Life-history genotype explains variation in migration activity in Atlantic salmon (Salmo salar)

Niemelä, Petri T.

2022-07-13

Niemelä , P T , Klemme , I , Karvonen , A , Hyvärinen , P , Debes , P V , Erkinaro , J , Sinclair-Waters , M , Pritchard , V L , Härkönen , L S & Primmer , C R 2022 , ' Life-history genotype explains variation in migration activity in Atlantic salmon (Salmo salar) ' , Proceedings of the Royal Society B: Biological Sciences , vol. 289 , no. 1978 . https://doi.org/10.1098/rspb.2022.085

http://hdl.handle.net/10138/346356
https://doi.org/10.1098/rspb.2022.0851

Life-history genotype explains variation in migration activity in Atlantic salmon (*Salmo salar*).

Petri T. Niemelä[1], Ines Klemme[2], Anssi Karvonen[2], Pekka Hyvärinen[3], Paul V. Debes[1,4,5], Jaakko Erkinaro[6], Marion Sinclair-Waters[1], Victoria L. Pritchard[1,7], Laura Härkönen[3,6], Craig R. Primmer[1,4]

[1]Organismal and Evolutionary Biology Research Program, Faculty of Biological and Environmental Sciences, University of Helsinki, Helsinki, Finland.

[2]University of Jyvaskyla, Department of Biological and Environmental Science, P.O. Box 35, 40014 University of Jyvaskyla, Finland.

[3]Natural Resources Institute Finland (Luke), Migratory fish and regulated rivers, Manamansalontie 90, 88300 Paltamo, Finland.

[4]Institue of Biotechnology, Helsinki Institute of Life Sciences (HiLIFE), University of Helsinki, Finland.

[5] Department of Aquaculture & Fish Biology, Hólar University, Háeyri 1, 551 Sauðárkrókur, Iceland.

[6]Natural Resources Institute Finland (Luke), Migratory fish and regulated rivers, Paavo Havaksen tie 3, 90570 Oulu, Finland.

[7]Rivers and Lochs Institute, Inverness College, University of the Highlands and Islands, United Kingdom.

Abstract

One of the most well-known life-history continuums is the fast–slow axis, where "fast" individuals mature earlier than "slow" individuals. "Fast" individuals are predicted to be more active than "slow" individuals because high activity is required to maintain a fast life-history strategy. Recent meta-analyses revealed mixed evidence for such integration. Here, we test whether known life-history genotypes differ in activity expression by using Atlantic salmon (*Salmo salar*) as a model. In salmon, variation in Vgll3, a transcription co-factor, explains ~40% of variation in maturation timing. We predicted that the allele related to early maturation (*vgll3**E) would be associated with higher activity. We used an automated surveillance system to follow ~1900 juveniles including both migrants and non-migrants (i.e. smolt and parr fish, respectively) in semi-natural conditions over 31 days (~580 000 activity measurements). In migrants, but not in non-migrants, *vgll3* explained variation in activity according to our prediction in a sex-dependent manner. Specifically, in females the *vgll3**E allele was related to increasing activity, whereas in males the *vgll3**L allele (later maturation allele) was related to increasing activity. These sex-dependent effects might be a mechanism maintaining within-population genetic life-history variation.

Introduction

Life-history trade-offs characterize the lives of nearly every organism and differing individual solutions to trade-offs can result in the emergence of different life history strategies (Stearns 1992). One of the most studied life-history strategy continuums is the fast–slow continuum, where “fast” life-history strategies have faster developmental rates, younger maturation age and shorter lifespan compared to “slow” strategies with opposite expression of life-history (Stearns 1992; Healy et al. 2019). The fast-slow continuum is one of the most important life-history axes explaining as much as 70% of life-history variation among animal species (Healy et al. 2019). For the last decade, the fast-slow continuum has also been studied at the within-species and within-population levels, with a goal to understand whether and why such continuums exist and how behaviours are associated with them (Réale et al. 2010; Dammhahn et al. 2018a). So far, within-population studies of fast-slow continuums have focused on estimating trait correlation mainly at the un-partitioned phenotypic, but also increasingly at the among-individual, level of (co)variation (Royauté et al. 2018; Moiron et al. 2020). However, to advance our evolutionary understanding of the fast-slow continuum, studies where the genetic underpinning of life-history strategies is known are needed. This would shed more light on the genetic versus environmental contribution on the expression of the continuum and, exclude the need to directly observe life-history events that occur in stages that are difficult or time consuming to track.

Recently, the role of behaviour in the expression of a fast-slow life-history continuum at the within-population level has received considerable attention (Réale et al. 2010; Dammhahn et al. 2018a; Royauté et al. 2018; Moiron et al. 2020). Behavioural expression is assumed to coevolve with life-history and is considered as a mechanism mediating costs and benefits involved in life-history trade-offs (Stamps 2007; Dammhahn et al. 2018a; Montiglio

et al. 2018). For example, individuals maturing at an early age are predicted to be highly explorative and active in order to maintain their "fast" life-history strategy, but might be more vulnerable to predation due to their "risky" behavioural expression. Nevertheless, the results from studies associating behavioural and life-history strategies at the within-population level are mixed (Royauté et al. 2018). This has led to recent criticism indicating that the pace of life syndrome theory is too simplistic (Montiglio et al. 2018, Laskowski et al. 2021). For example, the presence of alternative life-history strategies (e.g. fast, slow) or trade-offs are assumed a priori in the majority of empirical studies (Dammhahn et al. 2018). Moreover, recent theoretical literature suggests the existence of sex-specific expression of life-history variation, highlighting the importance to include sex in the models (Immonen et al. 2018, Hämäläinen et al. 2018). Studying behavioural expression across confirmed life-history genotypes in both sexes can therefore advance our understanding of whether behaviours and life-history are integrated as suggested by theory.

Salmonid fishes have been a model species group for life-history research (Hendry and Stearns 2004) and this research has contributed substantially to our understanding of the evolution and genetic underpinnings of life-history strategies. For example, in Atlantic salmon (*Salmo salar*), variation in a genome region including the vestigial-like family member 3 gene (*vgll3*) on chromosome 25, has been shown to explain a large proportion of variation in the sea-age at maturity in males and females (Barson et al. 2015). Since *vgll3* is involved in fat cell regulation (Halperin et al. 2013), potentially controlling resource allocation between energy reserves and somatic growth, and its effects are at least partially phylogenetically conserved, it potentially contributes to moderating the expression of life-history strategies across species (Debes et al. 2021). Indeed, *vgll3* is associated with size, as well as age, at maturity in both salmon and humans (Cousminer et al. 2013; Barson et al. 2015). In Atlantic salmon, *vgll3*

explains ~40% of the variation in sea age at maturation so that the *vgll3**E allele is linked with early, and the *vgll3**L allele with late maturation (Barson et al. 2015). Moreover, early maturing individuals are smaller at maturation compared to late maturing individuals (Barson et al. 2015; Reed et al. 2019). Generally, the life-history of salmon is extremely complex. For example, most Atlantic salmon go through a major life-history transition from the non-migrant (i.e. freshwater *parr* stage) into the migrant life-history stage (i.e. marine *smolt* stage), where physiology, morphology and behavioural expression change dramatically, preparing individuals for transition to the marine environment (Stradmeyer and Thorpe 1987; Huntingford et al. 1988; Thorstad et al. 2012). The age at which individuals undergo this demanding transition varies, and the different freshwater and subsequent marine life-history stages can last for 1-8 and 0-5 years, respectively (Klemetsen et al. 2003; Mobley et al. 2021), with over 100 different life-history strategies observed in a single population complex (Erkinaro et al. 2019).

