Early life exploration behavior and life-history loci are co-localized in an adaptive genomic hotspot in Atlantic salmon.

Tutku Aykanat[1], Jaakko Erkinaro[2]

1. Organismal and Evolutionary Biology Research Program, Faculty of Biological and Environmental Sciences, University of Helsinki, Finland.
2. Natural Resources Institute Finland (Luke), Oulu, Finland

Abstract

1) The traits that are important for adaptation may exhibit genetic correlation due to pleiotropy or as a result of linkage. Understanding the genetic architecture of such correlations is important for predicting the selection response of populations. Exploration in fishes is a behavioral trait by which individuals may find habitats with better foraging and growth opportunities that subsequently improve their fitness. For example, in Atlantic salmon (*Salmo salar),* all individuals originate in spawning rivers where females lay eggs, but some juveniles migrate to small tributaries which are not spawning areas but provide favorable habitat patches for young salmon. The increased growth in these nursery streams may facilitate earlier sexual maturation, implying a potential correlation between exploration and maturation traits.
2) In this study, by sampling juveniles from two wild populations in the large Teno River catchment in northernmost Fennoscandia, we tested the genetic association between exploration behavior with nursery streams across four SNPs that span a 70-kb long genomic region with a major effect on age at maturity variation. Three of these SNPs are missense mutations in the *vgll3* and *akap11* genes, and one SNP tags a putative regulatory region with the strongest association with the age-at-maturity trait.

3) We show that the exploration behavior was linked to the genomic region in one of the two studied populations. However, the genetic association was substantial in the missense SNP located in the *akap11* gene, which is farthest away from the *vgll3* SNPs and previously ruled out as being linked to the age at maturity. We also detected a marginal interaction effect between SNPs in the *vgll3* gene and *akap11*, indicating a potentially complex genetic architecture underlying the trait variation.
4) Our results suggest that exploration and age at maturity are co-inherited within the same haplotype block, but we find no evidence for direct causality. These two traits may form a co-adapted trait complex that may be instrumental in local adaptation processes.

Keywords: Correlated traits, exploration, habitat shift, age at maturity, epistasis, pleiotropy, Atlantic salmon

Introduction

Elucidating the genetic architecture of adaptive traits is essential to predict the evolutionary trajectories linked to natural selection in the wild. While genome-wide scans are essential for locating genomic regions associated with phenotypic variation or adaptation, their utility to assess fine-scale adaptive landscape is limited, especially in natural populations. For example, a genomic region may harbor multiple loci associated with trait variation and, depending on the number of loci and the linkage disequilibrium between them, the predicted response to selection will vary. Close genomic proximity or close genetic linkage distances between adaptive genetic loci can constrain adaptation (Connallon & Hall 2018), but may also be selected for to preserve co-adapted allele combinations in the form of epistatic interaction (Yeaman 2013; Bank 2022). For example, the evolution of inversions reduces recombination along the inversion and allows gene complexes to be preserved over large genomic distances (Kirkpatrick 2010; Küpper et al. 2015). Such an epistasis has been suggested as an important form of genetic architecture that facilitates the coevolution of coadapted trait complexes, such as behavior and reproduction or behavior and life history (Küpper et al. 2015; Tuttle et al. 2016; Funk et al. 2021).

46 Likewise, population models suggest such nonrecombining regions may be preserved even without a need for
47 coadaptation or epistasis (Kirkpatrick & Barton 2006; Hoffmann & Rieseberg 2008), suggesting their potential
48 prevalence in the natural populations.

49 Loci that are in close proximity have inherently low recombination rate. Hence, similar to long nonrecombining
50 genomic regions, they could also harbor coadapted gene complexes or independent adaptive loci. However,
51 the prevalence of such mechanisms is not well understood in natural populations. For example, it is challenging
52 to distinguish whether multiple traits are genetically associated with independent loci within the region
53 (spurious pleiotropy) or due to true pleiotropy (linked to one causal genic polymorphism, see, e.g., Solovieff et
54 al. 2013). Distinguishing these two modes of inheritance has implications. In the evolutionary sense, pleiotropic
55 loci are harder to decouple than tightly linked independent loci (Chebib & Guillaume 2021) hence may be less
56 responsive to evolutionary pressures. On the other hand, synergistic pleiotropy may evolve as a result of strong
57 natural selection, in which case mutations effecting multiple fitness traits may be selected for (McGee et al.
58 2016). Likewise, multivariate phenotypes associated with tightly linked loci might indicate coadaptation
59 (between traits) within local demes (Yeaman & Whitlock 2011), while phenotypes under a pleiotropic effect of
60 a gene may have a developmental basis (Wagner, Pavlicev & Cheverud 2007). Therefore, linking genetic
61 architecture to ecological processes and adaptation requires information not only on the phenotypes
62 associated with the genomic region, but also on the fine-scale genetic association between phenotypes and
63 polymorphisms within genomic regions.

64 The *vgll3* locus in Atlantic salmon (*Salmo salar*) has strong potential as a genomic tool to better understand the
65 adaptive dynamics in the wild associated with a small linked genomic region. The *vgll3* genomic region, which
66 spans approximately 70 kb and encompasses the *vgll3* and *akap11* genes, was initially identified as a major
67 genomic region that explains age at maturity, a life history trait with substantial fitness effects (Ayllon et al.
68 2015; Barson et al. 2015). Further research identified that variation in other traits was also linked with genetic
69 variation in the region, such as precocious male maturation (Debes et al. 2021), repeat spawning (Aykanat et al.

70 2019), metabolism (Prokkola et al. 2022; Prokkola et al. 2024), foraging behavior (Aykanat et al. 2024),
71 exploration and aggression (Bangura et al. 2022; Bangura et al. 2024), morphology (Aykanat et al. 2025) and
72 early life fitness (Aykanat et al. 2024). The region harbors a large number of single nucleotide polymorphisms
73 (SNP), as revealed by whole genome sequencing (e.g., Barson et al. 2015), but four SNPs remain the most
74 important candidates for the association of phenotypes. These include two potentially significant functional
75 missense polymorphisms within the coding regions in the *vgll3* gene ($vgll3_{\text{Met54Thr}}$ and $vgll3_{\text{Asn323Lys}}$), one
76 missense polymorphism in the *akap11* gene ($akap11_{\text{Val214Met}}$), and a putatively regulatory SNP with the
77 strongest association with maturation age, so-called $vgll3_{\text{TOP}}$ (Barson et al. 2015). However, in most of these
78 studies, the trait-gene association was not further refined. For example, in studies that involved cross-breeding
79 designs, parental fish were usually selected to have a homogeneous *vgll3* haplotype block with full linkage
80 among these four important SNPs, primarily to increase the inference power to detect the additive genetic
81 relation. In one exceptional case, cross-breeding was designed to segregate the genetic variation between the
82 *vgll3* and *akap11* genes, which allowed further refinement of the location of causal SNPs within the genomic
83 region (Sinclair-Waters et al. 2022). Genetic variation across tightly linked loci can also be refined in wild
84 populations by exploiting natural segregation within the region. For example, Aykanat et al. (2019) attempted
85 to narrow down the genetic variation in the *vgll3* region associated with the repeat spawning phenotype along
86 four important SNPs in the region, but none of the four SNPs explained the phenotypic variation better than
87 the others, indicating insufficiency of power. Taken together, the presence of multiple adaptive traits and
88 putatively functionally important SNPs linked to the genomic region signify the importance of better
89 characterizing the genetic architectures. This will provide insight into the dynamics of evolutionary change of
90 the genomic region within and among Atlantic salmon populations.

91 Exploration in fishes is an important behavioral trait, enabling populations to spread and occupy new habitat
92 patches and resources. It can reduce the negative effects of density dependence (Einum, Sundt-Hansen & H.
93 Nislow 2006), and improve population stability (Baker et al. 2025). In juvenile Atlantic salmon, exploration

within freshwater (before emigration to the ocean) has the potential to contribute to improved feeding opportunities, better growth, and ultimately higher survival (Erkinaro & Niemelä 1995; Erkinaro & Erkinaro 1998; Johansen, Elliott & Klemetsen 2005a; Johansen, Elliott & Klemetsen 2005b). Such habitat shifts may also affect individual life history patterns (Erkinaro et al. 1997) via improved feeding and growth opportunities (e.g., Udea et al. 2025), making the individuals more likely to exceed the maturation threshold (Metcalfe 1998; Thorpe et al. 1998; Jonsson & Jonsson 2014). At the genetic level, exploration and covarying traits such as metabolism and aggression have been linked with the major loci affecting age at maturity, *vgll3* (Bangura et al. 2022; Prokkola et al. 2022; Bangura et al. 2024; Prokkola et al. 2024). For example, using a common garden design in an aquarium setting, Bangura et al. (2024) showed that juvenile Atlantic salmon with the late-maturing *vgll3*^{LL} genotype (L referring to the allele associated with late maturation) were significantly more active in the 30-minute period after their release into a novel environment than individuals with the early-maturing *vgll3*^{EE} genotype (E referring to the allele associated with early maturation). This indicates that exploration and maturation could be influenced by the same genetic locus. However, in the cross-design, the *vgll3* haplotype block was in complete linkage, and the study could not further refine the genetic basis within the genomic region.

