsimonious model. In cases where a simpler model was not significantly different from the fuller model (by checking AIC scores using the drop1 function, and using the “ANOVA” function to compare models), we chose the simpler.

Results

Length, weight, condition factor and fat content

No differences in fish length were found between treatments until May. In May fish length in treatments that were starved in spring were significantly lower than the high control ($T = -3.28, p < 0.01$; $T = -3.89, p < 0.01$; $T = -3.96, p < 0.01$ for treatments HHL, HLL and LLL respectively). Fish length in treatments LHH and LLH did not differ significantly from the high control (Figure 1).

Differences in fish mass were found between treatments in both March and May. In March fish mass was significantly lower in all treatments compared with the high control ($T = -3.22, p < 0.01$; $T = -2.23, p < 0.05$; $T = -2.50, p < 0.05$ for treatments HL, LH and LL respectively). In May fish mass was significantly lower in treatments HHL ($T = -6.41, p < 0.01$), HLL ($T = -7.77, p < 0.01$), LHH ($T = -2.43, p < 0.05$) and LLL ($T = -7.46, p < 0.01$) compared with the

high control. Fish mass in treatment LLH did not differ significantly from the high control in May (Figure 1).

Differences in fish condition factor were found between treatments in December, March and May. In December fish fed low food rations had a significantly lower condition than fish fed high rations ($T = -3.77, p < 0.01$). In March fish condition was significantly lower in treatments starved over winter compared with the high control ($T = -6.20, p < 0.01$; $T = -6.79, p < 0.01$ for treatments HL and LL respectively). Fish condition in treatment LH did not differ significantly from the high control. In May fish from all the treatments starved over spring had a significantly lower condition compared with the high control ($T = -9.15, p < 0.01$; $T = -11.30, p < 0.01$; $T = -10.26, p < 0.01$ for treatments HHL, HLL and LLL respectively). Fish condition in treatments LHH and LLH did not differ significantly from the high control (Figure 1).

Differences in fish lipid content were found between treatments in March and May. In March fish lipid content was significantly lower in treatments starved over winter compared with the high control ($T = -3.22, p < 0.01$; $T = -2.67, p < 0.01$; for treatments HL and LL respectively). In May fish from all the treatments starved over spring had a significantly lower condition compared with the high control ($T = -5.41, p < 0.01$; $T = -8.48, p < 0.01$; $T = -5.41, p < 0.01$ for treatments HHL, HLL and LLL respectively). Fish condition in treatments LHH and LLH did not differ significantly from the high control (Figure 1).

Proportion of smolts

The proportion of smolts in May was greater for the three treatments in which trout were starved over spring (93-95%) than for the high control treatment (79%). Treatment alone was not sufficient to predict whether or not a fish became a smolt. A series of GLMMs used to predict the proportion of smolts (S_m), based on starvation period (autumn, winter, spring), fish

length at time of sampling, and interactions between starvation period and fish length, were run and resulted in a best fit model containing the terms spring starved (S_s), length (L) and the interaction term $S_s L$.

$$S_m = S_s + L + S_s * L$$

Fish starved in autumn and winter were not significantly more likely to be smolts in spring, and both were also discarded from the best model according to AIC scores. Starvation in spring significantly increased the likelihood of smoltification ($z = 3.05$, $p < 0.01$; Table 2, Figure 2). Fish length had a significant effect on the proportion of smolts; longer fish were more likely to be classified as smolts ($z = 6.95$, $p < 0.01$; Figure 2), the spring starved * length interaction term was also significant; longer fish in spring starved treatments were more likely to be classified as smolts ($z = 2.28$, $p < 0.05$). Treatment had a negligible amount of variance and was discarded as a random variable from the best model.

Discussion

The present study indicates that spring food availability influences smolt status in brown trout. Recent studies have shown that food availability is one factor that influences whether brown trout becomes a migrant or not (Olsson et al. 2006, Wysujack et al. 2009). However, these studies did not investigate when the decision was made (sensu Metcalfe et al. 1986, 1988, Vainikka et al. 2012 for Atlantic salmon), just that food restrictions prior to migration increased the number of migrants in the population. Our study demonstrates that less food increases the probability of becoming a smolt, i.e. a migrant, but it also pinpoints that food availability during the spring is important.

Metcalfe et al. (1986, 1988) reported that Atlantic salmon decide whether or not to smolt soon after midsummer of the previous year, which differs from our result. It is difficult to know why the conclusions from our work and that of Metcalfe et al. (1986, 1988) differ.