Even though many aspects of the association between *vgll3* and life-history are still unknown (e.g. life-history stage-dependent *vgll3* effects on trait expression; difference between migrant and non-migrant), the broad patterns discussed above suggest that generally the *vgll3**E allele is linked to “fast” and the *vgll3**L allele to “slow” life-histories. This leads to the prediction that the *vgll3**E allele is linked to higher activity compared to the *vgll3**L allele (Réale et al. 2010; Dammhahn et al. 2018a). So far, there is only indirect evidence that suggest *vgll3* genotypes to differ in their behavioural phenotypes. For example, at sea, *vgll3* homozygote genotypes associate marginally with different prey content in the stomach (Aykanat et al. 2020), which might indicate differences in behaviours contributing to resource acquisition. However, direct behavioural observations are required to fully understand

whether behaviours, such as general activity, differ across life-history genotypes or, whether the associations are life-history stage specific.

Using juvenile Atlantic salmon as a model with *vgll3* genotype as a predictor of the life-history strategy, our main objective was to test whether the *vgll3**E genotype is linked with activity. We predicted that the *vgll3**E allele would be associated with higher activity in both migrant and non-migrant fish (see above). We measured general movement activity behaviour of 1932 *vgll3*-genotyped, migrant and non-migrant, fish for 31 days using an automatic RFID-surveillance system (i.e. radio frequency identification). Our semi-natural setting (artificial streams) with natural food, water flow and water temperature connects the recorded activity with an ecologically relevant function: activity most likely represents general local, or even territorial, activity in non-migrant fish and migration activity in migrant fish (Stradmeyer and Thorpe 1987; Huntingford et al. 1988; Thorstad et al. 2012). Thus, our study links genetically defined life histories with ecologically relevant behaviours. Further, our study takes into account the abovementioned pace-of-life theory criticism by testing how life-history explains behavioral expression between pre-defined life-history genotypes, incorporating also potential effect of sex-differences.

Methods

Origin of fish

The parents of the experimental fish originated from two broodstocks (Oulujoki; OUL and Tornionjoki; TOR, broodstocks: generation 0), that were hatchery raised at the Natural Resources Institute Finland (Luke), Taivalkoski, but whose parents had successfully completed a sea migration in the Baltic Sea. Individuals of these broodstocks had been tagged and genotyped as described below, allowing identification of unrelated individuals with specific *vgll3* genotypes. The breeding design involved crossing only *vgll3* heterozygote individuals,

144 resulting in all possible *vgll3* genotypes occurring within a family in a Mendelian 1:2:1 ratio,
145 thus controlling for genetic background when estimating *vgll3* effects. Eggs and sperm were
146 stripped from suitable *vgll3*EL* females and males and a series of 2 x 2 factorial crosses were
147 created via external fertilization, i.e. "crossing groups", using two sires and two dams (one
148 from each parental river) of the *vgll3**EL genotype so the sperm of each male was used to
149 fertilize a separate batch of eggs of each female. This generated four crossing group types:
150 OUL-OUL, TOR-TOR, TOR-OUL, OUL-TOR with 24 families of each crossing group type. Fish
151 were experimentally crossed in October 2017 and eggs incubated at the Taivalkoski hatchery
152 until hatching (8000 per crossing group, 32000 in total), after which eyed eggs were
153 transferred to a commercial fish hatchery (Montan Lohi Ltd), where they were maintained for
154 one year in eight fiberglass tanks (3.14 m^2) (two replicate tanks per crossing group) in similar
155 conditions until February 2019. None of the fish became sexually mature prior to start of the
156 experiment. For the tagging period (i.e. for 4 days; see below), fish from the two replicate
157 tanks of each cross-type were combined into one tank on 20th February 2019, leading to one
158 tank per crossing group, i.e. total of four tanks. In total 3200 randomly selected fish (800 per
159 crossing group, without any trait preference) were tagged between 20-25th February 2019
160 (mean (SD): total length = 111.96 mm (17.33) & body mass = 12.58 g (5.75)). Fish were
161 anaesthetized (using Benzocaine, 40 mg L^{-1}) and a 12 mm passive integrated transponder
162 (HDX PIT-tag, Oregon RFID, Oregon, USA) inserted into the body cavity to enable re-
163 identification and activity recordings (see below). A fin clip was also taken to allow single
164 nucleotide polymorphism (SNP) genotyping and sex-determination. After tagging (20-25th
165 February 2019), fish were divided into two tanks, each with 400 individuals of each crossing-
166 group and 1600 fish in total. DNA was extracted from fin samples and 177 SNPs including the
167 *VGLL3*$_{TOP}$ SNP (Aykanat et al. 2016) were genotyped and the data subsequently used to assign

individuals to families as outlined in Debes et al. (2020). On 27th March 2019 fish were transferred to the Kainuu Fisheries Research Station (www.kfrs.fi, Paltamo, Finland) of the Natural Resources Institute Finland and kept in two fiberglass tanks (15 m^2) until 23th May 2019 when the experiment was started.

Experimental streams and data collection

The experimental outdoor streams were ring shaped (surface area = 40m^2, width = 1.5m from the outer edge of the ring towards the centre of the ring, length = ~26.15m at 0.75m from the outer edge of the ring) with water flow of 40.5 L s^{-1} (water depth ~0.3m, stream current velocity ~0.09m s^{-1}) (Supplementary figure 1). Water originated from a nearby Lake Kivesjärvi, mixed from depths of three and seven meters. Thus, the stream water temperature followed natural variation (Rodewald et al. 2011). The bottom of the stream was covered with gravel (30–80 mm grain size). The system has been running uninterruptedly for years, which allowed establishment of a natural food supply of benthic invertebrates in the tanks, supplemented also by additional natural food via incoming water (Rodewald et al. 2011, Hatanpää et al. 2020).

Prior to release into the experimental streams, 1932 experimental fish were selected with stratified randomization from a larger pool of 3200 fish of PIT tagged and genotyped individuals (see above). Individuals were allocated randomly to streams with respect to phenotype, but were assigned in a manner to ensure relatively even representation in each replicate stream of each cross and family, as well as sex and *vgll3* genotypes within each family. The fish were distributed in roughly equal numbers among 16 experimental streams (118-124 fish/stream) as outlined above and left to acclimatize between May 23 – Jun 3, 2019. During the data collection period (31 days; Jun 4 - Jul 4, 2019), fish activity was recorded in the streams. The selected timing of the experiment overlaps with the natural smolt migration

timing in Atlantic salmon (Karppinen et al. 2014; Otero et al. 2014). Each stream was equipped with four RFID-antennas, positioned in quadrats of the circular stream (Alioravainen et al. 2020). Since the system had the capacity to record data from maximum 32 antennas at a time, streams were monitored periodically in two sets of eight streams: recording was swapped between the two sets of streams every three days until the end of the data collection period. Thus, each individual stream was monitored on average for 357.4 hours across the 31-day period. The raw-RFID data (theoretical reading frequency 9 readings s^{-1}) was converted into one-hour resolution (www.pitdata.net). An individual was defined to have moved if it crossed at least two RFID antennae within the focal hour, i.e. moved through an area between two antennas. As the antennas were equally divided in the stream, the movement measured between two antennas was 6.54 m (one whole round 26.15 m). If an individual did not move during the focal hour, it got value zero (0) for the focal hour movement. We extracted three activity variables from the data. The hourly movement activity was calculated as the number of passes between two antennae in either 1) upstream direction (upstream movement) or 2) downstream direction (downstream movement) or 3) the number of passes between two antennae irrespective of the direction (total movement).

