# Interaction of two tightly linked loci in an adaptive genomic hotspot explains exploration behavior in juvenile Atlantic salmon in freshwater.

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## Abstract

1) 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. In Atlantic salmon (*Salmo salar*), for example, all individuals are originated in larger rivers that females can lay eggs, but some juveniles migrate to small tributaries that provide favorable habitat patches. The increased growth in these nursery streams may also 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 for genetic association between exploration behavior to nursery streams across four SNPs that spans 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 substantially stronger 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 significant interaction between SNPs at the *vgll3* gene and *akap11*, indicating a 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. The observed genetic interaction may indicate that these two traits 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 underlying adaptive traits is essential for understanding the mechanistic basis of natural selection in the wild. Genome-wide scans have been essential for locating genomic regions associated with phenotypic variation, or elucidating adaptive genetic differences within and among populations. However, assessing the adaptive landscape at a finer-scale resolution is challenging, especially in natural populations. 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 epistatic structure has been suggested as an important form of genetic architecture that facilitates the co-evolution of co-adapted trait complexes, such as behavior and

45 reproduction or behavior and life history (Küpper *et al.* 2015; Tuttle *et al.* 2016; Funk *et al.* 2021). Likewise,
46 population models suggest such non-recombining regions may be preserved even without a need for co-
47 adaptation or epistasis (Kirkpatrick & Barton 2006; Hoffmann & Rieseberg 2008), suggesting their potential
48 prevalence in the natural populations.

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

62 The *vgll3* locus in Atlantic salmon (*Salmo salar*) has strong potential as a genomic tool to better understand the
63 adaptive dynamics in the wild associated with a small linked genomic region. The *vgll3* genomic region, which
64 spans approximately 70 kb and encompasses *vgll3* and *akap11* genes, was initially identified as a major
65 genomic region explaining age at maturity, a life history trait with substantial fitness effects (Ayllon *et al.* 2015;
66 Barson *et al.* 2015). Further research identified that variation in other traits was also linked with the genetic
67 variation in the region, such as precocious male maturation (Debes *et al.* 2021), repeat-spawning (Aykanat *et*
68 *al.* 2019), metabolism (Prokkola *et al.* 2022a; Prokkola *et al.* 2024), foraging behavior (Aykanat et al. 2024),

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

89 Exploration in fishes is an important behavioral trait in that enables populations to spread and occupy new
90 habitat patches and resources. It can reduce the negative effects of density dependence (Einum, Sundt-Hansen
91 & H. Nislow 2006), and improve population stability (Baker *et al.* 2025). In juvenile Atlantic salmon, exploration
92 within freshwater (before emigration to the ocean) has the potential to contribute to improved feeding

93 opportunities, better growth, and ultimately higher survival (Erkinaro & Niemelä 1995; Erkinaro & Erkinaro
94 1998; Johansen, Elliott & Klemetsen 2005a; Johansen, Elliott & Klemetsen 2005b). Such habitat shifts may also
95 affect individual life history patterns (Erkinaro *et al.* 1997) via improved feeding and growth opportunities (e.g.,
96 Udea *et al.* 2025), making the individuals more likely to exceed the maturation threshold (Metcalfe 1998;
97 Thorpe *et al.* 1998; Jonsson & Jonsson 2014). At the genetic level, exploration and covarying traits such as
98 metabolism and aggression have been linked with the major loci affecting age-at-maturity, *vgll3* (Bangura *et al.*
99 2022; Prokkola *et al.* 2022a; Bangura *et al.* 2024; Prokkola *et al.* 2024). For example, using a common garden
100 design in an aquarium setting, Bangura *et al.* (2024) showed that juvenile Atlantic salmon with the late-
101 maturing *vgll3*$^{LL}$ genotype (L referring to the allele associated with late maturation) were significantly more
102 active in the 30-minute period following their release into a novel environment than individuals with the early-
103 maturing *vgll3*$^{EE}$ genotype (E referring to the allele associated with early maturation). This indicates that
104 exploration and maturation might be influenced by the same genetic locus. However, in their cross design, the
105 *vgll3* haplotype block was in complete linkage, and the study could not further refine the genetic basis within
106 the genomic region.