Traditionally, Atlantic salmon juveniles are considered relatively site-attached and sedentary in their early years in freshwater (see, e.g., Jonsson & Jonsson 2011). However, in some river systems, older age groups of juvenile salmon (parr) disperse to more favorable habitat patches within freshwater systems, including lacustrine areas and smaller tributaries (Erkinaro 1995; Erkinaro, Julkunen & Niemelä 1998; Halvorsen & Jørgensen 2006). These small tributaries are nursery streams that are not suitable for salmon reproduction but may provide favorable growth and survival conditions for salmon parr by means of increased food availability and decreased competition and predation (Erkinaro & Niemelä 1995; Erkinaro & Erkinaro 1998; Erkinaro, Julkunen & Niemelä 1998; Johansen, Elliott & Klemetsen 2005b). The extent of exploratory behavior to nursery streams and its adaptive importance may be influenced by various factors, including environmental conditions, genetic

118 predispositions, and population density (e.g., Erkinaro et al. 1997; Johansen, Erkinaro & Amundsen 2010). For
119 example, the use of nursery streams by juvenile Atlantic salmon has been observed especially in northern areas
120 with depauperate fish fauna that exhibit less competition and predation threat to juvenile salmon (Erkinaro
121 1995; Erkinaro & Gibson 1997; Shustov, Baryshev & Belyakova 2012).

122 Measuring the active migration of juvenile Atlantic salmon to nursery streams is a good proxy for quantifying
123 exploration behavior in natural settings (Erkinaro, Julkunen & Niemelä 1998) and may help us to quantify
124 genetic basis of the exploration across populations. Furthermore, such migratory behavior may be linked to
125 maturation age during adulthood. The relative proportion of early maturation is shown to be higher among
126 individuals that occupy nursery streams during the juvenile stage (Erkinaro et al. 1997), which may be
127 facilitated by improved growth opportunities and the likelihood of reaching the maturation threshold (e.g.,
128 Thorpe et al. 1998). Thus, a genetic covariation between exploration and maturation timing may be
129 hypothesized as the basis of this observation.

130 Here, we quantified the genetic basis of exploration to nursery streams in two wild Atlantic salmon populations
131 in the Teno River system in northernmost Fennoscandia. We first ask whether the *vgll3* genomic region is
132 associated with exploratory behaviors to nursery streams. By further exploring the genetic architecture within
133 the *vgll3* haploblock, we asked if exploration and age at maturity traits are pleiotropic or associated with
134 different genetic loci, and if epistasis within the region may play a role in shaping trait variation.

135

136 Material and Methods

137 *Study area and sampling*

138 The Teno River (Deatnu in Sámi, Tana in Norwegian) catchment is located in far-north Europe (68–70°N, 25–
139 27°E), runs northward between Finland and Norway, and drains into the Barents Sea (Supplementary Figure 1).
140 The Teno system supports a number of Atlantic salmon populations with wide diversity in life history

141 characteristics and genetic structure within and among populations (Vähä et al. 2017; Erkinaro et al. 2019).
142 Juvenile salmon samples used in this study were originally collected for a series of studies characterizing the
143 exploration behaviors of juvenile salmon from the main stem spawning areas into small nursery streams in
144 relation to environmental conditions and fish age (Erkinaro & Niemelä 1995; Erkinaro, Julkunen & Niemelä
145 1998). Samples were collected from two populations that reproduce in the Teno main stem and Inarijoki
146 (Anárjohka in Sámi and Norwegian), a large headwater tributary of the Teno River. These two populations
147 exhibit a low level of genetic divergence (F_{ST} = 0.012, Vähä et al. 2008; Aykanat et al. 2015), but have
148 substantial differences in their life histories, with the former population having high proportions of large, later-
149 maturing individuals, and the latter population primarily consisting of younger individuals at maturity (Czorlich
150 et al. 2018, Erkinaro et al. 2019). In the spawning rivers, the Teno main stem and Inarijoki, where adult Atlantic
151 salmon reproduce and females lay eggs, juvenile salmon were captured using 600- to 900-V pulsed DC
152 electrofishing equipment. Scales were sampled (initially for age determination, but later used for DNA
153 extraction) and after sampling, the fish were released unharmed at the site of capture.

154 The sampling sites in both spawning rivers were located in close proximity (up to 100 meters) to the outlets of
155 two nursery streams, Baðđá and Guoldnájohka (Supplementary Figure 1), which drain into the Teno main stem
156 and Inarijoki, respectively (Erkinaro, Julkunen & Niemelä 1998). Juvenile salmon in the streams were captured
157 with a counting fence installed at the lowest parts of the streams, 20–50 m from the outlets, and as above, the
158 scales were sampled. After sampling, fish were released in the direction in which they had been heading (*cf.*,
159 Erkinaro, Julkunen & Niemelä 1998). Migrant fish were classified as smolt or parr based on external
160 characteristics, especially coloration, visibility of parr marks, and size (Erkinaro & Niemelä 1995). Overall, we
161 sampled and genotyped 785 individuals, of which 635 were used in the main analysis after filtering out IDs with
162 missing genotype information in focal SNPs (see below) or missing cohort year information (i.e., due to poor-
163 quality scale samples; Supplementary Table 1).

164 *DNA extraction, SNP genotyping by targeted sequencing*

165 DNA was extracted from juvenile Atlantic salmon scales using QIAamp 96DNA QIAcube HTKit (Qiagen)
166 following the manufacturer's protocol. Individuals were genotyped by targeted sequencing using a SNP panel
167 consisting of 173 SNP markers using a GTSeq approach (Campbell, Harmon & Narum 2015) as described in
168 (Aykanat et al. 2020). The SNP panel contained four SNPs from the *vgll3* genomic regions including the SNP that
169 is most highly associated with age at maturity ($vgll3_{TOP}$), two missense mutations in the *vgll3* gene ($vgll3_{Met54Thr}$
170 and $vgll3_{Asn323Lys}$), and one missense mutation in the *akap11* gene ($akap11_{Val214Met}$, Barson et al. 2015). These
171 SNPs are located on chromosome 25 and are 0.8 kb ($vgll3_{Met54Thr}$), 2.9 kb ($vgll3_{Asn323Lys}$), 10.9 kb ($vgll3_{TOP}$), and
172 65.5 kb ($akap11_{Val214Met}$) downstream of the transcription start site of the *vgll3* gene. The SNP panel also
173 included *six6* locus, a SNP highly spatially divergent between Atlantic salmon populations (Barson et al. 2015),
174 and the so-called outlier and baseline SNPs. The outlier module includes 53 highly differentiated SNPs between
175 the Inarijoki and Teno main stem populations, allowing to confirm the population of origin of individuals
176 between these two closely related populations (data not shown). The baseline module included 136 putatively
177 neutral markers in low linkage disequilibrium, distributed throughout the whole genome and previously
178 filtered to have a minor allele frequency greater than 0.05 and heterozygosity greater than 0.2 for these two
179 populations (Aykanat et al. 2016). Individuals who did not have genotype information on any of these SNPs
180 were excluded from the analysis. Bonferroni correction was applied when multiple SNPs were compared.

181 *Statistical analysis*

182 We first tested if the exploration trait is colocalized in the *vgll3* genomic region by comparing single SNP
183 association to exploration behavior, which may also address whether exploration and age at maturity are
184 pleiotropic or associated with different loci within the region. We modeled this separately for the Teno main
185 stem and Inarijoki populations using a generalized linear mixed model with a binomial error structure as
186 follows:

187 $Y_{tenoMS} = \mu + age + SNP + \varepsilon_{error}$ for Teno main stem,

188 $Y_{inari} = \mu + age + SNP + \varepsilon_{hatchyear} + \varepsilon_{error\ for}$ Inarijoki,

189 where Y is a Boolean response variable for the explorative behavior of individuals, in which individuals sampled
190 in the main stem were assumed to be sedentary, and coded as "0", and individuals sampled in the streams,
191 either descending or ascending, were assumed to be explorative and coded as "1". SNP is the genotype score
192 of SNPs, coded as 0 when individuals are homozygous for the reference alleles, 1 when homozygous for the
193 alternative alleles, and 0.5 when heterozygous. Age of the fish was determined from the sampled scales. For
194 the Inarijoki population, $\varepsilon_{hatchyear}$ is the random variance associated with the hatch year (i.e., cohort year)
195 calculated as the year sampled minus the age of the fish. Hatch year controls for potential cohort specific allele
196 frequency differences between different years. Neither the hatch year nor the sampling year overlapped for
197 the Teno main stem populations between nursery streams and main stem collections, so for this population,
198 the model did not include the random term $\varepsilon_{hatchyear}$. The model was implemented for four focal SNPs in the
199 vgll3 genomic region (*vglll3*$_{TOP}$, *vgll3*$_{Met54Thr}$, *vgll3*$_{Asn323Lys}$, *akap1*$_{Val214Met}$), , *six6 locus* that is shown to be
200 associated with age at maturity and metabolism (Sinclair-Waters et al. 2020; Prokkola et al. 2022; Prokkola et
201 al. 2024), and the rest of 169 SNPs in the SNP panel to assess baseline association levels in the putatively
202 unrelated loci. Using a similar model structure as above, we then implemented a set of models to quantify the
203 effect of epistasis within the genomic region by modeling pairwise interactions of SNPs within the *vgll3*
204 genomic regions:

205 $Y_{tenoMS} = \mu + age + SNP_1 * SNP_2 + \varepsilon_{error}$ for Teno main stem,

206 $Y_{inari} = \mu + age + SNP_1 * SNP_2 + \varepsilon_{hatchyear} + \varepsilon_{error\ for}$ Inarijoki,

207 Whereby, SNP_1 and SNP_2 are two of the four focal SNPs, and we all possible models that included any pairwise
208 comparisons between them.