During the observation period, 288 fish disappeared. Either they were missing at the end of the experiment (273 fish) or were observed dead (15 fish) (per genotype: missing; EE=91, EL=87, LL=95, dead; EE=5, EL=7, LL=3). As this resulted in incomplete RFID data from these fish as well as from additional 21 fish that most likely lost their RIFD-tags during the experiment, these fish were removed from the RFID-data. This resulted in a final sample size of 1625 fish (580893 hourly observations of movement), including 500 migrants (i.e. smolts during the experiment period) (178494 hourly observations) and 1125 non-migrants (i.e. parr during the experiment period) (402399 hourly observations). The status of being a migrant

during the experiment was determined based on a combination of 1) colouration of the fish at the end of the observation period and 2) their movement patterns during the observation period. The transformation of salmon into the migrant saltwater phenotype (i.e. smolt) is typically associated with an appearance of silvery colouration and orientation to downstream movement (Thorstad et al. 2012; Debes et al. 2020; Mobley et al. 2021). Here, all individuals with a fully silvery colouration, based on visual inspection, were classified as migrants (N=202). Additionally, non-silvery individuals with average downstream movement of at least 5 stream rounds $hour^{-1}$ (i.e. 120 rounds $24h^{-1}$) were considered as migrant phenotypes (Klemme et al. unpublished) (N=292, i.e. 20.9% of all non-silvery fish). This threshold value was selected since 95% of the fish with silvery coloration showed movement patterns that exceeded this threshold (Klemme et al. 2022). All other individuals were categorized as non-migrants. It is good to note that non-migrants have potential to become migrants in coming years. The weight and length of the fish (to the nearest gram and millimetre, respectively) was measured just before (21.05.2019) and directly after (12.07.2019) the experimental period. At the end of the observation period, fish were used in other experiments. All data were collected according to guidelines of Finnish legislation.

Statistical methods

Generalized linear mixed effect models were used to study whether *vgll3**E allele was linked with higher hourly movement activity. Upstream movement, downstream movement and total movement (see above) were each fitted as a response variable in three separate univariate models. Migrant and non-migrant fish are generally known to differ in their behavioural expression and the biological meaning of the recorded activity likely differs between individuals with different migrant status (e.g. migration activity versus local activity) (Stradmeyer and Thorpe 1987; Huntingford et al. 1988; Thorstad et al. 2012). Thus, we ran

separate univariate models for i) only migrant fish and ii) only non-migrant fish for each three activity traits.

The main models were fitted with *vgll3* having additive (i.e. EE = 1, EL = 0 and LL = -1; continuous covariate) and dominance (i.e. EE & LL = 0 and EL = 1; continuous covariate) effects on activity (Xiang et al. 2018). Fitting both additive and dominance *vgll3* effects in the model estimates whether there are dominance effects on top of additive effects (Xiang et al. 2018). Additionally, fixed effect for sex (categorical) was fitted with *vgll3* interactions. Interaction terms between *vgll3* and sex were considered since in some cases, the *vgll3**E allele has been observed to be dominant in males, but not in females (Barson et al. 2015). All main models can be found in Table 1 and Supplementary Table 1.

In all models, we included the same random effects structure. We fitted individual identity as a random effect to control for pseudo-replication. To control for variation in the data caused by family structure and potential spatiotemporal variation caused by the experimental setup, we fitted mother identity (34 mothers), father identity (42 fathers), crossing group (i.e. parental source population combination (four levels: OUL-OUL, TOR-TOR, TOR-OUL, OUL-TOR), stream identity (16 streams), date (31 days) and time of day (hour identity; 24 levels) as random effects.

All models were run in the R statistical environment R, version 3.6.3. (R core team 2020), using the package glmmTMB (Brooks et al. 2017) with negative binomial error distribution and log-link function, which fits well for zero-inflated count data.

Results

In migrant fish, *vgll3* effects on upstream, downstream and total activity were sex-dependent (Table 1, Figure 1). More specifically, the *vgll3**E allele, which relates to earlier maturation, was linked with higher activity in females. However, in males *vgll3**L, which relates to later

maturation, was linked with higher activity (Table 1, Figure 1) (see Supplementary Table 2 for data scale predictions, used in Figure 1, and for activity expressed as distance moved in meters). In non-migrant fish, the *vgll3* effects were absent.

The dominance effects were non-significant (Table 1), although the effect sizes for additive and dominance effects were quite similar and statistical significance for dominance was close to the threshold value. Thus, our results are inconclusive.

Variation for date effects on activity was significantly larger for migrant fish and variation for individual effects (i.e. among-individual differences) was marginally larger for non-migrant fish compared to other random effects, when 95% credible intervals across random effects are being compared (Table 1, Supplementary Figure 2). This means that day-to-day differences dominated activity variation in migrant fish (Supplementary Figure 2). To test whether date effects explain the observed *vgll3* effects, we ran an additional model where we included *vgll3*-date interaction in the main model (Supplementary Table 3). Nevertheless, when we added *vgll3*-date interaction as a random effect in the migrant fish model, the *vgll3* effect estimate on migrant activity remained the same (Supplementary Table 3). We also ran an additional model where we included date and time as normal linear covariates (Supplementary table 4). This model did not show any differences in the *vgll3* effects compared to the main models described in Table 1. The models where we additionally tried to fit non-linear date and time as covariates did not converge.

Discussion

In this study, we tested whether individuals with genetically determined life-history strategies differ in their activity levels as predicted by pace-of-life theory (Réale et al. 2010; Dammhahn et al. 2018b; Laskowski et al. 2021), specifically whether the *vgll3**E allele, which associates with earlier maturation, is linked with higher activity. Interestingly, *vgll3* effects on activity

288 differed between males and females within migrant fish and our predictions were supported
289 only in migrant females, where the *vgll3**E allele was indeed linked with higher activity. In
290 migrant males, conversely, the *vgll3**L allele, which relates to later maturation, was linked
291 with higher activity. In non-migrant fish, *vgll3* effects were absent. Thus, our results indicate
292 that *vgll3* effects on activity depend on migrant status and sex.

293 *Migrant status and sex-dependent vgll3 effects on activity*

294 Our results indicate that variation in *vgll3* genotype explains variation in migration
295 activity. High hourly migration activity might allow individuals to reach the marine
296 environment considerably faster compared to more slowly migrating conspecifics. Indeed, the
297 literature acknowledges considerable variation in the duration of the (smolt) migration among
298 individuals (Thorstad et al. 2012; Karppinen et al. 2014; Harbicht et al. 2021; Simmons et al.
299 2021). Our results indicate that sex-dependent variation in *vgll3* genotype might partly explain
300 this variation so that the *vgll3**E allele is linked with higher migration activity in females, while
301 in males the pattern is opposite (the result could also be explained by genotype and sex-
302 specific onset of migration, but no such *vgll3*-sex interaction was observed: Supplementary
303 Table 5). Generally, smolt migration takes several days (Thorstad et al. 2012, Harbicht et al.
304 2021), even up to 8 weeks, depending on the river length (Thorstad et al. 2012). Thus, even
305 small differences in hourly migration activity across genotypes could lead to large differences
306 in the overall migration duration in long rivers. Lower migration activity can be considered as
307 a more “risky” behaviour compared to high migration activity (Thorstad et al. 2012; Hyvärinen
308 and Rodewald 2013; Karppinen et al. 2014). Indeed, fast migration through estuaries or other
309 high-risk areas has been suggested to reduce mortality during migration to the sea (reviewed
310 in Thorstad et al. 2012). For example, multiple fish, bird and mammal species prey on
311 migrating fish in the river (Thorstad et al. 2012; Karppinen et al. 2014; Flávio et al. 2020) and

indeed, mortality during river migration can be very high (Lothian et al. 2018, Flávio et al. et al. 2020). Faster migrating *vgll3* genotypes might be able to (temporarily) reduce migration-related mortality costs, compared to other genotypes, leading to genotype-dependent survival during the river-to-sea migration. Our finding of a sex-genotype interaction for migration activity most likely arises due to sex-dependent expression of life-history and life-history trade-offs (see below), which affects the costs and benefits of behavioural expression in a sex-dependent manner (Immonen et al. 2018). Interestingly, under the assumption that variation in migration speed generates variation in survival, the sex-*vgll3* interaction in migration activity might act as a mechanism maintaining variation in *vgll3* genotypes: opposite genotypes in males (i.e. LL) and females (i.e. EE) might be selected for due to viability selection acting via migration duration/speed. On the other hand, such antagonistic selection can make sex-specific adaptations, linked to *vgll3* genotypes, inherently difficult.