107 Traditionally, Atlantic salmon juveniles are considered relatively site-attached and sedentary in their early years
108 in freshwater (e.g., Jonsson & Jonsson 2011). However, in some river systems, older age groups of juvenile
109 salmon (parr) disperse to more favorable habitat patches within freshwater systems, including lacustrine areas
110 and smaller tributaries (Erkinaro 1995; Erkinaro, Julkunen & Niemela 1998; Halvorsen & Jørgensen 2006).
111 These small tributaries are nursery streams that are not suitable for salmon reproduction but may provide
112 favorable growth and survival conditions for salmon parr by means of increased food availability and decreased
113 competition and predation (Erkinaro & Niemelä 1995; Erkinaro & Erkinaro 1998; Erkinaro, Julkunen & Niemela
114 1998; Johansen, Elliott & Klemetsen 2005b). The extent of exploratory behavior to nursery streams and its
115 adaptive importance may be influenced by various factors, including environmental conditions, genetic
116 predispositions, and population density (e.g., Erkinaro *et al.* 1997; Johansen, Erkinaro & Amundsen 2010). For

117 example, the use of nursery streams by juvenile Atlantic salmon have been observed especially in northern
118 areas with depauperate fish fauna that exhibit less competition and predation threat to juvenile salmon
119 (Erkinaro 1995; Erkinaro & Gibson 1997; Shustov, Baryshev & Belyakova 2012).

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

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

133

## 134 Material and Methods

135 *Study area and sampling*

136 The Teno River (Deatnu in Sámi, Tana in Norwegian) catchment is located in far-north Europe (68–70°N, 25–
137 27°E), runs northwardly between Finland and Norway, and drains into the Barents Sea. The Teno system
138 supports a number of Atlantic salmon populations with wide diversity in life history characteristics and genetic
139 structure within and among populations (Vähä *et al.* 2017; Erkinaro *et al.* 2019). Juvenile salmon samples used

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

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

162 *DNA extraction, SNP genotyping by targeted sequencing*

163 DNA was extracted from the scales of the juvenile Atlantic salmon using QIAamp 96DNA QIAcube HTKit
164 (Qiagen) following the manufacturer's protocol. Individuals were genotyped by targeted sequencing using a
165 SNP panel consisting of 173 SNP markers using a GTSeq approach (Campbell, Harmon & Narum 2015) as
166 outlined in (Aykanat *et al.* 2020). The SNP panel contained four SNP from the *vgl3* genomic regions including
167 the SNP that is most highly associated with age at maturity ($vgll3_{TOP}$), two missense mutations in the *vgll3* gene
168 ($vgll3_{Met54Thr}$ and $vgll3_{Asn323Lys}$), and one missense mutation in the *akap11* gene ($akap11_{Val214Met}$, Barson *et al.*
169 2015). These SNPs are located on chromosome 25 and are 0.8 kb ($vgll3_{Met54Thr}$), 2.9 kb ($vgll3_{Asn323Lys}$), 10.9 kb
170 ($vgll3_{TOP}$), and 65.5 kb ($akap11_{Val214Met}$) downstream from the transcription start site of the *vgll3* gene. The SNP
171 panel also included *six6* locus, a SNP highly spatially divergent between Atlantic salmon populations (Barson *et*
172 *al.* 2015), and so-called outlier and baseline SNPs. The outlier module includes 53 SNPs highly differentiated
173 between the Inarijoki and Teno main stem populations, allowing for a more powerful assignment of the
174 population of origin between these two closely related populations. The baseline module included 136
175 putatively neutral markers in low linkage disequilibrium, distributed throughout the whole genome and
176 previously filtered to have a minor allele frequency larger than 0.05 and heterozygosity larger than 0.2 for
177 these two populations (Aykanat *et al.* 2016). Individuals missing genotype information in any of these SNPs
178 were excluded from the analysis. Bonferroni correction was applied when multiple SNPs were compared.

179 *Statistical analysis*

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

184 $Y_{tenoMS} = \mu + SNP + \varepsilon_{error}$ for Teno main stem,

185 $Y_{inari} = \mu + SNP + \varepsilon_{hatchyear} + \varepsilon_{error\ for}$ Inarijoki,