209 Finally, we compared the differences in gene trait association between populations, i.e., Inarijoki and Teno
210 main stem, which are in close proximity and genetically similar, but with substantial differences in their life

211 histories. Such a difference may potentially indicate gene-by-environmental, gene-by-gene (i.e., due to
212 populations genetic background), or a combination of these two effects.

213 All models were run using the glmmTMB package, version 1.1.5, (Brooks et al. 2017) in R software version 4.4.1
214 (R Core Team 2019), using binomial error structure. Marginal means for genotype effects and their confidence
215 intervals were calculated using the emmeans package, version 1.8.5 (Lenth, 2023). Model diagnostics were
216 performed using the DHARMa package, version 0.4.6 (Hartig 2022).

217

218 Results

219 Overall, the genotyping success rate was generally low (85%, Supplementary Figure 2), mainly due to the small
220 amount of material available for DNA extraction. After removing individuals with no genotype success in any of
221 the focal SNPs (N=143) and those with no scale aging data (N=15, of which eight also did not have genotype
222 success), 635 individuals remained in the final dataset out of an initial 785.

223 In the Teno main stem population, exploration behavior towards the nursery stream, Baðđá, was not
224 significantly associated with any of the four SNPs in the *vgll3* genomic region, or any other SNPs in the panel
225 after the Bonferroni correction for multiple comparisons (Figure 1a). In the Inarijoki population, the only SNP
226 that reached the Bonferroni-corrected threshold was $akap11_{\mathrm{Val214Met}}$ (Figure 1b). Specifically, the
227 $akap11_{\mathrm{Val214Met}}^{\mathrm{EE}}$ genotype was 8.04 times (95% CI: 2.13 – 30.34) more likely to explore the nursery stream,
228 Guoldnájohka, than the $akap11_{\mathrm{Val214Met}}^{\mathrm{LL}}$ allele ($p < 0.001$, Figure 2a). The *six6* locus did not exhibit a significant
229 association in any of the populations.

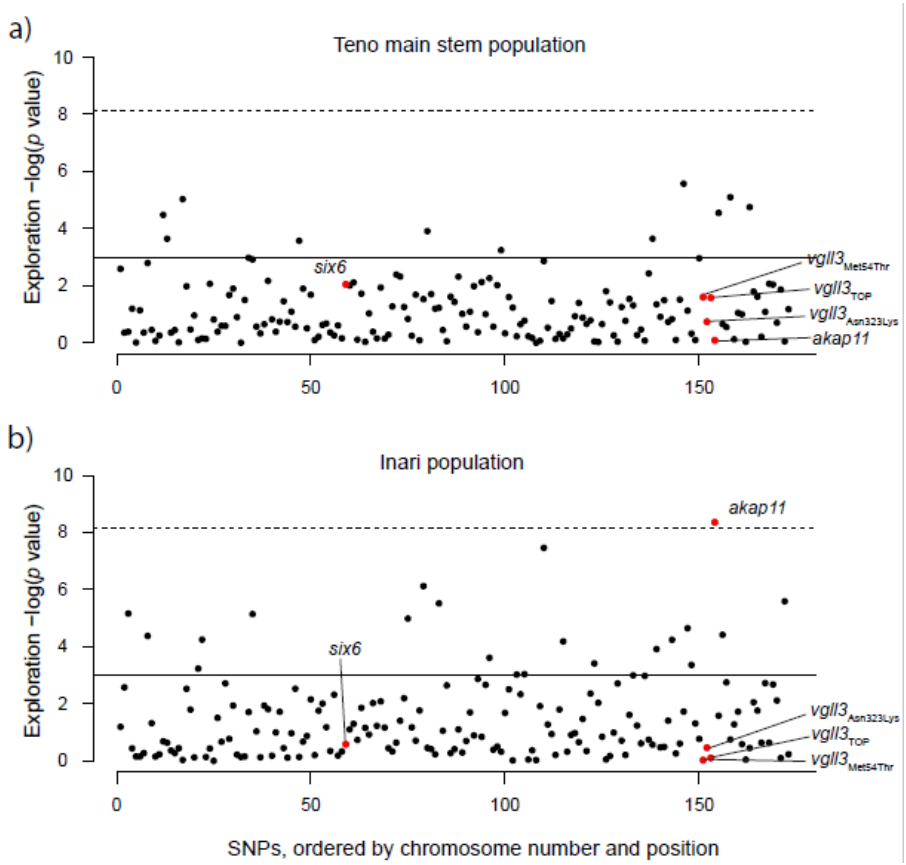


Figure 1: SNP - exploration association across 173 SNPs in Teno main stem (a) and Inarijoki (b) populations in Atlantic salmon. Focal SNPs are colored red. Uncorrected (p = 0.05) and Bonferroni corrected p-value thresholds are indicated with dashed and continuous lines.

When pairwise interactions within the *vgll3* genomic region were modeled in the Teno main stem population, none of the models were more significant than the null model that did not contain genetic effects. For the Inarijoki population, the most parsimonious model explaining the exploration included the interaction of *akap11*$_{\text{Val214Met}}$ and *vglll3*$_{\text{TOP}}$, which was superior to the null model (ΔAIC = 13.07), but only marginally to the model that only included *akap11*$_{\text{Val214Met}}$ (ΔAIC = 1.12, p = 0.077). This model was also not significantly better than the interaction between *akap11*$_{\text{Val214Met}}$ and two other SNPs in the *vgll3* genomic region (ΔAIC < 2, Supplementary Figure 3). This marginal interaction effect was driven by a decrease in exploration behavior associated with the genotype combination of *akap11*$_{\text{Val214Met}}^{\text{EL}}$ and *vgll3*$_{\text{TOP}}^{\text{EL}}$ (Figure 2b, Supplementary Figure 4). As such, the model predicts that the odds of exploration for individuals with *akap11*$_{\text{Val214Met}}^{\text{EL}}$ and *vgll3*$_{\text{TOP}}^{\text{EL}}$

243 was 3.69 (95% CI 1.63-8.36, p<0.001) and 3.04 (95% CI 0.80-11.47, p=0.14) times less than for *akap11*$_{Val214Met}^{EE}$

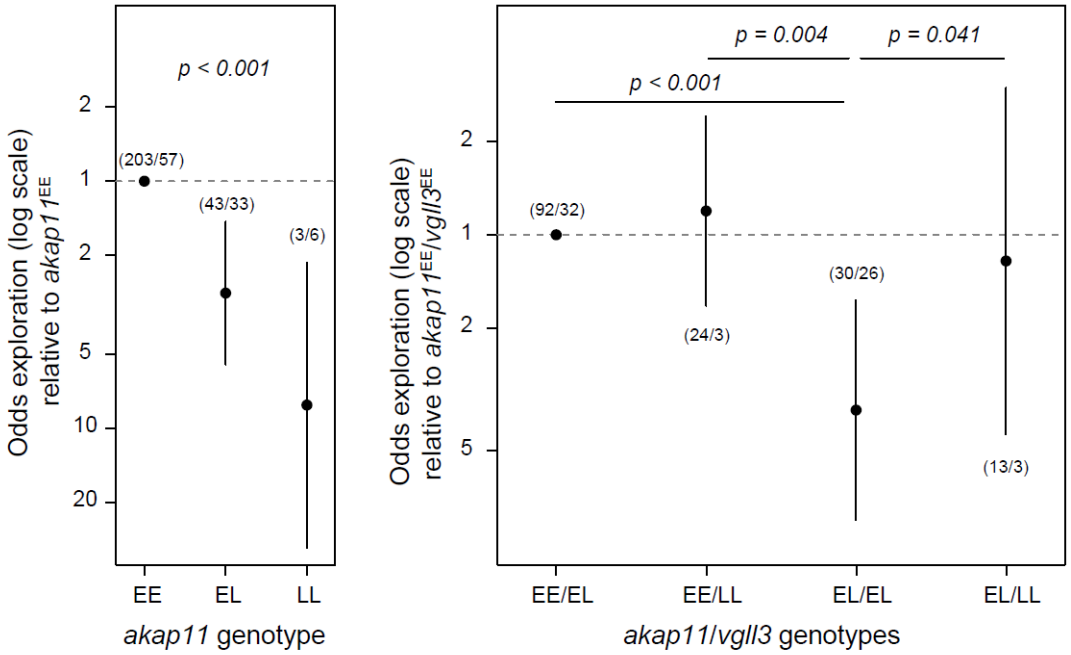
244 and *vgll3*$_{TOP}^{EL}$ and *akap11*$_{Val214Met}^{EL}$ and *vgll3*$_{TOP}^{EL}$, respectively (Figure 2b). The fit of the model with only *akap11*

245 genotype modelled, nor the model with the *vgll3*$_{TOP}$ and *akap11* interaction did not exhibit substantial

246 deviation from model assumption, as assessed visually by DHARMa package's (Hartig 2022) diagnostics plots

247 (Supplementary Figure 5). For both rivers, exploration to nursery streams increased with age (p< 0.001 for both

248 rivers), concordant with the previous reports (Erkinaro 1995).