Potential (partial) mechanisms explaining variation in migration activity linked to *vgll3* genotype might be variation in body condition as it might affect behavioural expression in salmon (Thorstad et al. 2012, Debes, et al. 2021). Furthermore, if the effects of body condition on migration activity are sex-dependent, that might partly explain the patterns found in the current study. Indeed, when testing this *a posteriori* hypothesis, adding an interaction between sex and body condition in our (migrant fish) models rendered the *vgll3* effects on activity smaller (Supplementary Table 1). Amongst individuals in poorer condition, males had higher migration activity than females while amongst individuals with higher condition, we found the opposite pattern (Supplementary figure 3). It has been previously shown that the *vgll3**E allele is associated with higher condition (Debes et al. 2021), which was also confirmed by our *a posteriori* analysis in migrant fish (Supplementary Figure 4). Thus, variation in body condition might explain the sex - *vgll3* interaction in migration activity: in females, the *vgll3**E

allele, which relates to higher condition, is also associated with higher migration activity while in males, the *vgll3**L allele, which relates to lower condition, is associated with higher migration activity. Interestingly, body condition has been suggested to, at least partly, be a factor contributing to the detected *vgll3* effects on maturation timing of male parr (Debes et al. 2021). Our results add more evidence supporting the notion that *vgll3* effects on trait expression might be mediated by body condition, although more research on the topic is needed.

Fast-slow life-history continuum and movement activity

Our results indicate that only in migrant females does *vgll3* genotype explain movement activity as predicted by pace-of-life theory (Réale et al. 2007; Dammhahn et al. 2018a). Sex-dependent expression of the pace-of-life continuum, e.g. integration of life-history and behavioural expression, has been predicted before, but rarely studied (Immonen et al. 2018; Tarka et al. 2018). The potential dependence of this life history-behaviour integration on ecology might explain why the *vgll3*-activity association is expressed in opposite ways in males and females (Immonen et al. 2018; Montiglio et al. 2018; Tarka et al. 2018; Laskowski et al. 2021). In Atlantic salmon, males and females differ in the expression of key life-history traits and how these traits affect fitness. For example, males generally mature earlier compared to females (Fleming and Einum 2011; Erkinaro et al. 2019) and females benefit more from larger maturation size compared to males (Fleming and Einum 2011; Mobley et al. 2020). In addition, sexes differ in expression of the trade-off between time spent in freshwater versus marine environments (Mobley et al. 2020). Sex differences in life-history or life-history trade-offs might lead to males destined to mature late and females destined to mature early to adopt high migration activity. The current general theory predicting links between life-history and behavioural expression is quite broad and not sufficiently detailed to explain why there are so

many exceptions to the fast-slow continuum (Immonen et al. 2018; Montiglio et al. 2018; Laskowski et al. 2021). Our work sheds more light on why the results from the pace-of-life literature might show mixed evidence for its support. Indeed, as also discussed in the recent theoretical literature (Immonen et al. 2018, Hämäläinen et al. 2018), our results show that the life-history strategy – behavioural expression relationship can depend on sex.

Conclusions

Variation in *vgll3* in Atlantic salmon has previously been shown to explain variation in the expression of life-history strategies in males and females (Barson et al. 2015). Here, we show that *vgll3* explains variation in movement activity. Our work reveals complex behaviour – life history integration, as the prediction from the pace-of-life theory was supported only on migrant females, where higher activity rate relates to the genetic predisposition for earlier maturation age. As suggested by recent theoretical work (Immonen et al. 2018, Hämäläinen et al. 2018), and confirmed by our study, it is recommended that future empirical and modelling work considers the study of sex and life-history stage-dependent expression of behaviour-life history integration to make pace-of-life research more biologically realistic.

Acknowledgements

We thank the personnel of Montan Lohi Oy fish farm, Taivalkoski fish farm and Kainuu fisheries research station for raising and maintaining the salmon population. We thank Jyrki Oikarinen, Olli van der Meer, Juuso Meriläinen, Mikko Jaukkuri, Ari Leinonen, Kanerva Korhonen, Tapio Laaksonen, Pekka K. Korhonen, Rauno Hokki and Vesa Rantanen for assisting with marking of the fish and organizing the experimental setup. We thank Andrew House, Annukka Ruokolainen, Jacqueline Moustakas-Verho, Johanna Kurko, Ksenia Zueva, Nico Lorenzen, with their help in generating the crossed families. We also thank Annukka Ruokolainen and Seija

Tillanen for conducting the SNP genotyping and Neil Metcalfe and an anonymous reviewer for constructive comments on an earlier manuscript version.

Funding

This work was supported by the Academy of Finland (project numbers 284941, 286334, 310632, 314254 and 314255), the European Research Council under the European Articles Union's Horizon 2020 research and innovation program (grant no. 742312), European Maritime and Fisheries Fund (grant no. 43521) and the University of Helsinki.

Open data

The data and R-script related to this study are stored in public repository (Niemelä 2022).

Competing interests

We declare we have no competing interests.

Authors' contributions

PTN wrote the first draft of the manuscript, ran all the statistical models and generated figures and tables. CRP helped to draft the manuscript. PVB participated in data analysis. IK, AK, PH, JK, MS-W, VLP, LH and CRP participated in design of the study, data collection and coordinated the data collection. All authors critically revised the manuscript. All authors gave final approval for publication and agree to be held accountable for the work performed therein.

Ethics

All applicable international, national and institutional guidelines for the care and use of animals were followed.

References

Alioravainen N, Prokkola JM, Lemopoulos A, et al (2020) Postrelease exploration and diel activity of hatchery, wild, and hybrid strain brown trout in seminatural streams. Can J

Fish Aquat Sci 77:1772–1779. https://doi.org/10.1139/cjfas-2019-0436

Aykanat T, Lindqvist M, Pritchard VL, Primmer CR (2016) From population genomics to conservation and management: a workflow for targeted analysis of markers identified using genome-wide approaches in Atlantic salmon Salmo salar. J Fish Biol 89:2658–2679. https://doi.org/10.1111/jfb.13149

Aykanat T, Rasmussen M, Ozerov M, et al (2020) Life-history genomic regions explain differences in Atlantic salmon marine diet specialization. J Anim Ecol In press: https://doi.org/10.1111/1365-2656.13324

Ayllon F, Kjærner-Semb E, Furmanek T, et al (2015) The vgll3 Locus Controls Age at Maturity in Wild and Domesticated Atlantic Salmon (Salmo salar L.) Males. PLoS Genet 11:. https://doi.org/10.1371/journal.pgen.1005628

Barson NJ, Aykanat T, Hindar K, et al (2015) Sex-dependent dominance at a single locus maintains variation in age at maturity in salmon. Nature 528:405–408. https://doi.org/10.1038/nature16062

Brooks ME, Kristensen K, van Benthem KJ, et al (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J 9:378–400. https://doi.org/10.32614/rj-2017-066

Cousminer DL, Berry DJ, Timpson NJ, et al (2013) Genome-wide association and longitudinal analyses reveal genetic loci linking pubertal height growth, pubertal timing and childhood adiposity. Hum Mol Genet 22:2735–2747. https://doi.org/10.1093/hmg/ddt104