186 where Y is a Boolean response variable for individuals' explorative behavior, in which individuals sampled in the
187 main stem were assumed to be sedentary, and coded as "0", and individuals sampled in the streams, either
188 descending or ascending, were assumed to be explorative and coded as "1". SNP is the genotype score of SNPs,
189 coded as 0 when individuals are homozygous for the reference alleles, 1 when homozygous for the alternative
190 alleles, and 0.5 when heterozygous. For the Inarijoki population, $\varepsilon_{hatchyear}$ is the random variance associated
191 with the hatch year calculated as the year sampled minus the age of the fish. Neither hatch year nor sampling
192 year overlapped for the Teno main stem populations between nursery streams and main stem collections, so
193 for this population, the model did not include the random term $\varepsilon_{hatchyear}$. The model was implemented for four
194 focal SNPs in the vgll3 genomic region (*vglll3*$_{TOP}$, *vgll3*$_{Met54Thr}$, *vgll3*$_{Asn323Lys}$), *akap1*$_{Val214Met}$*)*, and 169 SNPs in the
195 SNP panel, including *six6*, which is shown to be associated with age at maturity and metabolism (Sinclair-
196 Waters *et al.* 2020; Prokkola *et al.* 2022b; Prokkola *et al.* 2024). Using the same model structure as above, we
197 then implemented a second model to quantify the effect of epistasis within the genomic region by modeling
198 pairwise interactions of SNPs within the *vgll3* genomic regions. Finally, we tested for potential gene-by-
199 environment effects by examining if results were consistent across the two populations, i.e., Inarijoki and Teno
200 main stem, which are in close proximity and genetically similar, but with substantial differences in their life
201 histories.

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

206

## 207 Results

208 Overall, the genotyping success rate was generally low (85%, Supplementary Figure 1), mostly due to the small

209 amount of material available for DNA extraction. After removing individuals with no genotype success in any of
210 the focal SNPs (N=143) and those with no scale aging data (N=15, of which eight also had no genotype success),
211 635 individuals remained in the final dataset out of an initial 785.

212 In the Teno main stem population, exploration behavior toward the nursery stream, Baðđá, was not
213 significantly associated with any of the four SNPs in the *vgll3* genomic region, or any other SNPs in the panel
214 after the Bonferroni correction for multiple comparisons (Figure 1a). In the Inarijoki population, the only SNP
215 that reached the Bonferroni-corrected threshold was $akap11_{\mathrm{Val214Met}}$ (Figure 1b). Specifically, the
216 $akap11_{\mathrm{Val214Met}}^{\mathrm{EE}}$ genotype was 7.36 times (95% CI: 3.22 – 17.26) more likely to explore the nursery stream,
217 Guoldnájohka, than the $akap11_{\mathrm{Val214Met}}^{\mathrm{LL}}$ allele ($p < 0.001$, Figure 2a). The *six6* loci did not exhibit a significant
218 association in any of the populations.