Whilst they are different species, they share a near identical life history and their habitats often overlap. Both species demonstrate residency, migration or partial migration, though Atlantic salmon appear more predisposed to a migratory life history (Klemetsen et al. 2003, Jonsson and Jonsson 2011b). It is not unreasonable to assume that common environmental conditions cause migration across these species (Jonsson and Jonsson 2011b). One possible explanation is that the present work is performed in an inland system, whereas Metcalfe et al. (1986, 1988) studied anadromous fish. Another explanation may be because brown trout are more facultative than Atlantic salmon in their migratory response (Bohlin et al. 2001, Klemetsen et al. 2003). A meta-analysis of the effects of food rationing on out-migration in salmonids revealed contrasting migratory strategies in response to food limitation (D. A. Jones, G. P. Closs, M. Lagisz and S. Nakagawa unpublished). This meta-analysis revealed that some salmonid species such as Atlantic salmon do not readily increase out-migration in response to food limitation, whereas other species such as brown trout do. Smoltification in the present system appears to be more facultative and influenced by current food availability. In contrast to Metcalfe et al. (1986, 1988), and similar to our results on brown trout, Vainikka et al. (2012) found that there was a facultative element to smoltification and migration in Atlantic salmon. They found that a change in food rations in winter and spring prior to migration could affect smoltification and migratory speed. These variable findings underscore the complexity of migratory decision making and might be an indication of high inter- and intraspecies variability in migratory response to environmental conditions.

The relationship between growth, migration and maturation is complex. For more obligate migrators the conditional strategy states that if individuals attain a threshold value the previous year, migration may take place the following spring. However, maturation should be favoured over smolting when resource availability is high (Thorpe 1994, Thorpe and Metcalfe 1998). Indeed, Vainikka et al. (2012) showed that decreasing abundant food rations

in the hatchery could reduce maturation and increase migration in Atlantic salmon. Fish in our experiment had access to unlimited food resources prior to autumn, yet the number of mature fish was low (~5%). Also, food limitation in the autumn reduced mass and significantly reduced condition factor but did not affect the proportion of smolts the following spring.

Generally, fast growing fish are more likely to migrate (Acolas et al. 2012) than slow growing fish, although Jonsson (1985) and Ricker (1975) showed that both the fastest growing and the slowest growing fish (brown trout and sockeye salmon) smolt and fish with intermediate growth rates become sexually mature as parr instead (see also Fig. 5.9 in Jonsson and Jonsson (2011a)). Our study showed that it was not only fast growth that caused increased smoltification, but rather the combination of high growth and reduced rations in spring. A likely interpretation of this discrepancy is that under full rations, as in our experiment, individuals are in good condition, able to maintain growth, and thus fewer smolt (Jonsson and Jonsson 1993, Forseth et al. 1999).

That trout smolted even in the full ration treatments might indicate that not all individuals in these treatments were able to maintain growth. In general longer fish were more likely to be classified as smolts, regardless of treatment, which could indicate that larger individuals have a more difficult time maintaining growth. We also found that longer fish were more likely to become smolts, especially if the longer individuals were starved over spring, as indicated by our significant spring starved * length interaction in our GLMM. Such plasticity in the decision to migrate, based on food availability, can be described as a probabilistic reaction norm for migration, analogous to the situation described for maturation in white-spotted charr, *Salvelinus leucomaenis* (Morita et al. 2009). Thus, when food is abundant, fish with a lower growth rate presumably have little need to migrate to a resource-rich environment (lakes or the sea).

It is important to remember that our findings are the result of experiments on fish in a hatchery environment. As always, a level of caution is required before extrapolating these results to natural fish populations. However, we think the results are relevant given the importance of hatchery-derived restocking schemes. Also, it is most likely that in natural environments where competition is high, the effect of spring limitation would be felt more acutely, and its effect on smoltification could be greater.

The amount of food fish received affected indices of growth, condition factor and smolt status. Significant differences in fish condition were evident between high and low ration treatments after just one season (autumn), and mass after two seasons (autumn and winter). Differences were more pronounced after winter and, especially, spring. It is worth noting that fish that were previously starved were able to recover mass and condition factor if placed on a high ration diet. Fat content was less sensitive to changes in food rationing but differences were evident after winter, and markedly different by May. Length was least sensitive to food rationing. Only in May were differences in fish length observed between fish fed high and low rations. Length depends on inherited growth rates (Thorpe and Morgan 1978), but starvation during spring appears to limit length growth. Despite an overall reduced growth in spring starved treatments, larger individuals in these treatments were more likely to migrate than in treatments where fish were administered full rations in spring. That starvation in spring had the largest effect on growth metrics and the proportion of smolts, suggests that individuals smolted because they were unable to maintain growth in their current environment. This is in full agreement with work carried out on brook charr (Morinville and Rasmussen 2003) and brown trout (Jonsson and Jonsson 1993, Forseth et al. 1999).