Dammhahn M, Dingemanse NJ, Niemelä PT, Réale D (2018a) Pace-of-life syndromes: a framework for the adaptive integration of behaviour, physiology and life history. Behav Ecol Sociobiol 72:62. https://doi.org/10.1007/s00265-018-2473-y

Dammhahn M, Dingemanse NJ, Niemelae PT, Reale D (2018b) Pace-of-life syndromes: a framework for the adaptive integration ofbehaviour, physiology and life history. Behav Ecol Sociobiol 72:. https://doi.org/10.1007/s00265-018-2473-y

Debes P V., Piavchenko N, Erkinaro J, Primmer CR (2020) Genetic growth potential, rather than phenotypic size, predicts migration phenotype in Atlantic salmon. Proc R Soc B Biol Sci 287:20200867. https://doi.org/10.1098/rspb.2020.0867

Debes P V., Piavchenko N, Ruokolainen A, et al (2021) Polygenic and major-locus contributions to sexual maturation timing in Atlantic salmon. Mol Ecol Early View: https://doi.org/10.1111/MEC.16062

Erkinaro J, Czorlich Y, Orell P, et al (2019) Life history variation across four decades in a diverse population complex of atlantic salmon in a large subarctic river. Can J Fish Aquat Sci 76:42–55. https://doi.org/10.1139/cjfas-2017-0343

Flávio H, Caballero P, Jepsen N, Aarestrup K (2021). Atlantic salmon living on the edge: Smolt behaviour and survival during seaward migration in River Minho. Ecol Freshw Fish 30: 61-72.

Fleming IA, Einum S (2011) Reproductive Ecology: A Tale of Two Sexes. In: Aas Ø, Einum S, Klemetsen A, Skurdal J (eds) Atlantic Salmon Ecology. Wiley-Blackwell, pp 33–65.

Halperin DS, Pan C, Lusis AJ, Tontonoz P (2013) Vestigial-like 3 is an inhibitor of adipocyte differentiation. J Lipid Res 54:473–481. https://doi.org/10.1194/jlr.M032755.

Hatanpää A, Huuskonen H, Kekäläinen J. et al. 2020. Early winter foraging success, swimming performance, and morphology of juvenile landlocked Atlantic salmon reared under semi-wild and hatchery conditions. Can. J. Fish. Aquat. Sci. 77: 770–778.

Harbicht AB, Nilsson PA, Österling M, Calles O (2021) Environmental and anthropogenic correlates of migratory speeds among Atlantic salmon smolts. River Res Applic 37:358–

372.

Healy K, Ezard THG, Jones OR, et al (2019) Animal life history is shaped by the pace of life and the distributionof age-specific mortality and reproduction. Nat Ecol Evol 3:1217+. https://doi.org/10.1038/s41559-019-0938-7

Hendry AP, Stearns SC (2004) Evolution Illuminated: Salmon and Their Relatives. Oxford University Press, New York, USA

Huntingford FA, Metcalfe NB, Thorpe JE (1988) Choice of feeding station in Atlantic salmon, Salmo salar, parr: effects of predation risk, season and life history strategy. J Fish Biol 33:917–924. https://doi.org/10.1111/j.1095-8649.1988.tb05540.x

Hyvärinen P, Rodewald P (2013) Enriched rearing improves survival of hatchery-reared Atlantic salmon smolts during migration in the River Tornionjoki. Can J Fish Aquat Sci 70:1386–1395. https://doi.org/10.1139/cjfas-2013-0147

Immonen E, Hamalainen A, Schuett W, Tarka M (2018) Evolution of sex-specific pace-of-life syndromes: genetic architectureand physiological mechanisms. Behav Ecol Sociobiol 72:. https://doi.org/10.1007/s00265-018-2462-1

Karppinen P, Jounela P, Huusko R, Erkinaro J (2014) Effects of release timing on migration behaviour and survival of hatchery-reared Atlantic salmon smolts in a regulated river. Ecol Freshw Fish 23:438–452. https://doi.org/10.1111/eff.12097

Klemetsen A, Amundsen PA, Dempson JB, et al (2003) Atlantic salmon Salmo salar L., brown trout Salmo trutta L. and Arctic charr Salvelinus alpinus (L.): A review of aspects of their life histories. Ecol Freshw Fish 12:1–59. https://doi.org/10.1034/j.1600-0633.2003.00010.x

Klemme I, Debes PV, Hyvärinen P, Erkinaro J, Härkönen L, Primmer CR, Karvonen A (2022) Host developmental stage effects on parasite resistance and tolerance. Am. Nat. In

press.

Laskowski KL, Moiron M, Niemelä PT (2021) Integrating Behavior in Life-History Theory: Allocation versus Acquisition? Trends Ecol. Evol. 36:132–138

Lothian AJ, Newton M, Barry J, et al. (2018). Migration pathways, speed and mortality of Atlantic salmon (Salmo salar) smolts in a Scottish river and the near-shore coastal marine environment. Ecol Freshw Fish 27:549-558.

Mobley KB, Aykanat T, Czorlich Y, et al (2021) Maturation in Atlantic salmon (Salmo salar, Salmonidae): a synthesis of ecological, genetic, and molecular processes. Rev FISH Biol Fish In press

Mobley KB, Granroth-Wilding H, Ellmén M, et al (2020) Time spent in distinct life history stages has sex-specific effects on reproductive fitness in wild Atlantic salmon. Mol Ecol 29:1173–1184. https://doi.org/10.1111/mec.15390

Moiron M, Laskowski KL, Niemelä PT (2020) Individual differences in behaviour explain variation in survival: a meta-analysis. Ecol Lett 23:399–408. https://doi.org/10.1111/ele.13438

Montiglio P-O, Dammhahn M, Messier GD, Reale D (2018) The pace-of-life syndrome revisited: the role of ecological conditionsand natural history on the slow-fast continuum. Behav Ecol Sociobiol 72:. https://doi.org/10.1007/s00265-018-2526-2

Niemelä, Petri. (2022). Life-history genotype explains variation in migration activity in Atlantic salmon (Salmo salar) [Data set]. Zenodo. https://doi.org/10.5281/zenodo.6518674

Otero J, L'Abée-Lund JH, Castro-Santos T, et al (2014) Basin-scale phenology and effects of climate variability on global timing of initial seaward migration of Atlantic salmon (Salmo salar). Glob Chang Biol 20:61–75. https://doi.org/10.1111/gcb.12363

503 R core team (2020) R: A language and environment for statistical computing. R Found Stat
504 Comput Vienna, Austria.
505 Réale D, Garant D, Humphries MM, et al (2010) Personality and the emergence of the pace-
506 of-life syndrome concept at the population level. Philos Trans R Soc B Biol Sci 365:4051–
507 4063. https://doi.org/10.1098/rstb.2010.0208
508 Réale D, Reader SM, Sol D, et al (2007) Integrating animal temperament within ecology and
509 evolution. Biol Rev 82:291–318. https://doi.org/10.1111/j.1469-185X.2007.00010.x
510 Reed TE, Prodöhl P, Bradley C, et al (2019) Heritability estimation via molecular pedigree
511 reconstruction in a wild fish population reveals substantial evolutionary potential for
512 sea age at maturity, but not size within age classes. Can J Fish Aquat Sci 76:790–805.
513 https://doi.org/10.1139/cjfas-2018-0123
514 Rodewald P, Hyvärinen P, Hirvonen H (2011) Wild origin and enriched environment promote
515 foraging rate and learning to forage on natural prey of captive reared Atlantic salmon
516 parr. Ecol Freshw Fish 20:569–579. https://doi.org/10.1111/j.1600-0633.2011.00505.x
517 Royaute R, Berdal MA, Garrison Courtney R.and Dochtermann NA (2018) Paceless life? A
518 meta-analysis of the pace-of-life syndrome hypothesis. Behav Ecol Sociobiol 72:.
519 https://doi.org/10.1007/s00265-018-2472-z
520 Royauté R, Berdal MA, Garrison CR, Dochtermann NA (2018) Paceless life? A meta-analysis
521 of the pace-of-life syndrome hypothesis. Behav Ecol Sociobiol 72:64
522 Simmons OM, Gregory SD, Gillingham PK (2021) Biological and environmental influences on
523 the migration phenology of Atlantic salmon Salmo salar smolts in a chalk stream in
524 southern England. Freshw Biol 66:1581–1594.
525 Stamps JA (2007) Growth-mortality tradeoffs and “personality traits” in animals. Ecol. Lett.
526 10:355–363