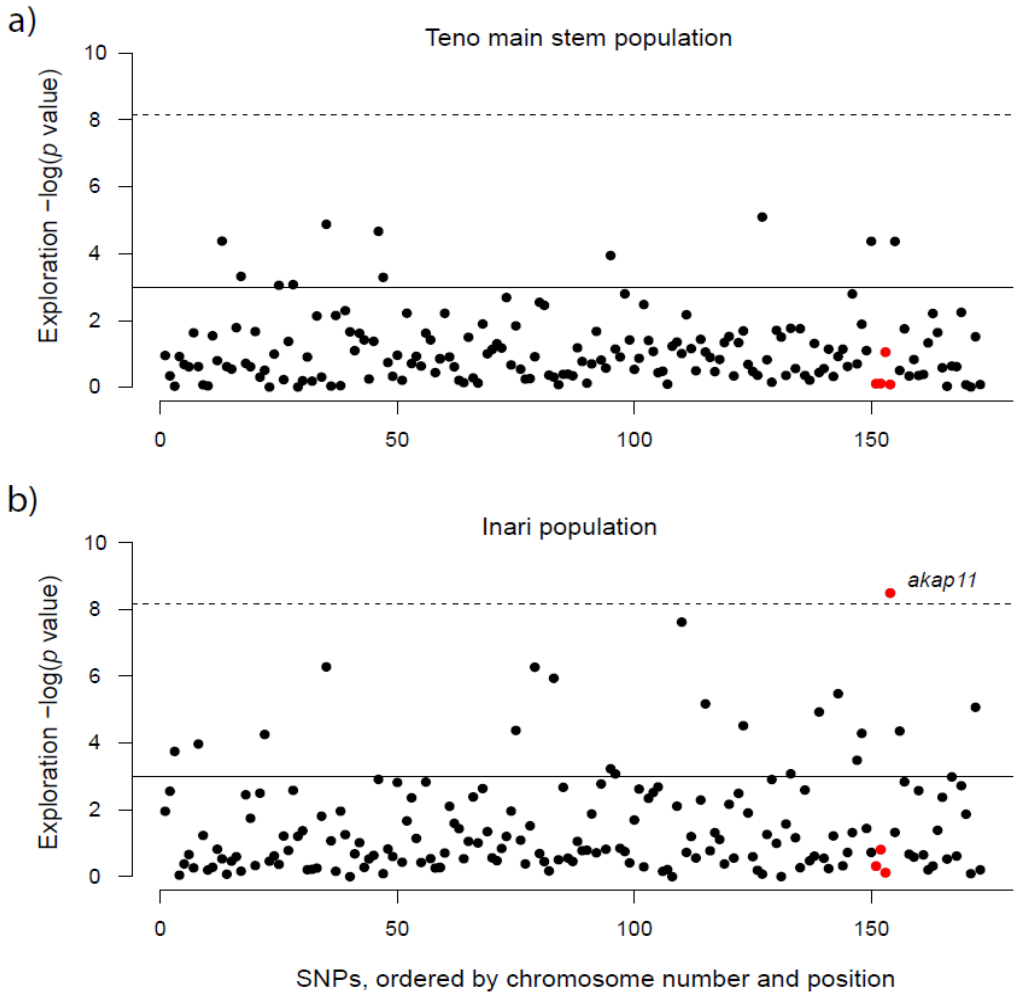



**Figure 1:** SNP - exploration association across 173 SNPs in Teno main stem (a) and Inarijoki (b) populations in Atlantic salmon. Focal SNPs are colored in red. Uncorrected (p = 0.05) and Bonferroni corrected p-value thresholds are indicated with dashed and continuous lines.

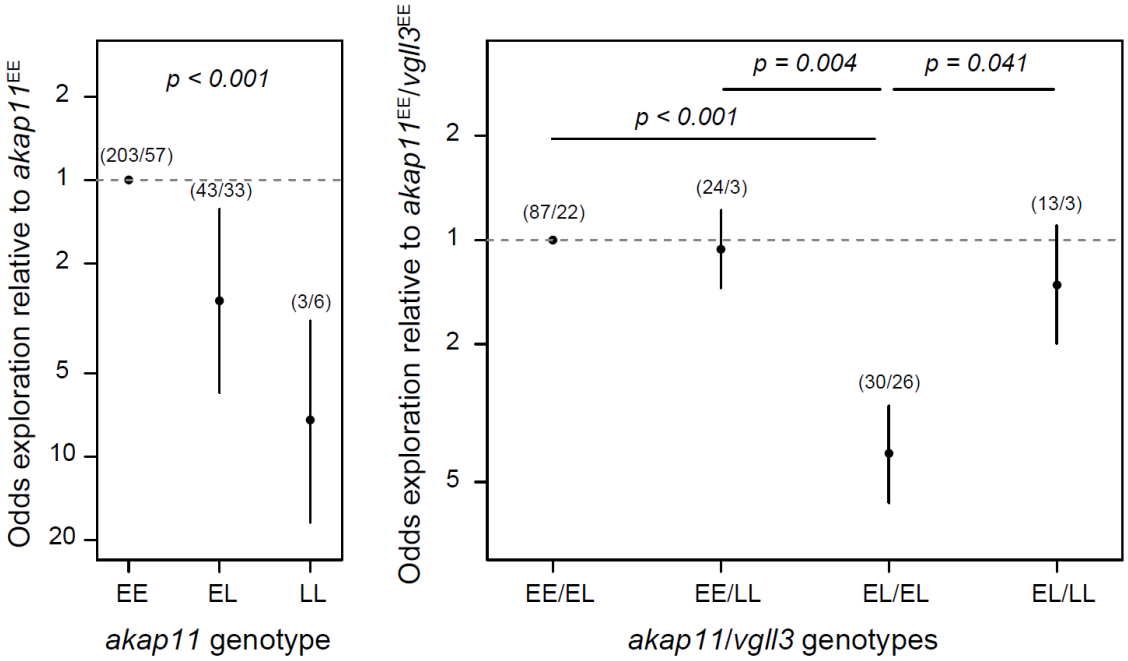
When pairwise interactions within the *vgll3* genomic region were modeled in the Teno main stem population, none of the models were more significant than the null model that did not contain genetic effects. For the Inarijoki population, the most parsimonious model explaining the exploration included the interaction of *akap11*$_{\text{Val214Met}}$ and *vgll3*$_{\text{Asn323Lys}}$, which was superior to the null model (ΔAIC = 16.36), or the model that only included *akap11*$_{\text{Val214Met}}$ (ΔAIC = 4.47), but not significantly better than the interaction between *akap11*$_{\text{Val214Met}}$ and two other SNPs in the *vgll3* genomic region (ΔAIC < 2, Supplementary Figure 3). The effect was driven by a substantial decrease in exploration behavior associated with the genotype combination of *akap11*$_{\text{Val214Met}}^{\text{EL}}$ and

