

1 Genotype-specific variation in seasonal body condition at a large-effect maturation locus

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34 **Conflict of Interest Statement**

35 The authors declare no conflicts of interest.

36 **Author Contributions**

37 Conceptualization: CRP, PVD, AHH , Data curation: AHH, PVD, CRP, Formal Analysis:  
38 PVD, AHH, Funding acquisition: CRP, Investigation: AHH, CRP, PVD, JK, Methodology:  
39 CRP, PD, AHH, JK, Project administration: CRP, Resources: CRP, JE, Software: PVD,  
40 AHH, Supervision: CRP, Visualization: AHH, Writing – original draft: AHH, Writing – review  
41 & editing: CRP, PVD, AHH, JK, JE

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## 74 Abstract

- 75 1. Organisms utilize varying lipid resource allocation strategies as a means to survive  
76 seasonal environmental changes and life-history stage transitions. In Atlantic  
77 salmon, a certain lipid threshold is needed to initiate sexual maturation. Because of  
78 this, an individual's maturation schedule may be affected by changes in  
79 temperature and food availability across the seasons that create natural fluctuations  
80 of lipid reserves.
- 81 2. Recent studies have found a genome region, including the gene *vgll3*, that explains  
82 a large proportion of variation for size and age at maturity. *Vgll3* encodes a  
83 transcription co-factor that acts as an inhibitor of adipogenesis in mice and also  
84 affects condition factor and other phenotypes in juvenile salmon. However, even  
85 with many studies investigating varying temperature effects, there is a lack of  
86 temporal studies examining the effects of seasonality on such phenotypes, nor have  
87 the effects of *vgll3* genotype on condition factor and maturation in different  
88 temperatures at different life stages.
- 89 3. Here, we investigate the influence of different larval and juvenile incubation  
90 temperatures, *vgll3* genotype and their interactions on juvenile salmon phenotypes  
91 including body condition, and sexual maturation rate. We reared Atlantic salmon for  
92 2 years in varying temperatures with an average 1.76 °C difference between warm  
93 and cold treatments in four different larval-juvenile phase treatment groups (Warm-  
94 Warm, Warm-Cold, Cold-Warm, and Cold-Cold) until the first occurrence of  
95 maturation in males.
- 96 4. We found no effect of larval temperature on the measured phenotypes or  
97 maturation rate, suggesting the occurrence of growth compensation over the course  
98 of the experiment. Agreeing with previous studies, an increased maturation rate  
99 was observed in individuals of the warm juvenile temperature treatment.
- 100 5. In addition, we observed differences in condition factor associated with *vgll3*  
101 genotype, whereby *vgll3\*EE* individuals (the genotype associated with early  
102 maturation) had a less variable condition factor across the seasons compared to the  
103 *vgll3\*LL* (associated with late maturation) individuals.
- 104 6. This result suggests a *vgll3* influence on resource acquisition and allocation  
105 strategies, possibly linked with the early maturation process, with individuals

106 carrying the early maturation *vgll3* genotype having a higher early maturation rate  
107 and a higher condition factor in the spring.

108

## 109 **Keywords**

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111 Resource allocation, Atlantic salmon, body condition, seasonal variation, maturation,  
112 temperature

113

## 114 **Introduction**

115 Resource acquisition and allocation strategies are important for enabling organisms to  
116 respond to environmental fluctuations (Mogensen and Post 2012). In ectotherms,  
117 temperature is an important abiotic factor that can directly influence food availability but  
118 also growth and metabolism, and thereby development rate (Castañeda, Lardies, and  
119 Bozinovic 2004; Finstad and Jonsson 2012; Jonsson, Jonsson, and Finstad 2014).

120 Because of the many influences temperature has it also can affect an individual's ability to  
121 use or store acquired energy (Geissinger et al. 2021; Mogensen and Post 2012; Post and  
122 Parkinson 2001). The amount and usage of the stored energy reserves plays a role in  
123 initiating and progressing developmental processes, such as life-history stage transitions  
124 associated with smoltification (i.e., acquiring seawater tolerance) and sexual maturation  
125 (Jonsson and Jonsson 2005; reviewed in Wang, Hung, and Randall 2006). Therefore,  
126 understanding the processes that determine the allocation of acquired energy will  
127 contribute to understanding variation in initiation and progression of major life-history  
128 transitions (Post and Parkinson 2001; Rowe, Thorpe, and Shanks 1991).