249

250 **Figure 2: a)** Odds of exploration in Inarijoki Atlantic salmon as a function of the *akap11*$_{Val214Met}$ SNP, and **b)** as a
251 function of the *akap11*$_{Val214Met}$ and *vgll3*$_{TOP}$ interaction. The error bars indicate 95% CI of the marginal estimates,
252 and the first and second numbers in parentheses indicate the sample sizes in the nursery stream and the main
253 stream, respectively. The Y axis is drawn on a logarithmic scale.

254 The fish sampled in Guoldnájohka contained 83 individuals that had undergone smoltification (or were in the

255 process of becoming smolt), which is a suite of physiological, morphological, and behavioral changes in Atlantic

256 salmon juveniles for becoming ready for seaward migration (McCormick & Saunders 1987), which may have

257 altered their exploration behavior. However, when the smolts were excluded from the analysis, the results

258 were mostly qualitatively similar (Supplementary Figure 6). One notable difference was that a model with the
259 *akap11*$_{Val214Met}$ and *vgll3*$_{TOP}$ interaction was the best model. As in the full dataset, the fit of the interaction
260 model the was not significantly better than the fit of the model with only additive effects of only a*kap11*$_{Val214Met}$
261 (p = 0.12, ΔAIC = 0.19, Supplementary Figure 6). However, the change was not meaningfully different from an
262 effect that might have resulted from a reduced sample size in a random manner. As such, when 83 parr were
263 randomly sampled and excluded from the dataset (i.e., the same number as the smolts in the dataset) or 83
264 randomly selected parrs in the dataset were used as a replacement for the excluded smolts, the ΔAIC range of
265 these models (each permuted 1000 times) was similar to the ΔAIC values obtained in the original model
266 (Supplementary Figure 7).

267

268 Discussion

269 The factors shaping the genetic architecture of ecologically important traits are fundamentally important to
270 understand adaptive dynamics in the wild. We have demonstrated that the exploration behavior in juvenile
271 Atlantic salmon is linked to a genomic region on chromosome 25 in one of the two populations in the Teno
272 River. This region contains the *vgll3* and *akap11* genes and is associated with a suite of traits involved in salmon
273 adaptation (reviewed in Mobley et al. 2021) including age at maturity (Barson et al. 2015). We have found that
274 a missense SNP in the *akap11* gene (*akap11*$_{Val214Met}$) was substantially linked to exploratory behavior, while
275 SNPs in the *vgll3* gene exhibited a marginally supported epistasis with this SNP, suggesting a complex genetic
276 architecture in the region. Furthermore, the genetic effect was only observed in one of the two populations
277 studied, indicating the importance of environment or population-specific factors in triggering gene-dependent
278 exploration behavior.

279 Our results showed that the early maturation allele in the *akap11* gene was associated with increased
280 exploration to nursery streams in the Inarijoki population. This is consistent with the findings of Erkinaro et al.

281 (1997) who, by analyzing freshwater growth patterns of salmon, suggested that juveniles entering nursery
282 streams had a greater tendency to mature and return from their sea journey earlier than those that stayed in
283 the main stem for their juvenile years. Differences in growth opportunity in Atlantic salmon juveniles, which is
284 linked to efficient acquisition of resources, may be instrumental in exceeding the maturation threshold in
285 subsequent years (Metcalfe 1998; Thorpe et al. 1998; Jonsson & Jonsson 2014). As such, causality between
286 exploration and migrating to nursery streams may be suggested based on the increased likelihood of
287 individuals in the streams to reach the maturation threshold (e.g., Thorpe et al. 1998) upon increased growth
288 opportunities. However, the association was predominantly driven by genetic variation in the *akap11*$_{\text{Val214Met}}$
289 SNP, which is about 70 kb downstream of the *vgll3* gene and exhibits a weaker association with sea age at
290 maturity (Barson et al. 2015). The *akap11*$_{\text{Val214Met}}$ SNP was also previously ruled out as the genetic basis for
291 early male maturation in Atlantic salmon in controlled settings (Sinclair-Waters et al. 2022). Combined, while
292 exploration behavior may facilitate earlier maturation in a context-dependent manner, our results do not
293 provide evidence to support a direct genetic causation between the two, but that a small region explains both
294 maturation and exploration behaviors, and that the two traits are genetically correlated by linkage.

295 A multitude of phenotypic traits may be linked within a genomic region via pleiotropy or linkage disequilibrium
296 (that is, spurious pleiotropy, Solovieff et al. 2013). This makes it challenging to identify the phenotypic traits
297 under selection, e.g., by using genomic scans (Paaby & Rockman 2013; Solovieff et al. 2013). Our results
298 indicate that the *vgll3* genomic region contains multiple independent SNPs linked to adaptive traits, ruling out
299 pleiotropy as the basis of multi-trait association. The presence of multiple adaptive traits within a tightly linked
300 genomic region raises the question of whether the genetic covariation between these loci harbors coadapted
301 trait combinations. Linked architectures may facilitate adaptation by enabling co-inheritance of adapted gene
302 complexes (Mullon, Keller & Lehmann 2017; Oomen, Kuparinen & Hutchings 2020). For example, genomic
303 inversions have been shown to be important in maintaining coadapted trait combinations, including migratory
304 strategies and dispersal (Mullon, Keller & Lehmann 2017; Wellenreuther & Bernatchez 2018; Rubenstein et al.

305 2019). Similarly, genetic variation in migratory ecotypes in rainbow trout (*Oncorhynchus mykiss*, Pearse et al.
306 2014) and Atlantic cod (*Gadus morhua*) have been shown to be associated with genetic markers in a large
307 inverted region (Kirubakaran et al., 2016). A tight linkage between adaptive traits might also be selected for
308 when locally adapted populations may have varying local fitness optima (for these traits) and exhibit high gene
309 flow between them (Yeaman & Whitlock 2011). In this case, a tight linkage between locally adapted traits
310 would help in purging maladaptive genetic variants with a relatively reduced genetic load.

311 In a practical sense, our results also highlight the insufficiency of drawing conclusions when only one SNP is
312 used as a tag marker to represent the genetic makeup of tightly linked genomic regions. In common garden
313 cross-breeding designs, one SNP marker may be utilized to tag the whole region when exploring the trait-
314 genotype association of the region (e.g., Prokkola et al., 2022; Bangura et al., 2024). While such designs provide
315 substantial statistical and cost reduction benefits, they would not be able to discern associations across SNPs in
316 close proximity, and their interactions. For example, using a common garden setup, Bangura et al., (2024),
317 suggested that *vgll3* is likely to play a role in exploration behaviors. However, in the cross-breeding design,
318 parents were chosen to be in complete linkage regarding the genetic variation in *akap11* and *vgll3* SNPs,
319 thereby deduction of SNP effects independently is not possible (see also, Bangura et al., 2022). In fact, when
320 Sinclair-Waters et al., (2022) refined the association of SNPs in the vgll3 genomic region, in relation to their
321 effect on male parr maturation, they found an opposite effect of SNPs in the *vgll3* and *akap11* gene, whereby
322 the early maturation allele in the *akap11* gene was indeed marginally associated with reduced maturation,
323 further signifying the importance of refining genetic associations when multiple candidate SNPs may underlie
324 the phenotypic variation.