527 Stearns SC (1992) The evolution of life-histories. Oxford University Press, Oxford, UK
528 Stradmeyer L, Thorpe JE (1987) Feeding behaviour of wild Atlantic salmon, Salmo salar L.,
529 parr in mid- to late summer in a Scottish river. Aquac Res 18:33–49.
530 https://doi.org/10.1111/j.1365-2109.1987.tb00123.x
531 Tarka M, Guenther A, Niemelae PT, et al (2018) Sex differences in life history, behavior, and
532 physiology along aslow-fast continuum: a meta-analysis. Behav Ecol Sociobiol 72:.
533 https://doi.org/10.1007/s00265-018-2534-2
534 Thorstad EB, Whoriskey F, Uglem I, et al (2012) A critical life stage of the Atlantic salmon
535 Salmo salar: Behaviour and survival during the smolt and initial post-smolt migration. J
536 Fish Biol 81:500–542. https://doi.org/10.1111/j.1095-8649.2012.03370.x
537 Xiang T, Christensen OF, Vitezica ZG, Legarra A (2018) Genomic model with correlation
538 between additive and dominance effects. Genetics 209:711–723.
539 https://doi.org/10.1534/genetics.118.301015
540
541
542
543
544
545
546
547
548
549

550

1. Parameter estimates for additive and dominance models for migrant and non-migrant fish for all three behaviours: upstream activity, downstream activity and total activity. We present fixed parameter estimates (i.e. β, on the log scale) with standard error (i.e. SE) and *P*-values and, random parameter estimates (i.e. standard deviation = σ) with 95% credible intervals (i.e. CI). Genotypes modeled as: *vgll3**EE = 1, *vgll3**EL = 0, *vgll3**LL = -1.

Migrant fish	*Upstream*		*Downstream*		*Total activity*	
Fixed effects	β (SE)	*P*	β (SE)	*P*	β (SE)	*P*
Intercept	0.658 (0.309)	0.033	2.448 (0.317)	<0.001	2.774 (0.306)	<0.001
*vgll3*_ADDITIVE	0.049 (0.029)	0.097	0.065 (0.036)	0.073	0.064 (0.036)	0.072
Sex[1]	-0.038 (0.039)	0.335	-0.022 (0.049)	0.649	-0.025 (0.048)	0.595
*vgll3*_DOMINANCE	0.082 (0.048)	0.087	0.111 (0.059)	0.063	0.109 (0.059)	0.064
*vgll3*_ADDITIVE:Sex[1]	-0.108 (0.039)	0.006	-0.131 (0.048)	0.007	-0.131 (0.047)	0.006
*vgll3*_DOMINANCE:Sex[1]	-0.099 (0.068)	0.143	-0.127 (0.085)	0.134	-0.130 (0.166)	0.118
Random Effects	σ (95% CI)		σ (95% CI)		σ (95% CI)	
Individual	0.340 (0.316, 0.365)		0.424 (0.395, 0.454)		0.416 (0.388, 0.446)	
Date	1.566 (1.221, 2.009)		1.574 (1.227, 2.019)		1.511 (1.177, 1.938)	
Stream	0.308 (0.210, 0.452)		0.291 (0.193, 0.437)		0.280 (0.186, 0.421)	
Crossing group	0.165 (0.069, 0.394)		0.201 (0.084, 0.481)		0.200 (0.084, 0.476)	
Mother	0.051 (0.014, 0.178)		0.055 (0.012, 0.252)		0.055 (0.012, 0.244)	
Father	0.072 (0.026, 0.203)		0.106 (0.047, 0.238)		0.102 (0.045, 0.235)	
Hour	0.212 (0.158, 0.283)		0.266 (0.199, 0.355)		0.259 (0.194, 0.346)	

Non-migrant fish	*Upstream activity*		*Downstream activity*		*Total activity*	
Fixed effects	β (SE)	*P*	β (SE)	*P*	β (SE)	*P*
Intercept	-0.856 (0.237)	<0.001	0.642 (0.231)	0.006	1.106 (0.216)	<0.001
*vgll3*_ADDITIVE	-0.061 (0.071)	0.387	-0.047 (0.069)	0.496	-0.048 (0.064)	0.451
Sex[1]	-0.141 (0.095)	0.136	-0.123 (0.093)	0.186	-0.127 (0.086)	0.141
*vgll3*_DOMINANCE	-0.094 (0.0117)	0.418	-0.071 (0.0115)	0.537	-0.070 (0.106)	0.508

*vgll3*_ADDITIVE:Sex[1]	0.091 (0.094)	0.334	0.097 (0.092)	0.293	0.098 (0.085)	0.248
*vgll3*_DOMINANCE:Sex[1]	0.099 (0.159)	0.533	0.060 (0.156)	0.703	0.073 (0.144)	0.612
Random Effects	σ (95% CI)		σ (95% CI)		σ (95% CI)	
Individual	1.028 (0.974, 1.085)		1.013 (0.960, 1.068)		0.936 (0.888, 0.987)	
Date	0.822 (0.640, 1.056)		0.785 (0.611, 1.009)		0.734 (0.571, 0.943)	
Stream	0.262 (0.159, 0.433)		0.280 (0.172, 0.456)		0.256 (0.157, 0.417)	
Crossing group	0.177 (0.062, 0.511)		0.170 (0.057, 0.506)		0.158 (0.053, 0.467)	
Mother	0.289 (0.176, 0.477)		0.290 (0.176, 0.479)		0.269 (0.164, 0.443)	
Father	0.316 (0.211, 0.471)		0.320 (0.216, 0.474)		0.292 (0.196, 0.434)	
Hour	0.493 (0.370, 0.657)		0.476 (0.357, 0.635)		0.456 (0.342, 0.608)	

[1] Reference sex is female, [2] Reference migrant status is non-migrant

Supplementary material:

Life-history genotype explains variation in migration activity in Atlantic salmon (*Salmo salar*).

Petri T. Niemelä, Ines Klemme, Anssi Karvonen, Pekka Hyvärinen, Paul V. Debes, Jaakko Erkinaro, Marion Sinclair-Waters, Victoria L. Pritchard, Laura Härkönen, Craig R. Primmer

Glossary:

Supplementary Table 1. Parameter estimates for additive and dominance models for downstream acitivity when body condition is added as a covariate in the migrant fish model. We present fixed parameter estimates (i.e. β) with standard error (i.e. SE) and *P*-values and, random parameter estimates (i.e. standard deviation = σ) with 95% credible intervals (i.e. CI). Genotypes modeled as: *vgll3**EE = 1, *vgll3**EL = 0, *vgll3**LL = -1. Condition was defined as the residuals from the model: weight~length+lenth^2 (weight and length were measured directly after the experimental period: see methods for more detail).