230 *vgll3*$_{Asn323Lys}^{EL}$ (Figure 2b). As such, the model predicts that the odds of exploration for individuals with

231 *akap11*$_{Val214Met}^{EL}$ and *vgll3*$_{Asn323Lys}^{EL}$ were 4.13 (95% CI 2.24-7.84, $p$<0.001) and 3.10 (95% CI 1.34-7.15, $p$=0.041)

232 times less than for *akap11*$_{Val214Met}^{EE}$ and *vgll3*$_{Asn323Lys}^{EL}$ and *akap11*$_{Val214Met}^{EL}$ and *vgll3*$_{Asn323Lys}^{LL}$, respectively (Figure

233 2b)




234

235 **Figure 2: a)** Odds of exploration in Inarijoki Atlantic salmon as a function of *akap11*$_{Val214Met}$ SNP, and **b)** as a
236 function of *akap11*$_{Val214Met}$ and *vgll3*$_{Asn323Lys}$ interaction. Error bars indicate 95% CI of the marginal estimates, and
237 first and second numbers in parenthesis indicates the sample sizes in the nursery stream and the main stream,
238 respectively. Y axis is drawn in log scale.

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

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

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

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

243 were mostly qualitatively similar (Supplementary Figure 4). One notable difference was that a model with the

244 *akap11*$_{Val214Met}$ and *vgll3*$_{Asn323Lys}$ interaction was only marginally more significant than a model with

245 independent, additive effects of these SNPs ($p$ = 0.085, ΔAIC = 0.93, Supplementary Figure 4). However, the

246 change in significance was not meaningfully different from an effect that might have resulted from a reduced
247 sample size in a random manner. As such, when 83 parr were randomly sampled and excluded from the
248 dataset (i.e., the same number as the smolts in the dataset) or 83 randomly selected parrs in the dataset were
249 used as a replacement for excluded smolts, the ΔAIC range of these models (each permuted 1000 times) was
250 similar to the ΔAIC values obtained in the original model (Supplementary Figure 5).

251

## 252 Discussion

253 Factors shaping the genetic architecture of ecologically important traits are fundamentally important for
254 understanding adaptive dynamics in the wild. We have demonstrated that exploration behavior in juvenile
255 Atlantic salmon is linked to a genomic region on chromosome 25 in one of the two populations in the Teno
256 River. This region contains *vgll3* and *akap11* genes and is associated with a suite of traits involved in salmon
257 adaptation (reviewed in Mobley *et al.* 2021) including age at maturity (Barson *et al.* 2015). We have found that
258 a missense SNP in the *akap11* gene ($akap11_{Val214Met}$) was substantially linked to exploratory behavior, while
259 SNPs in the *vgll3* gene exhibited epistasis with this SNP, suggesting a complex genetic architecture in the
260 region. Furthermore, the genetic effect was only observed in one of the two studied populations, indicating the
261 importance of environment or population-specific factors in triggering gene-dependent exploration behavior.

262 Our results showed that the early maturation allele in the *akap11* gene was associated with increased
263 exploration to nursery streams in the Inarijoki population. This is consistent with the findings of Erkinaro *et al.*
264 (1997) who, by analyzing freshwater growth patterns of salmon, suggested that juveniles entering nursery
265 streams had a greater tendency to mature and return from their sea journey earlier than those that stayed in
266 the main stem for their juvenile years. Differences in growth opportunity in Atlantic salmon juveniles, which is
267 linked to efficient acquisition of resources, may be instrumental in exceeding the maturation threshold in
268 subsequent years (Metcalfe 1998; Thorpe *et al.* 1998; Jonsson & Jonsson 2014). As such, causality between