325 Our study provides a further outlook on the dynamics of behavioral syndromes and correlated behaviors
326 (Höjesjö, Johnsson & Bohlin 2004; Garamszegi, Markó & Herczeg 2013; Mathot, Dingemanse & Nakagawa
327 2019; Axling et al., 2023). The classic paradigm suggests that dispersal is negatively correlated with dominance
328 and aggression, whereby dominant individuals monopolize favorable habitat patches and force subordinate

329 individuals to displace in search of new habitats (Stamps 1994; Stamps 1999). However, in Atlantic salmon,
330 migration to nursery streams might be carried out by individuals holding higher positions in the dominance
331 hierarchy (Erkinaro & Niemelä 1995). Using seasonal growth in scale depositions, Erkinaro and Niemelä (1995)
332 estimated growth in previous seasons, a trait correlated with dominance and aggression in early life stages
333 (Cutts et al., 2005), and showed that faster growing individuals are more likely to migrate to the small nursery
334 streams. A similar tendency in individual growth patterns has also been identified in individuals shifting their
335 juvenile rearing habitat to lacustrine areas of the catchment (Erkinaro et al., 1998). A niche shift, i.e., by
336 migrating to nursery streams, may be hypothesized to be a mechanism to overcome potential resource
337 mismatch in the original habitat. Therefore, we would predict that the EE allele in the *vgll3* genomic region is
338 likely associated with behavioral traits correlated with exploration in salmon, such as dominance.

339 On the other hand, common garden experiments under controlled conditions do not support our prediction.
340 For example, by quantifying the exploration of new environments in a confined space (an aquarium with a
341 surface area of 25 x 30 cm), Bangura et al., (2024) found that the *vgll3* L allele was associated with greater
342 exploration in a novel environment. Similarly, using a similar experimental setup, Bangura et al., (2022) also
343 found increased aggression associated with the *vgll3* L allele. These results suggest that there is a genetic
344 covariation between aggression and novel environmental exploration, but with an opposite direction of allelic
345 effect to our study. (Note that in the crosses used by Bangura et al., (2022) and Bangura et al., (2024) *akap11*
346 and *vgll3* were in full linkage, so conclusions related to the genetic variation in the *vgll3* SNPs are equally valid
347 for the *akap11* SNP.) These contrasting results can reflect contextual differences between natural and common
348 garden settings. As such, a meta-analysis has shown that these two personality traits (aggression and
349 exploration) only correlate when there is a contextual overlap that underlies the similarity of trait expression
350 (Garamszegi, Markó & Herczeg 2013). Therefore, the contrasting conclusions in these two settings (natural vs.
351 laboratory) may stem from different functional physiological processes. Alternatively, strong environment
352 (common garden vs. natural setting) by genotype, or population by genotype interactions may explain the

353 contrast. For the latter, for example, the parental fish used in Bangura et al., (2022) and Bangura et al., (2024)
354 are obtained from a hatchery broodstock of salmon managed by the Natural Resources Institute Finland
355 (LUKE), initially originated from a Baltic Sea population (River Neva). Therefore, differences in the genetic
356 background of fish may also explain the discrepancies. In fact, the genetic association between SNPs in the
357 *vgll3* genomic region and exploration was significant only in the Inarijoki population, while no detectable effect
358 was found in the Teno main stem population, further highlighting a potential role of population-specific
359 differences in the genetic basis of trait variation. Our study illustrates the complex dynamics of the correlated
360 behaviors of Atlantic salmon and their genetic background.

361 Finally, we found a marginal support for epistasis between *akap11* and the *vgll3* gene, in which the fit of the
362 interaction model was better than the fit model with only *akap11* SNP, but this did not reach to a significance
363 at alpha value = 0.05. The statistical power was also insufficient to determine which of the SNPs in the *vgll3*
364 gene are the most likely candidates. However, the suggestive signals of epistasis may be an indication of a
365 complex genetic architecture within the genomic region. Epistasis contributes to the trait variance and helps
366 maintain additive genetic variation upon selection (Cheverud & Routman 1995). Furthermore, the trait
367 complex between exploration and age at maturity may contribute to the adaptation dynamics. For example,
368 optimal trait combinations (of traits co-inherited within a haplotype block) may be locally variable among
369 populations and may improve overall fitness compared to what would be predicted by only additive gene
370 action. Such an epistatic interaction would also facilitate purging of maladapted genetic combinations (Yeaman
371 & Whitlock 2011).

372 We used historical field data that were not originally intended for a genetic study such as this. Therefore, the
373 design has some drawbacks. For example, the hatching year, which represents the year that the offspring
374 originate from, was not modelled for the Teno main stem and Baðða stream due to the lack of temporal
375 overlap between sites. Therefore, we cannot rule out the possibility that the (lack of) difference in genetic
376 response is due to temporal changes in allele frequencies between cohorts, even though the time span

377 between sampling periods is only a few years. However, the hatch year was accounted for in the model for the
378 Inarijoki population, by which we controlled for temporal genetic changes between cohort years. Second,
379 genotype calling failed for a substantial portion of individuals due to the suboptimal amount of tissue
380 remaining in the storage envelopes. In addition, we used a targeted genotyping approach by scoring only the
381 most likely candidate SNPs in the genomic region. An alternative approach to sequence the whole genomic
382 region might provide finer resolution in trait association and help to better narrow down the causal region.

383 In this study, two life history genomic regions were the primary focus (*vgll3* and six6), and other SNPs
384 genotyped was used to account for potential inflation in the statistical tests. Therefore, by design, we did not
385 perform large scale scans to explore the signals of association at genomic scale, which may provide insights to
386 the molecular mechanisms underlying the trait variation. Genome wide association analyses have identified a
387 number small effect loci linked to age-at-maturity (Ayllon et al., 2015; Gutierrez et al., 2015; Sinclair-Waters et
388 al., 2020), but such studies for traits such as movement or exploration are mostly missing in non-model
389 organisms, e.g., Atlantic salmon. Theory of omnigenic genetic architecture predicts that major regulatory
390 proteins may drive covariation in multiple traits via highly pleiotropic function (Boyle et al., 2017; Liu et al.,
391 2019). In humans, genome-wide meta-analyses have been used to genetically link personality traits to larger
392 psychological disorders (Lo et al., 2017; Gupta et al., 2024). Such approaches as in human studies may help to
393 better understand to linking exploration and life-history at the molecular level and potential regulatory
394 networks shared by these two traits (Liu et al., 2019; Boyle et al., 2017*;* Mathieson 2021), once the genome-
395 wide association are available for the trait of interests (i.e., exploration).

396 Our system included only two populations from a northern River which are generally low-nutrient, low
397 productivity areas with depauperate fish species communities, and whether the observed genetic effects are
398 parallel across the species range is unclear. The association between age-at-maturity and the *vgll3* genomic
399 region is sex and region specific for the North American populations (Kusche et al., 2017; Kess et al., 2024), and
400 may have an environmental component in some European populations (Bersnier et al., 2019; Ayllon et al.,

401 2019). Exploration behavior may alter life-history variation context dependently, e.g., via means of enabling
402 improved feeding opportunities (Wright et al., 2007; Chapman et al., 2012). Therefore, it is intriguing to ask
403 whether such context dependent association between the *vgll3* genomic region and age-at-maturity may have
404 linked to the *akap11* gene.

405 Movement patterns in the Salmonidae family are mostly studied in the context of the phenology of migration,
406 which is central to their life histories, has a heritable component, and has strong fitness consequences
407 (Niemelä et al., 2006; Stewart, Middlemas & Youngson 2006). Many species exhibit a strong dichotomy of the
408 trait within and among populations, as evidenced by the presence of both resident and migratory forms in,
409 e.g., brown trout, rainbow/steelhead trout, and Arctic char (Jonsson & Jonsson 1993). Movement within the
410 freshwater habitat at the juvenile stage and its association with migration at later stages are much less
411 explored. Our study demonstrates a complex genetic interaction between freshwater exploration and maturity
412 age. The linked inheritance of these two functional traits (exploration and maturation) may help to maintain
413 coadapted trait complexes, and may be instrumental in local adaptation processes, fitness, and the long-term
414 survival of populations.

415

416 Acknowledgement

417 We thank Susanna Ukonaho and Meri Lindquist from the University of Turku for help with DNA extraction,
418 Matti Kylmäaho from Luke for scale aging, and Lars Paulin from the University of Helsinki for coordinating the
419 genotyping-by-sequencing assays. Funding came from the Research Council of Finland (353388 and 325964 to
420 T.A.). We thank to Craig Primmer for his communication during the making of the study.

421

422 Conflict of Interest

423 The authors declare no competing interests.

References

Axling, J., Vossen, L.E., Peterson, E. & Winberg, S. (2023) Boldness, activity, and aggression: Insights from a large-scale study in Baltic salmon (*Salmo salar* L). *PLoS One,* **18,** e0287836. 10.1371/journal.pone.0287836.

Ayllon, F., Solberg, M.F., Glover, K.A., Mohammadi, F., Kjaerner-Semb, E., Fjelldal, P.G., Andersson, E., Hansen, T., Edvardsen, R.B. & Wargelius, A. (2019) The influence of vgll3 genotypes on sea age at maturity is altered in farmed mowi strain Atlantic salmon. BMC Genetics, 20, 44. 10.1186/s12863-019-0745-9.