Migratory phenotype	*Downstream*	
Fixed effects	β (SE)	*P*
Intercept	2.435 (0.319)	>0.001
vgll3_ADDITIVE	0.074 (0.035)	0.036
Sex[1]	-0.001 (0.047)	0.989
vgll3_DOMINANCE	0.086 (0.058)	0.139
Condition	-0.049 (0.0220)	0.027
vgll3_ADDITIVE:Sex[1]	-0.113 (0.047)	0.016
vgll3_DOMINANCE:Sex[1]	-0.077 (0.162)	0.346
Condition:Sex[1]	-0.068 (0.030)	0.024
Random Effects	σ (95% CI)	
Individual	0.407 (0.380, 0.436)	
Date	1.574 (1.227, 2.020)	
Pool	0.297 (0.198, 0.447)	
Cross	0.212 (0.090, 0.500)	
Mother	0.025 (<0.001, >10.00)	
Father	0.122 (0.063, 0.234)	
Hour	0.266 (0.199, 0.355)	

[1] Reference sex is Female

Supplementary Table 2. Data scale predictions and hourly distance moved in meters for *vgll3* and sex effects on activity. Predictions are extracted from models presented in Table 1. The conversion to meters was done by multiplying the activity estimates by 6.54, i.e. the distance between two adjacent antennae at the center of the pool.

	FEMALE		**MALE**	
	Upstream activity (SE)	***Meters/hour***	***Upstream activity (SE)***	***Meters/hour***
Migrant fish				
LL	1.89 (0.58)	12.3	1.96 (0.61)	12.8
EL	1.98 (0.61)	13.0	1.85 (0.57)	12.1
EE	2.08 (0.64)	13.6	1.74 (0.54)	11.4
Non-migrant fish				
LL	0.44 (0.11)	2.9	0.36 (0.09)	2.3
EL	0.41 (0.10)	2.7	0.37 (0.09)	2.4
EE	0.39 (0.09)	2.5	0.38 (0.09)	2.5
	Downstream activity (SE)	***Meters/hour***	***Downstream activity (SE)***	***Meters/hour***
Migrant fish				
LL	11.24 (3.58)	73.5	12.02 (3.83)	78.6
EL	12.00 (3.80)	78.5	11.26 (3.56)	73.6
EE	12.80 (4.08)	83.7	10.54 (3.36)	68.9
Non-migrant fish				
LL	1.94 (0.46)	12.7	1.59 (0.37)	10.4
EL	1.85 (0.42)	12.1	1.67 (0.38)	10.9
EE	1.77 (0.42)	11.6	1.76 (0.41)	11.5
	Total activity (SE)	***Meters/hour***	***Total activity (SE)***	***Meters/hour***
Migrant fish				
LL	15.57 (4.79)	101.8	16.59 (5.09)	108.5
EL	16.61 (5.07)	108.6	15.52 (4.74)	101.5

EE	17.71 (5.45)	115.8	14.52 (4.46)	95.0
Non-migrant fish				
LL	3.10 (0.69)	20.2	2.53 (0.56)	16.6
EL	2.95 (0.63)	19.3	2.66 (0.56)	17.4
EE	2.81 (0.62)	18.4	2.80 (0.61)	18.3

Supplementary Table 3. Parameter estimates for a model where a *vgll3*-date interaction is fitted as a random effect for the model presented in Table 1. We present fixed parameter estimates (i.e. β) standard errors (i.e. SE) and P-values. As the results were qualitatively the same across all three behaviours, we present here only the estimates for downstream activity.

Migratory fish	*Downstream activity*	
Fixed effects	β (SE)	*P*
Intercept	2.447 (0.317)	<0.001
*vgll3*_ADDITIVE	0.087 (0.038)	0.022
Sex[1]	-0.022 (0.049)	0.647
*vgll3*_DOMINANCE	0.111 (0.060)	0.063
*vgll3*_ADDITIVE:Sex[1]	-0.133 (0.048)	0.006
*vgll3*_DOMINANCE:Sex[1]	-0.126 (0.085)	0.136
Random Effects	σ	r
Individual	0.424	
Date	1.574	
vgll3_ADDITIVE	0.054	-0.61
Stream	0.290	
Crossing group	0.202	
Mother	0.054	
Father	0.106	
Hour	0.266	

[1] Reference sex is Female

Supplementary Table 4. Parameter estimates for additive and dominance models for upstream and downstream movement for migrants when date and hour are added as covariates. We present fixed parameter estimates (i.e. β) with standard error (i.e. SE) and *P*-values and, random parameter estimates (i.e. standard deviation = σ) with 95% credible intervals (i.e. CI). Genotypes modeled as: *vgll3**EE = 1, *vgll3**EL = 0, *vgll3**LL = -1.

Migrant fish	*Upstream*		*Downstream*	
Fixed effects	β (SE)	*P*	β (SE)	*P*
Intercept	0.055 (0.112)	0.623	1.502 (0.134)	<0.001
vgll3_ADDITIVE	0.059 (0.029)	0.042	0.074 (0.037)	0.047
Date	0.075 (<0.001)	<0.001	0.090 (<0.001)	<0.001
Hour	0.008 (<0.001)	<0.001	0.010 (<0.001)	<0.001
Sex[1]	-0.027 (0.039)	0.497	-0.008 (0.050)	0.880
vgll3_DOMINANCE	0.072 (0.048)	0.134	0.106 (0.061)	0.082
vgll3_ADDITIVE:Sex[1]	-0.119 (0.039)	0.002	-0.140 (0.049)	0.005
vgll3_DOMINANCE:Sex[1]	-0.091 (0.068)	0.181	-0.138 (0.086)	0.110
Random Effects	σ (95% CI)		σ (95% CI)	
Individual	0.335 (0.312, 0.360)		0.428 (0.400, 0.459)	
Stream	0.284 (0.195, 0.415)		0.325 (0.220, 0.479)	
Cross	0.151 (0.066, 0.342)		0.185 (0.081, 0.422)	
Mother	0.054 (0.016, 0.179)		0.063 (0.017, 0.233)	
Father	0.089 (0.041, 0.194)		0.122 (0.062, 0.242)	

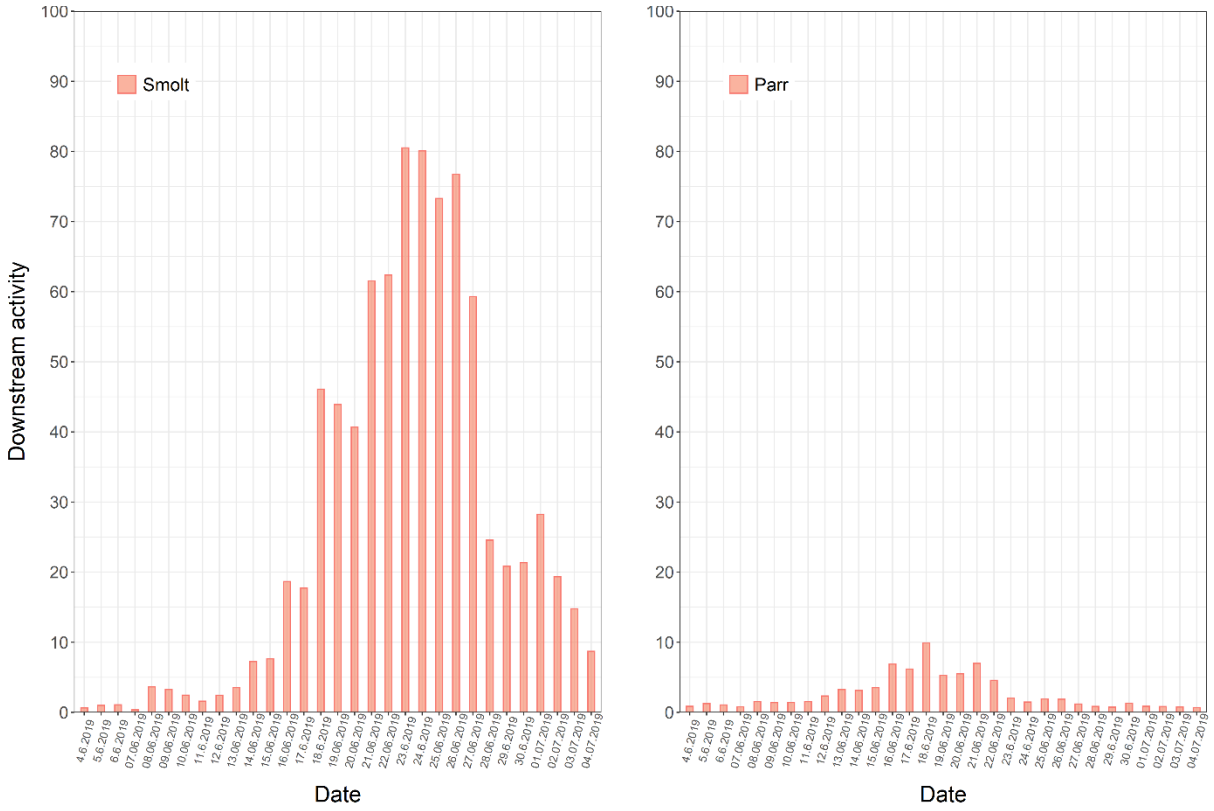
Supplementary Table 5. Parameter estimates for *vgll3* and sex effects on onset of migration. We present fixed parameter estimates (i.e. β) standard errors (i.e. SE) and P-values. Onset of migration was defined as date when the downstream movement reached 120 stream rounds day^{-1} (i.e. 5 rounds hour^{-1}) among migrant fish (see methods).