It is probable that environment shapes migratory decisions by salmonids, as has also been shown for insects (Taylor and Taylor 1977). Migration may be a mechanism used to avoid metabolic adversity (Forseth et al. 1999), and obtain energy required to grow and mature

(Thorpe 1994, Thorpe and Metcalfe 1998). We found that larger fish on reduced rations were more likely to smolt. Fish with higher growth rates have greater metabolic requirements and are more likely to migrate when resources are limiting (Forseth et al. 1999). Larger fish are also most likely to survive migratory journeys (Bohlin et al. 1993, Jonsson and Jonsson 2014). A restriction in food availability in natal streams promotes migration; a life history which is sustained if food availability is higher at migratory destinations. Conversely, if there is no growth advantage from migrating then residency is favoured. Switches between migratory and resident life histories have been observed in wild populations of Arctic charr and brown trout (Näslund et al. 1993, Sandlund and Jonsson 2014).

In conclusion, this study demonstrates that smolting is flexible in brown trout and can be influenced by feeding conditions in spring. The situation for brown trout does not seem to resemble that of Atlantic salmon as described by Metcalfe et al. (1986, 1988), namely that the decision to migrate in spring depends on whether an energetic or a size threshold is reached in the previous summer, but is in line with work carried out by Vainikka et al. (2012). The majority of studies investigating the effect of food availability show that brown trout respond to reduced food by increasing smoltification and outmigration. According to the conditional strategy, individuals migrate if they are able to achieve a predetermined threshold; individuals that cannot achieve this delay migration. Instead we found that smolting in spring was highest in treatments where measures of growth were reduced.

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468 **Figure 1.** Seasonal development of the **a)** length, **b)** condition, **c)** mass, and **d)** fat content of
469 trout from all treatments during the experiment. Grey bars indicate high rations in the
470 preceding season, white bars indicate low rations in the preceding season. Treatment labels
471 are included; L represents low food rations, H represents high rations. Values are means
472 $\pm 95\%$ confidence intervals.

Figure 2. Probability of the fish being classified as a smolt based on length in May according to our Generalised Linear Mixed Effects Model. Dashed line represents spring starved fish, solid line is fish fed full rations. Panel to the right shows the probability of a 242 mm (mean length of fish in May) long fish being classified as a smolt, based on food rations. Shading around lines and the error bars in the bar graph represent $\pm 95\%$ confidence intervals. Note that greater differences likely occur in fish at lower lengths, but since we had few fish in these size classes estimates are less accurate and confidence intervals are larger.

Table 1. Six different food ration treatments with details of food treatments for autumn, winter and spring periods. Approximate rations for each season (grams per individual per week) are given in brackets.

Treatment	Food ration autumn (~ g ind ⁻¹ week ⁻¹ / ~ % mass ind ⁻¹)	Food ration winter (~ g ind ⁻¹ week ⁻¹ / ~ % mass ind ⁻¹)	Food ration spring (~ g ind ⁻¹ week ⁻¹ / ~ % mass ind ⁻¹)
HHH (high ration control)	High (6.9/0.72)	High (2.9/0.31)	High (7.3/1.00)
LLL (low ration control)	Low (2.1/0.22)	Low (0.9/0.10)	Low (2.2/0.30)
HLL		Low (0.9/0.10)	Low (2.2/1.00)
LHH		High (2.9/0.31)	High (7.3/0.30)
HHL			Low (2.2/1.00)
LLH			High (7.3/0.30)

Table 2. Coefficients and their standard errors for the proportion of smolts.

Effect	Lower 95 % CI	Coefficient estimate	Upper 95 % CI	z – value
Spring fed	1.28	1.70	2.12	7.96
Spring starved	2.06	2.71	3.36	3.05
Length*fed	0.03	0.05	0.06	6.95
Length*starved	0.04	0.07	0.10	2.28

Note: Response is migrant or not migrant. The estimates for the categorical spring fed and spring starved are for the intercepts. Length*fed and Length*starved are numerical and their estimates are coefficients for the slope. The z - value and probabilities of obtaining the z-value by chance are provided. The z - value is the number of standard deviations from the reference value. Note that values are the logit of predicted values.