Ayllon, F., Kjaerner-Semb, E., Furmanek, T., Wennevik, V., Solberg, M.F., Dahle, G., Taranger, G.L., Glover, K.A., Almen, M.S., Rubin, C.J., Edvardsen, R.B. & Wargelius, A. (2015) The *vgll3* Locus Controls Age at Maturity in Wild and Domesticated Atlantic Salmon (*Salmo salar L.*) Males. *PLoS Genetics*, 11, e1005628. 10.1371/journal.pgen.1005628.

Aykanat, T., Debes, P.V., Jansouz, S., Gueguen, L., House, A.H., Ruokolainen, A., Erkinaro, J., Pritchard, V.L., Primmer, C.R. & Bolstad, G.H. (2025) Large effect life-history genomic regions are associated with functional morphological traits in Atlantic salmon. *G3 (Bethesda)*.

Aykanat, T., Johnston, S.E., Orell, P., Niemelä, E., Erkinaro, J. & Primmer, C.R. (2015) Low but significant genetic differentiation underlies biologically meaningful phenotypic divergence in a large Atlantic salmon population. *Molecular Ecology,* **24,** 5158-5174. 10.1111/mec.13383.

Aykanat, T., Lindqvist, M., Pritchard, V.L. & Primmer, C.R. (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*. *Journal of Fish Biology,* **89,** 2658-2679. 10.1111/jfb.13149.

Aykanat, T., McLennan, D., Metcalfe, N.B. & Prokkola, J.M. (2024) Early survival in Atlantic salmon is associated with parental genotypes at loci linked to timing of maturation. *Evolution,* **78,** 1441-1452. 10.1093/evolut/qpae072.

Aykanat, T., Ozerov, M., Vähä, J.P., Orell, P., Niemelä, E., Erkinaro, J. & Primmer, C.R. (2019) Co-inheritance of sea age at maturity and iteroparity in the Atlantic salmon *vgll3* genomic region. *Journal of Evolutionary Biology,* **32,** 343-355. 10.1111/jeb.13418.

Aykanat, T., Rasmussen, M., Ozerov, M., Niemelä, E., Paulin, L., Vähä, J.P., Hindar, K., Wennevik, V., Pedersen, T., Svenning, M.A. & Primmer, C.R. (2020) Life-history genomic regions explain differences in Atlantic salmon marine diet specialization. *Journal of Animal Ecology,* **89,** 2677-2691. 10.1111/1365-2656.13324.

Ayllon, F., Kjaerner-Semb, E., Furmanek, T., Wennevik, V., Solberg, M.F., Dahle, G., Taranger, G.L., Glover, K.A., Almen, M.S., Rubin, C.J., Edvardsen, R.B. & Wargelius, A. (2015) The *vgll3* Locus Controls Age at Maturity in Wild and Domesticated Atlantic Salmon (*Salmo salar* L.) Males. *PLoS Genetics,* **11,** e1005628. 10.1371/journal.pgen.1005628.

Baker, H.K., Obedzinski, M., Grantham, T.E. & Carlson, S.M. (2025) Variation in Salmon Migration Phenology Bolsters Population Stability but Is Threatened by Drought. *Ecology Letters,* **28,** e70081. 10.1111/ele.70081.

Bangura, P.B., Tiira, K., Aykanat, T., Niemelä, P.T., Erkinaro, J., Liljestrom, P., Toikkanen, A. & Primmer, C.R. (2024) Sex-specific associations of the maturation locus vgll3 with exploratory behavior and boldness in Atlantic salmon juveniles. *Ecology and Evolution,* **14,** e11449. 10.1002/ece3.11449.

Bangura, P.B., Tiira, K., Niemelä, P.T., Erkinaro, J., Liljestrom, P., Toikkanen, A. & Primmer, C.R. (2022) Linking vgll3 genotype and aggressive behaviour in juvenile Atlantic salmon (*Salmo salar*). *Journal of Fish Biology,* **100,** 1264-1271. 10.1111/jfb.15040.

468 Bank, C. (2022) Epistasis and Adaptation on Fitness Landscapes. *Annual Review of Ecology, Evolution, and*
469 *Systematics,* **53,** 457-479. 10.1146/annurev-ecolsys-102320-112153.
470 Barson, N.J., Aykanat, T., Hindar, K., Baranski, M., Bolstad, G.H., Fiske, P., Jacq, C., Jensen, A.J., Johnston, S.E.,
471 Karlsson, S., Kent, M., Moen, T., Niemelä, E., Nome, T., Naesje, T.F., Orell, P., Romakkaniemi, A.,
472 Saegrov, H., Urdal, K., Erkinaro, J., Lien, S. & Primmer, C.R. (2015) Sex-dependent dominance at a single
473 locus maintains variation in age at maturity in salmon. *Nature,* **528,** 405-408. 10.1038/nature16062.
474 Besnier, F., Skaala, O., Wennevik, V., Ayllon, F., Utne, K.R., Fjeldheim, P.T., Andersen-Fjeldheim, K., Knutar, S. &
475 Glover, K.A. (2024) Overruled by nature: A plastic response to environmental change disconnects a
476 gene and its trait. *Molecular Ecology*, 33, e16933. 10.1111/mec.16933.
477 Boyle, E.A., Li, Y.I. & Pritchard, J.K. (2017) An Expanded View of Complex Traits: From Polygenic to Omnigenic.
478 *Cell*, 169, 1177-1186. 10.1016/j.cell.2017.05.038.
479 Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Machler, M.
480 & Bolker, B.M. (2017) glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated
481 Generalized Linear Mixed Modeling. *R Journal,* **9,** 378-400. 10.32614/Rj-2017-066.
482 Campbell, N.R., Harmon, S.A. & Narum, S.R. (2015) Genotyping-in-Thousands by sequencing (GT-seq): A cost
483 effective SNP genotyping method based on custom amplicon sequencing. *Molecular Ecology Resources,*
484 **15,** 855-867. 10.1111/1755-0998.12357.
485 Chapman, B.B., Hulthen, K., Brodersen, J., Nilsson, P.A., Skov, C., Hansson, L.A. & Bronmark, C. (2012) Partial
486 migration in fishes: causes and consequences. *Journal of Fish Biology*, 81, 456-478. 10.1111/j.1095-
487 8649.2012.03342.x.
488 Chebib, J. & Guillaume, F. (2021) Pleiotropy or linkage? Their relative contributions to the genetic correlation of
489 quantitative traits and detection by multitrait GWA studies. *Genetics,* **219**. 10.1093/genetics/iyab159.
490 Cheverud, J.M. & Routman, E.J. (1995) Epistasis and its contribution to genetic variance components. *Genetics,*
491 **139,** 1455-1461. 10.1093/genetics/139.3.1455.
492 Connallon, T. & Hall, M.D. (2018) Genetic constraints on adaptation: a theoretical primer for the genomics era.
493 *Annals of the New York Academy of Sciences,* **1422,** 65-87. 10.1111/nyas.13536.
494 Cutts, C.J., Brembs, B., Metcalfe, N.B. & Taylor, A.C. (2005) Prior residence, territory quality and life-history
495 strategies in juvenile Atlantic salmon (*Salmo salar* L.). *Journal of Fish Biology,* **55,** 784-794.
496 10.1111/j.1095-8649.1999.tb00717.x.
497 Czorlich, Y., Aykanat, T., Erkinaro, J., Orell, P. & Primmer, C.R. (2018) Rapid sex-specific evolution of age at
498 maturity is shaped by genetic architecture in Atlantic salmon. *Nature Ecology and Evolution*, **2**, 1800-
499 1807. 10.1038/s41559-018-0681-5.
500 Debes, P.V., Piavchenko, N., Ruokolainen, A., Ovaskainen, O., Moustakas-Verho, J.E., Parre, N., Aykanat, T.,
501 Erkinaro, J. & Primmer, C.R. (2021) Polygenic and major-locus contributions to sexual maturation
502 timing in Atlantic salmon. *Molecular Ecology,* **30,** 4505-4519. 10.1111/mec.16062.
503 Einum, S., Sundt-Hansen, L. & H. Nislow, K. (2006) The partitioning of density-dependent dispersal, growth and
504 survival throughout ontogeny in a highly fecund organism. *Oikos,* **113,** 489-496. 10.1111/j.2006.0030-
505 1299.14806.x.
506 Erkinaro, H. & Erkinaro, J. (1998) Feeding of Atlantic salmon,*Salmo salar* L., parr in the subarctic River Teno and
507 three tributaries in northernmost Finland. *Ecology of Freshwater Fish,* **7,** 13-24. 10.1111/j.1600-
508 0633.1998.tb00168.x.
509 Erkinaro, J. (1995) The age structure and distribution of Atlantic salmon parr, *Salmo salar* L., in small tributaries
510 and main stems of the subarctic River Teno, northern Finland. *Ecology of Freshwater Fish,* **4,** 53-61.
511 10.1111/j.1600-0633.1995.tb00117.x.
512 Erkinaro, J., Czorlich, Y., Orell, P., Kuusela, J., Falkegård, M., Länsman, M., Pulkkinen, H., Primmer, C.R. &
513 Niemelä, E. (2019) Life history variation across four decades in a diverse population complex of Atlantic
514 salmon in a large subarctic river. *Canadian Journal of Fisheries and Aquatic Sciences,* **76,** 42-55.
515 10.1139/cjfas-2017-0343.