129

130 Lipid allocation patterns can affect the probability of survival to reproductive age as well as  
131 the probability of maturation at a given age (Post and Parkinson 2001). Condition factor,  
132 defined as the relative weight of an individual given its length, provides an indication of the  
133 relative level of lipid stores in Atlantic salmon during the freshwater stage (Herbinger and  
134 Friars 1991; Sutton, Bult, and Haedrich 2000). It has also been applied as a proxy for lipid  
135 reserve levels in a range of taxa including birds (Balbontín et al. 2012), amphibians  
136 (Cogălniceanu et al. 2021), mammals (Bright Ross et al. 2021), and fishes (Haraldstad et  
137 al. 2018; Mozsár et al. 2015; Sutton, Bult, and Haedrich 2000). Lipid reserves have been  
138 found to be especially important for Atlantic salmon due to their need to reach a certain

139 threshold of lipid reserves in order to initiate maturation (Rowe, Thorpe, and Shanks 1991;  
140 Rowe and Thorpe 1990a; 1990b) which may be affected by variation for replenishing  
141 reserves across seasonal changes, including periods of low temperatures and food  
142 availability (Gurney et al. 2003; Mogensen and Post 2012). For example, it has been  
143 shown that maturing males replenish and build up stores faster than individuals delaying  
144 maturation in the spring prior to maturation capability (Kadri et al. 1996; Rowe, Thorpe,  
145 and Shanks 1991).

146

147 Atlantic salmon is an excellent organism to understand energy allocation and effects of  
148 environmental variation at different life stages. The propensity to mature early has been  
149 associated with prior condition factor (Debes et al. 2021; Herbinger and Friars 1992;  
150 Rowe, Thorpe, and Shanks 1991). Further, the genetic basis of age at maturity in salmon  
151 has been well characterized, with a single genome region, including the *vgll3* gene,  
152 explaining 39% of the variation in the age at maturity (Barson et al. 2015; Czorlich et al.  
153 2018). *Vgll3* encodes a transcription cofactor and has been associated with adipocytes  
154 differentiation in mice (Halperin et al., 2013) and recently was also found to play a role in  
155 mediating maturation timing via condition factor in salmon (Debes et al. 2021). However,  
156 the effects of *vgll3* genotype on condition factor and maturation in different temperatures at  
157 different life stages has not been investigated.

158

159 To address this knowledge gap, we reared Atlantic salmon with different *vgll3* genotypes  
160 from fertilization for two years in four different temperature treatment combinations:  
161 warmer or colder (2°C difference) during the embryonic and larval endogenous feeding  
162 phase (fertilization to first feeding, hereafter 'larval') and warmer or colder during the  
163 externally feeding juvenile phase (hereafter 'juvenile'). This enabled us to study the relative  
164 effects of environmental temperature during larval and juvenile rearing on resource  
165 allocation relevant phenotypes, such as growth, body condition, maturation rate and size  
166 at maturity. We also investigated whether genetic effects or interactions with the  
167 environmental effects (GxE) exist in order to understand seasonal energy allocation and its  
168 effect on the maturation process.