269 exploration and migrating to nursery streams may be suggested based on the increased likelihood of
270 individuals in the streams to reach the maturation threshold (e.g., Thorpe *et al.* 1998) upon increased growth
271 opportunities. On the other hand, the association was predominantly driven by genetic variation in the
272 *akap11*$_{\text{Val214Met}}$ SNP, which is about 70 kb downstream of the *vgll3* gene and exhibits a weaker association with
273 sea age at maturity (Barson *et al.* 2015). The *akap11*$_{\text{Val214Met}}$ SNP was also previously ruled out as the genetic
274 basis of early male maturation in Atlantic salmon in controlled settings (Sinclair-Waters *et al.* 2022). Combined,
275 while exploration behavior may facilitate earlier maturation in a context-dependent manner, our results do not
276 provide evidence to support a direct genetic causation between the two, but that a small region explains both
277 maturation and exploration behaviors, and that the two traits are genetically correlated by linkage.

278 A multitude of phenotypic traits may be linked within a genomic region via pleiotropy or linkage disequilibrium
279 (i.e., spurious pleiotropy, Solovieff *et al.* 2013). This makes it challenging to identify the phenotypic traits under
280 selection, i.e., by using genomic scans (Paaby & Rockman 2013; Solovieff *et al.* 2013). Our results indicate that
281 the *vgll3* genomic region contains multiple independent SNPs linked to adaptive traits, ruling out pleiotropy as
282 the basis of multi-trait association. The presence of multiple adaptive traits within a tightly linked genomic
283 region raises the question of whether the genetic co-variation between these loci harbors co-adapted trait
284 combinations. Linked architectures may facilitate adaptation by enabling co-inheritance of adapted gene
285 complexes (Mullon, Keller & Lehmann 2017; Oomen, Kuparinen & Hutchings 2020). For example, genomic
286 inversions have been shown to be important in maintaining co-adapted trait combinations, including migratory
287 strategies and dispersal (Mullon, Keller & Lehmann 2017; Wellenreuther & Bernatchez 2018; Rubenstein *et al.*
288 2019). Similarly, genetic variation in life-history migratory ecotypes in rainbow trout (*Oncorhynchus mykiss*,
289 Pearse *et al.* 2014) and Atlantic cod (*Gadus morhua*) have been shown to be associated with genetic markers in
290 a large inverted region (Kirubakaran *et al.* 2016). A tight linkage between adaptive traits might also be selected
291 for when locally adapted populations may have varying local fitness optima (for these traits), and exhibit high

292 gene flow between them (Yeaman & Whitlock 2011). In this case, tight linkage between locally adapted traits
293 would help in purging maladaptive genetic variants with a relatively reduced genetic load.

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

308 Our study provides a further outlook on the dynamics of behavioral syndromes and correlated behaviors
309 (Höjesjö, Johnsson & Bohlin 2004; Garamszegi, Markó & Herczeg 2013; Mathot, Dingemanse & Nakagawa
310 2019; Axling *et al.* 2023). The classic paradigm suggests that dispersal is negatively correlated with dominance
311 and aggression, whereby dominant individuals monopolize favorable habitat patches, and force subordinate
312 individuals to displace in search of new habitats (Stamps 1994; Stamps 1999). However, in Atlantic salmon,
313 migration to nursery streams might be carried out by individuals holding higher positions in the dominance
314 hierarchy (Erkinaro & Niemelä 1995). Using seasonal growth in scale depositions, Erkinaro and Niemelä (1995)
315 estimated growth in previous seasons -a trait correlated with dominance and aggression in early life stages

316 (Cutts *et al.* 2005)-, and showed that faster growing individuals are more likely to migrate to the small nursery
317 streams. A similar tendency in individual growth patterns has also been identified in individuals shifting their
318 juvenile rearing habitat to lacustrine areas of the catchment (Erkinaro *et al.* 1998). A niche shift, i.e., by
319 migrating to nursery streams, may be hypothesized as a mechanism to overcome potential resource mismatch
320 in the original habitat. Therefore, we would predict that the EE allele in the *vgll3* genomic region is likely
321 associated with behavioral traits correlated with exploration in salmon, such as dominance.