Erkinaro, J., Dempson, J.B., Julkunen, M. & Niemelä, E. (1997) Importance of ontogenetic habitat shifts to juvenile output and life history of Atlantic salmon in a large subarctic river: an approach based on analysis of scale characteristics. *Journal of Fish Biology,* **51,** 1174-1185. 10.1111/j.1095-8649.1997.tb01134.x.

Erkinaro, J. & Gibson, R.J. (1997) Interhabitat migration of juvenile Atlantic salmon in a Newfoundland river system, Canada. *Journal of Fish Biology,* **51,** 373-388. 10.1111/j.1095-8649.1997.tb01673.x.

Erkinaro, J., Julkunen, M. & Niemelä, E. (1998) Migration of juvenile Atlantic salmon *Salmo salar* in small tributaries of the subarctic River Teno, northern Finland. *Aquaculture,* **168,** 105-119. 10.1016/S0044-8486(98)00343-3.

Erkinaro, J. & Niemelä, E. (1995) Growth Differences between the Atlantic Salmon Parr, *Salmo-Salar*, of Nursery Brooks and Natal Rivers in the River Teno Watercourse in Northern Finland. *Environmental Biology of Fishes,* **42,** 277-287. 10.1007/Bf00004921.

Erkinaro, J., Niemelä, E., Saari, A., Shustov, Y. & Jørgensen, L. (1998) Timing of habitat shift by Atlantic salmon parr from fluvial to lacustrine habitat: analysis of age distribution, growth, and scale characteristics. *Canadian Journal of Fisheries and Aquatic Sciences,* **55,** 2266-2273. 10.1139/f98-107.

Funk, E.R., Mason, N.A., Palsson, S., Albrecht, T., Johnson, J.A. & Taylor, S.A. (2021) A supergene underlies linked variation in color and morphology in a Holarctic songbird. *Nature Communications,* **12,** 6833. 10.1038/s41467-021-27173-z.

Garamszegi, L.Z., Markó, G. & Herczeg, G. (2013) A meta-analysis of correlated behaviors with implications for behavioral syndromes: relationships between particular behavioral traits. *Behavioral Ecology,* **24,** 1068-1080. 10.1093/beheco/art033.

Gutierrez, A.P., Yanez, J.M., Fukui, S., Swift, B. & Davidson, W.S. (2015) Genome-wide association study (GWAS) for growth rate and age at sexual maturation in Atlantic salmon (*Salmo salar*). *PLoS One*, 10, e0119730. 10.1371/journal.pone.0119730.

Gupta, P., Galimberti, M., Liu, Y., Beck, S., Wingo, A., Wingo, T., Adhikari, K., Kranzler, H.R., Program, V.A.M.V., Stein, M.B., Gelernter, J. & Levey, D.F. (2024) A genome-wide investigation into the underlying genetic architecture of personality traits and overlap with psychopathology. Nature Human Behaviour, 8, 2235-2249. 10.1038/s41562-024-01951-3.

Halvorsen, M. & Jørgensen, L. (2006) Lake-use by juvenile Atlantic salmon (*Salmo salar* L.) and other salmonids in northern Norway. *Ecology of Freshwater Fish,* **5,** 28-36. 10.1111/j.1600-0633.1996.tb00034.x.

Hartig F (2022). DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.4.6.

Höjesjö, J., Johnsson, J.r. & Bohlin, T. (2004) Habitat complexity reduces the growth of aggressive and dominant brown trout (Salmo trutta) relative to subordinates. *Behavioral Ecology and Sociobiology,* **56**. 10.1007/s00265-004-0784-7.

Hoffmann, A.A. & Rieseberg, L.H. (2008) Revisiting the Impact of Inversions in Evolution: From Population Genetic Markers to Drivers of Adaptive Shifts and Speciation? *Annual Reviews in Ecology, Evolution and Systematics,* **39,** 21-42. 10.1146/annurev.ecolsys.39.110707.173532.

Johansen, M., Elliott, J.M. & Klemetsen, A. (2005a) A comparative study of juvenile salmon density in 20 streams throughout a very large river system in northern Norway. *Ecology of Freshwater Fish,* **14,** 96-110. 10.1111/j.1600-0633.2004.00082.x.

Johansen, M., Elliott, J.M. & Klemetsen, A. (2005b) Relationships between juvenile salmon,*Salmo salar* L., and invertebrate densities in the River Tana, Norway. *Ecology of Freshwater Fish,* **14,** 331-343. 10.1111/j.1600-0633.2005.00107.x.

Johansen, M., Erkinaro, J. & Amundsen, P.-A. (2010) The When, What and Where of Freshwater Feeding. *Atlantic Salmon Ecology*, pp. 89-114. Wiley-Blackwell.

Jonsson, B. & Jonsson, N. (1993) Partial migration: niche shift versus sexual maturation in fishes. *Reviews in Fish Biology and Fisheries,* **3,** 348-365. 10.1007/bf00043384.

Jonsson, B. & Jonsson, N. (2011) Ecology of Atlantic salmon and brown trout : habitat as a template for life histories. Springer, Dordrecht.

Jonsson, B. & Jonsson, N. (2014) Early environment influences later performance in fishes. *Journal of Fish Biology,* **85,** 151-188. 10.1111/jfb.12432.

Kess, T., Lehnert, S.J., Bentzen, P., Duffy, S., Messmer, A., Dempson, J.B., Newport, J., Whidden, C., Robertson, M.J., Chaput, G., Breau, C., April, J., Gillis, C.A., Kent, M., Nugent, C.M. & Bradbury, I.R. (2024) Variable parallelism in the genomic basis of age at maturity across spatial scales in Atlantic Salmon. *Ecology and Evolution*, 14, e11068. 10.1002/ece3.11068.

Kirkpatrick, M. (2010) How and why chromosome inversions evolve. *PLoS Biology,* **8**. 10.1371/journal.pbio.1000501.

Kirkpatrick, M. & Barton, N. (2006) Chromosome inversions, local adaptation and speciation. *Genetics,* **173,** 419-434. 10.1534/genetics.105.047985.

Kirubakaran, T.G., Grove, H., Kent, M.P., Sandve, S.R., Baranski, M., Nome, T., De Rosa, M.C., Righino, B., Johansen, T., Ottera, H., Sonesson, A., Lien, S. & Andersen, O. (2016) Two adjacent inversions maintain genomic differentiation between migratory and stationary ecotypes of Atlantic cod. *Molecular Ecology,* **25,** 2130-2143. 10.1111/mec.13592.

Kusche, H., Cote, G., Hernandez, C., Normandeau, E., Boivin-Delisle, D. & Bernatchez, L. (2017) Characterization of natural variation in North American Atlantic Salmon populations (Salmonidae: *Salmo salar*) at a locus with a major effect on sea age. *Ecology and Evolution*, 7, 5797-5807. 10.1002/ece3.3132.

Küpper, C., Stocks, M., Risse, J.E., dos Remedios, N., Farrell, L.L., McRae, S.B., Morgan, T.C., Karlionova, N., Pinchuk, P., Verkuil, Y.I., Kitaysky, A.S., Wingfield, J.C., Piersma, T., Zeng, K., Slate, J., Blaxter, M., Lank, D.B. & Burke, T. (2015) A supergene determines highly divergent male reproductive morphs in the ruff. *Nature Genetics,* **48,** 79-83. 10.1038/ng.3443.

Lenth R (2023). emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.8.5.

Li, M.H. & Merila, J. (2011) Population differences in levels of linkage disequilibrium in the wild. *Molecular Ecology,* **20,** 2916-2928. 10.1111/j.1365-294X.2011.05154.x.

Lillehammer A (1974) Studie av laks og ørretyngelens forflytning over elvebunnen og evertebratfaunaen i temporært oversvømte områder. (Summary: Studies on the movement of salmon and trout fry and invertebrates into flooded areas). *Fauna* 27: 69-73.

Liu, X., Li, Y.I. & Pritchard, J.K. (2019) Trans Effects on Gene Expression Can Drive Omnigenic Inheritance. *Cell*, 177, 1022-1034 e1026. 10.1016/j.cell.2019.04.014.

Lo, M.T., Hinds, D.A., Tung, J.Y., Franz, C., Fan, C.C., Wang, Y., Smeland, O.B., Schork, A., Holland, D., Kauppi, K., Sanyal, N., Escott-Price, V., Smith, D.J., O'Donovan, M., Stefansson, H., Bjornsdottir, G., Thorgeirsson, T.E., Stefansson, K., McEvoy, L.K., Dale, A.M., Andreassen, O.A. & Chen, C.H. (2017) Genome-wide analyses for personality traits identify six genomic loci and show correlations with psychiatric disorders. *Nature Genetics*, 49, 152-156. 10.1038/ng.3736.