	Onset of migration	
Fixed effects	β (SE)	*P*
Intercept	15.092 (0.143)	<0.001
*vgll3*_ADDITIVE	-0.006 (0.178)	0.971
Sex[1]	-0.353 (0.198)	0.076
*vgll3*_ADDITIVE:Sex[1]	-0.208(0.243)	0.391

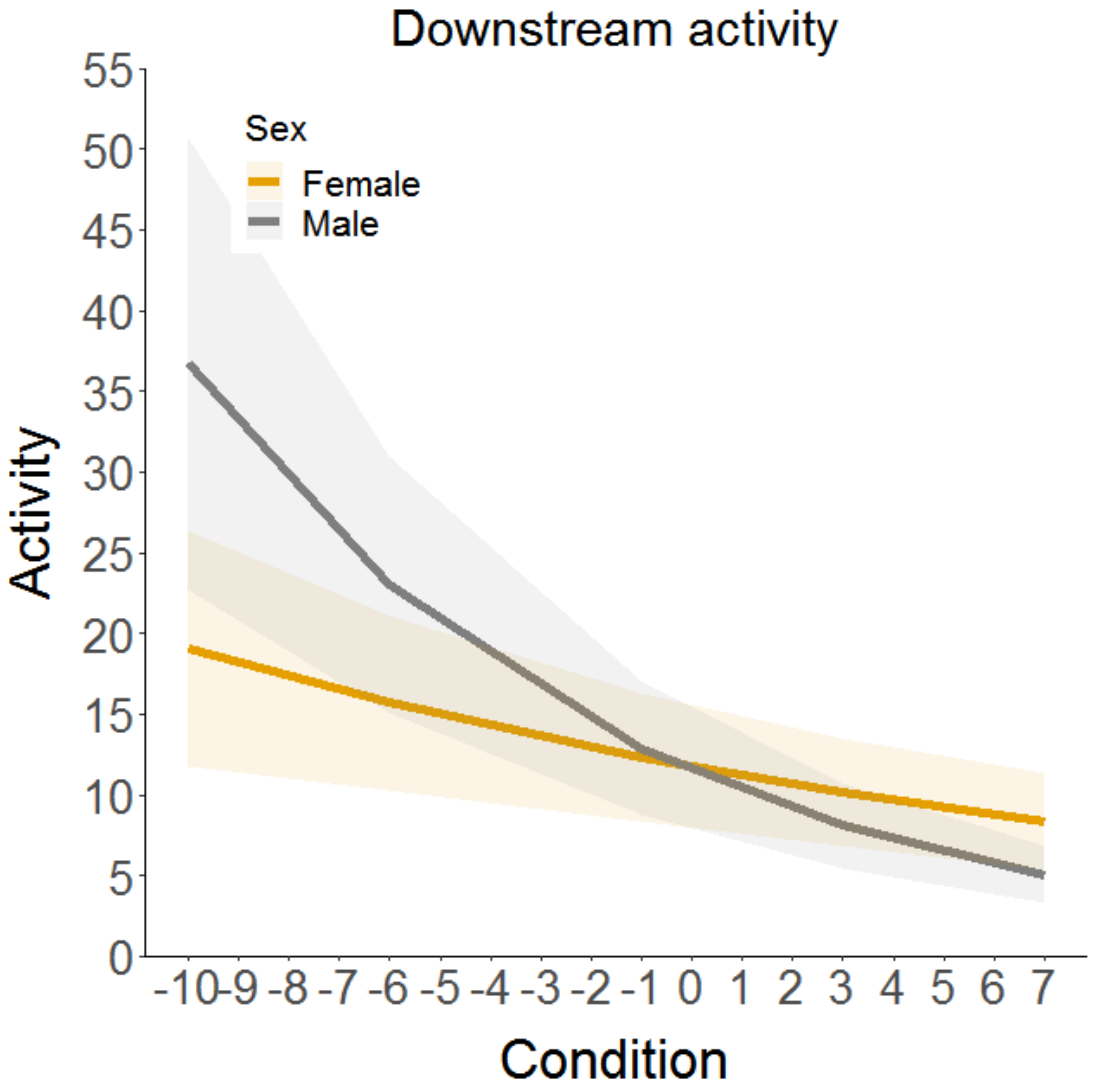
[1] Reference sex is female

Supplementary Figure 1. Photos of the ring-shaped experimental streams. Fish did not have access to the center pool in the middle of each ring-shaped stream, i.e. fish only occupied the outer ring of the stream. The picture at the bottom captures one of the four RFID-antennas in a stream covering the bottom, sides and top of the water bed in the stream. Photo credits: Ines Klemme.

Supplementary Figure 2. Best linear unbiased predictors (i.e. BLUPs) for downstream activity for each date. BLUPs are presented separately for migrant (i.e. smolt) and non-migrant (i.e. parr) fish. BLUPs for each date are extracted from models presented in Table 1. As the results were qualitatively the same across all three behaviours, we present here only the BLUPs for downstream activity.



Supplementary Figure 3. Linear predictions for sex-specific effects of body condition on recorded activity. Shaded areas represent standard errors around the predictions. The predictions are derived from model estimates presented in Supplementary Table 1. As the results were qualitatively the same across all three behaviours, we present here only the predictions for downstream activity. Condition (X-axis) was defined as the residuals from the model: weight~length+lenth^2 (weight and length were measured directly after the experimental period: see methods for more detail). In the X-axis, negative values refer to lower condition while positive values refer to higher condition.



Supplementary Figure 4. Linear prediction for the effect of *vgll3* genotype on condition among migrants. The shaded area represent standard errors around the prediction. The predictions are calculated from estimates delivered by a model: condition ~ *vgll3*_additive + Sex + (1|Stream) + (1|mother) + (1|father). Other random effects, as present in the main models, were omitted since only one condition measurement per individual was obtained (thus among-individual, date and hour variation are not present). In the Y-axis, negative values refer to lower condition while positive values refer to higher condition. Condition was defined as the residuals from the model: weight~length+lenth^2 (weight and length were measured directly after the experimental period: see methods for more detail).