322 On the other hand, common garden experiments in controlled conditions do not support our prediction. For
323 example, by quantifying novel environment exploration in a confined space (an aquarium with a 25 cm x 30 cm
324 surface area), Bangura *et al.* (2024) found that the *vgll3* L allele was associated with higher exploration in a
325 novel environment. Likewise, using a similar experimental setup Bangura *et al.* (2022) also found increased
326 aggression associated with the *vgll3* L allele. These results suggest a genetic covariation exists between
327 aggression and novel environmental exploration, but with an opposite direction of allelic effect to our study.
328 (Note that in the crosses used by Bangura *et al.* (2022) and Bangura *et al.* (2024) *akap11* and *vgll3* were in full
329 linkage, hence conclusions related to the genetic variation in the *vgll3* SNPs are equally valid for the *akap11*
330 SNP.) These contrasting results may reflect contextual differences between natural and common garden
331 settings. As such, a meta-analysis has shown that these two personality traits (aggression and exploration) only
332 correlate when there is a contextual overlap that underlies the similarity of trait expression (Garamszegi,
333 Markó & Herczeg 2013). Therefore, the contrasting conclusions in these two settings (natural vs. laboratory)
334 may stem from different functional physiological processes. Alternatively, strong environment (common
335 garden vs. natural setting) by genotype, or population by genotype interactions may explain the contrast. For
336 the latter, for example, the parental fish used in Bangura *et al.* (2022) and Bangura *et al.* (2024) are obtained
337 from a hatchery broodstock of salmon managed by the Natural Resources Institute Finland (LUKE), initially
338 originated from a Baltic Sea population (River Neva). Hence differences in the genetic background of fish may
339 also explain the discrepancies. In fact, the genetic association between SNPs in the *vgll3* genomic region and

340 exploration was significant only in the Inarijoki population, while no detectable effect was found in the Teno
341 main stem population, further emphasizing a potential role of population specific differences in the genetic
342 basis of trait variation. Our study illustrates the complex dynamics of correlated behaviors of Atlantic salmon
343 and their genetic background.

344 Finally, we demonstrated an epistasis between *akap11* and the *vgll3* gene. While the statistical power was
345 insufficient to which of the SNP in the *vgll3* gene are the most likely candidates, the presence of epistasis
346 suggests a complex genetic architecture within the genomic region. Epistasis contributes to the trait variance,
347 and help maintain additive genetic variation upon selection (Cheverud & Routman 1995). Further, the trait
348 complex between exploration and age at maturity may contribute to adaptation dynamics. For example,
349 optimal trait combinations (of traits co-inherited within a haplotype block) may be locally variable among
350 populations and may improve overall fitness compared to what would be predicted by only additive gene
351 action. Such an epistatic interaction would also facilitate purging maladapted genetic combinations (Yeaman &
352 Whitlock 2011).

353 In this study, we used historical field data that was not initially intended for a genetic study such as this one.
354 Hence, the design has some drawbacks. For example, the hatching years of individuals collected in the Teno
355 main stem and Baðða stream do not match, therefore we cannot rule out the possibility that the (lack of)
356 difference in genetic response is due to temporal changes in allele frequencies, even though the time span
357 between sampling periods is only a few years. Secondly, genotype calling failed for a substantial portion of
358 individuals due to the suboptimal amount of tissue remains in the storage envelopes. In addition, we employed
359 a targeted genotyping approach by scoring only the most likely candidate SNPs in the genomic regions. An
360 alternative approach to sequence the whole genomic region might provide finer resolution in trait association,
361 and help to better narrow down the causal region.

362 Movement patterns in the Salmonidae family are mostly studied in the context of the phenology of migration,
363 which is central to their life histories, has a heritable component, and strong fitness consequences (Niemelä *et*

364 *al.* 2006; Stewart, Middlemas & Youngson 2006). Many species exhibit a strong dichotomy of the trait within
365 and among populations, as evidenced by the presence of both resident and migratory forms in, e.g., brown
366 trout, rainbow/steelhead trout, and Arctic char (Jonsson & Jonsson 1993). Movement within the freshwater
367 habitat at the juvenile stage and its association with migration at later stages is much less explored. Our study
368 demonstrates a complex genetic interaction between exploration in the freshwater and age at maturity. This
369 may help to maintain co-adapted trait complexes (exploration and maturation) and may be instrumental in
370 local adaptation processes, fitness, and the long-term survival of populations.

371

## 372 Acknowledgement

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

377

## 378 Conflict of Interest

379 The authors declare no competing interests.

380

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