Mathot, K.J., Dingemanse, N.J. & Nakagawa, S. (2019) The covariance between metabolic rate and behaviour varies across behaviours and thermal types: meta-analytic insights. *Biological Reviews of the Cambridge Philosophical Society,* **94,** 1056-1074. 10.1111/brv.12491.

McCormick, S.D. & Saunders, R.L. (1987) Preparatory Physiological Adaptations for Marine Life of Salmonids: Osmoregulation, Growth, and Metabolism. *American Fisheries Society Symposium* 1, 211 – 229.

McGee, L.W., Sackman, A.M., Morrison, A.J., Pierce, J., Anisman, J. & Rokyta, D.R. (2016) Synergistic Pleiotropy Overrides the Costs of Complexity in Viral Adaptation. *Genetics*, 202, 285-295. 10.1534/genetics.115.181628.

Metcalfe, N.B. (1998) The interaction between behavior and physiology in determining life history patterns in Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences,* **55,** 93-103. 10.1139/d98-005.

Mathieson, I. (2021) The omnigenic model and polygenic prediction of complex traits. *American Journal of Human Genetics*, 108, 1558-1563. 10.1016/j.ajhg.2021.07.003.

Mobley, K.B., Aykanat, T., Czorlich, Y., House, A., Kurko, J., Miettinen, A., Moustakas-Verho, J., Salgado, A., Sinclair-Waters, M., Verta, J.-P. & Primmer, C.R. (2021) Maturation in Atlantic salmon (*Salmo salar*, Salmonidae): a synthesis of ecological, genetic, and molecular processes. *Reviews in Fish Biology and Fisheries,* **31,** 523-571. 10.1007/s11160-021-09656-w.

Mullon, C., Keller, L. & Lehmann, L. (2017) Social polymorphism is favoured by the co-evolution of dispersal with social behaviour. *Nature Ecology & Evolution,* **2,** 132-140. 10.1038/s41559-017-0397-y.

Niemelä, E., Orell, P., Erkinaro, J., Dempson, J.B., BrØrs, S., Svenning, M.A. & Hassinen, E. (2006) Previously spawned Atlantic salmon ascend a large subarctic river earlier than their maiden counterparts. *Journal of Fish Biology,* **69,** 1151-1163. 10.1111/j.1095-8649.2006.01190.x.

Oomen, R.A., Kuparinen, A. & Hutchings, J.A. (2020) Consequences of Single-Locus and Tightly Linked Genomic Architectures for Evolutionary Responses to Environmental Change. *Journal of Heredity,* **111,** 319-332. 10.1093/jhered/esaa020.

Paaby, A.B. & Rockman, M.V. (2013) The many faces of pleiotropy. *Trends in Genetics,* **29,** 66-73. 10.1016/j.tig.2012.10.010.

Pearse, D.E., Miller, M.R., Abadia-Cardoso, A. & Garza, J.C. (2014) Rapid parallel evolution of standing variation in a single, complex, genomic region is associated with life history in steelhead/rainbow trout. *Proc Biol Sci,* **281,** 20140012. 10.1098/rspb.2014.0012.

Prokkola, J.M., Asheim, E.R., Morozov, S., Bangura, P., Erkinaro, J., Ruokolainen, A., Primmer, C.R. & Aykanat, T. (2022a) Genetic coupling of life-history and aerobic performance in Atlantic salmon. *Proc Biol Sci,* **289,** 20212500. 10.1098/rspb.2021.2500.

Prokkola, J.M., Chew, K.K., Anttila, K., Maamela, K.S., Yildiz, A., Asheim, E.R., Primmer, C.R. & Aykanat, T. (2024) Tissue-specific metabolic enzyme levels covary with whole-animal metabolic rates and life-history loci via epistatic effects. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences,* **379,** 20220482. 10.1098/rstb.2022.0482.

R Core Team (2019) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rubenstein, D.R., Ågren, J.A., Carbone, L., Elde, N.C., Hoekstra, H.E., Kapheim, K.M., Keller, L., Moreau, C.S., Toth, A.L., Yeaman, S. & Hofmann, H.A. (2019) Coevolution of Genome Architecture and Social Behavior. *Trends in Ecology & Evolution,* **34,** 844-855. 10.1016/j.tree.2019.04.011.

Shustov, Y.A., Baryshev, I.A. & Belyakova, E.E. (2012) Specific features of the feeding of juvenile atlantic salmon (*Salmo salar* L.) in the subarctic varzuga river and its small tributaries (Kola Peninsula). *Inland Water Biology,* **5,** 288-292. 10.1134/s1995082912030121.

Sinclair-Waters, M., Odegard, J., Korsvoll, S.A., Moen, T., Lien, S., Primmer, C.R. & Barson, N.J. (2020) Beyond large-effect loci: large-scale GWAS reveals a mixed large-effect and polygenic architecture for age at maturity of Atlantic salmon. *Genetics Selection Evolution,* **52,** 9. 10.1186/s12711-020-0529-8.

Sinclair-Waters, M., Piavchenko, N., Ruokolainen, A., Aykanat, T., Erkinaro, J. & Primmer, C.R. (2022) Refining the genomic location of single nucleotide polymorphism variation affecting Atlantic salmon maturation timing at a key large-effect locus. *Molecular Ecology,* **31,** 562-570. 10.1111/mec.16256.

Solovieff, N., Cotsapas, C., Lee, P.H., Purcell, S.M. & Smoller, J.W. (2013) Pleiotropy in complex traits: challenges and strategies. *Nature Reviews: Genetics,* **14,** 483-495. 10.1038/nrg3461.

Stamps, J. (1994) Territorial Behavior: Testing the Assumptions. pp. 173-232.

Stamps, J.A. (1999) Dominance and Territoriality. *Proc. 22 Int. Ornithology Congress,* (eds N.J. Adams & R.H. Slotow), pp. 1592-1605. Durban.

Stewart, D.C., Middlemas, S.J. & Youngson, A.F. (2006) Population structuring in Atlantic salmon (*Salmo salar*): evidence of genetic influence on the timing of smolt migration in sub-catchment stocks. *Ecology of Freshwater Fish,* **15,** 552-558. 10.1111/j.1600-0633.2006.00197.x.

659 Thorpe, J.E., Mangel, M., Metcalfe, N.B. & Huntingford, F.A. (1998) Modelling the proximate basis of salmonid
660 life-history variation, with application to Atlantic salmon, *Salmo salar* L. *Evolutionary Ecology,* **12,** 581-
661 599. 10.1023/A:1022351814644.
662 Tuttle, E.M., Bergland, A.O., Korody, M.L., Brewer, M.S., Newhouse, D.J., Minx, P., Stager, M., Betuel, A.,
663 Cheviron, Z.A., Warren, W.C., Gonser, R.A. & Balakrishnan, C.N. (2016) Divergence and Functional
664 Degradation of a Sex Chromosome-like Supergene. *Current Biology,* **26,** 344-350.
665 10.1016/j.cub.2015.11.069.
666 Ueda, R., Kanaiwa, M., Terui, A., Takimoto, G. & Sato, T. (2025) Seasonal timing of ecosystem linkage mediates
667 life-history variation in a salmonid fish population. *Ecology*, **106**, e70114. 10.1002/ecy.70114.
668 Vähä, J.-P., Erkinaro, J., Falkegård, M., Orell, P. & Niemelä, E. (2017) Genetic stock identification of Atlantic
669 salmon and its evaluation in a large population complex. *Canadian Journal of Fisheries and Aquatic*
670 *Sciences,* **74,** 327-338. 10.1139/cjfas-2015-0606.
671 Vähä, J.P., Erkinaro, J., Niemelä, E. & Primmer, C.R. (2008) Temporally stable genetic structure and low
672 migration in an Atlantic salmon population complex: implications for conservation and management.
673 *Evolutionary Applications,* **1,** 137-154. 10.1111/j.1752-4571.2007.00007.x.
674 Wagner, G.P., Pavlicev, M. & Cheverud, J.M. (2007) The road to modularity. *Nature Reviews: Genetics,* **8,** 921-
675 931. 10.1038/nrg2267.
676 Wellenreuther, M. & Bernatchez, L. (2018) Eco-Evolutionary Genomics of Chromosomal Inversions. *Trends in*
677 *Ecology & Evolution,* **33,** 427-440. 10.1016/j.tree.2018.04.002.
678 Yeaman, S. (2013) Genomic rearrangements and the evolution of clusters of locally adaptive loci. *Proceedings*
679 *of the National Academy of Science USA,* **110,** E1743-1751. 10.1073/pnas.1219381110.
680 Yeaman, S. & Whitlock, M.C. (2011) The genetic architecture of adaptation under migration-selection balance.
681 *Evolution,* **65,** 1897-1911. 10.1111/j.1558-5646.2011.01269.x.

682

683