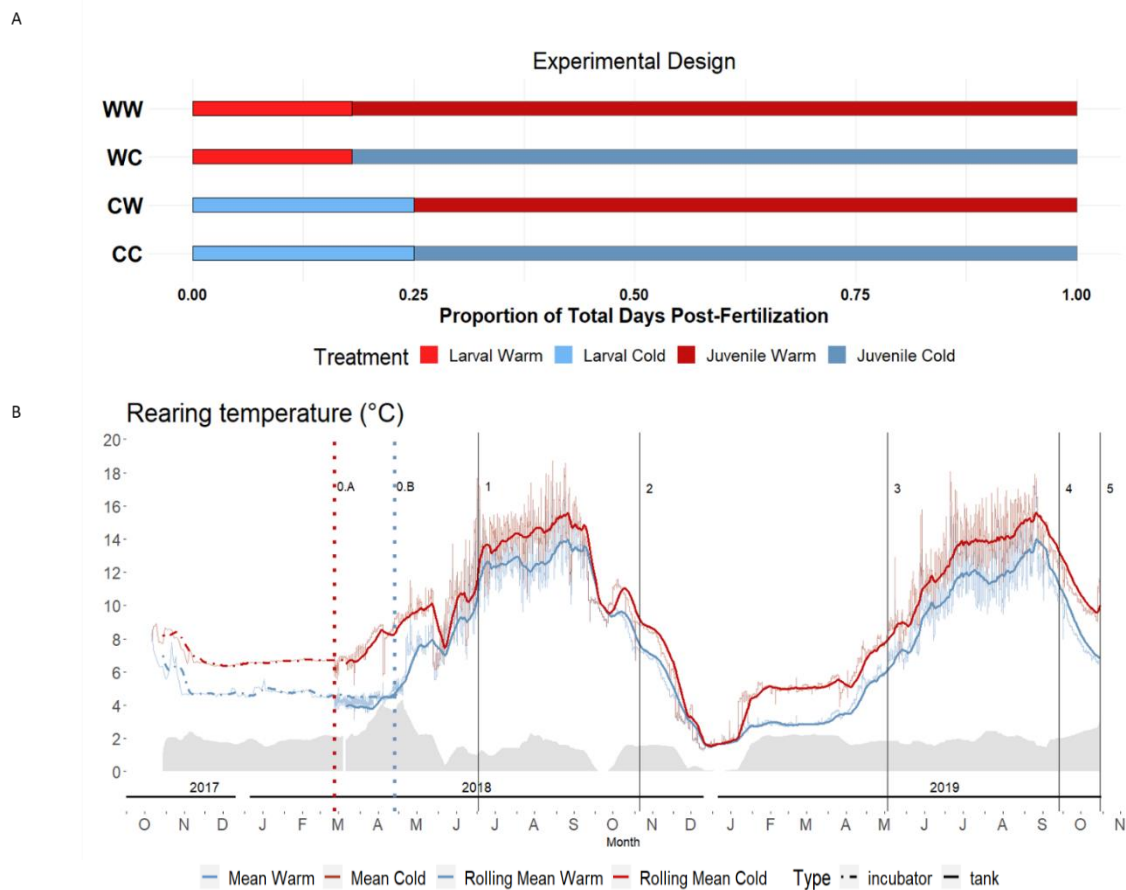
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## 170 **Methods**

### 171 ***Salmon rearing and measurement***

172 The Atlantic salmon used in this study derived from a first-generation hatchery stock  
173 maintained by the Natural Resources Institute Finland (62°24'50"N, 025°57'15"E, Laukaa,  
174 Finland), which originate from the River Neva, Russia. Fertilization took place in late  
175 October 2017 when unrelated parents with homozygous *vgll3* genotypes were crossed as  
176 six 2 × 2 factorials. Each factorial included a *vgll3\*EE* male and female and a *vgll3\*LL*  
177 male and female, where *E* and *L* refer to the alleles previously associated with earlier or  
178 later maturation, respectively (Barson et al. 2015), thus yielding four reciprocal same-*vgll3*-  
179 genotype offspring families in each 2x2 factorial (EE, 2EL, LL). Eggs of the 24 families  
180 were divided into four batches and incubated in each of two vertical incubators at each of  
181 two temperatures (2°C difference, hereafter referred to as the warm and cold larval  
182 treatments), i.e., with two replicates per family and temperature treatment. A water  
183 temperature difference of 2°C was maintained by using a combination of water chillers and  
184 room heating. At first feeding, juveniles from the two replicates were pooled and  
185 transported to the Lammi Biological Station (61°04'45"N, 025°00'40"E, Lammi, Finland) on  
186 10.03.2018 and 24.04.2018 for the warm- and cold-larval treatments, respectively. Half of  
187 the individuals of each larval temperature treatment were placed into the same  
188 temperature treatment for the juvenile phase (warm and cold juvenile treatments;  
189 maintaining a 2°C difference), and the other half of the individuals were transferred to the  
190 opposite temperature treatment, thus resulting in a total of four different larval phase-  
191 juvenile phase temperature treatment groups, Warm-Warm (WW), Warm-Cold (WC) ,  
192 Cold-Warm (CW), and Cold-Cold (CC) as shown in Figure 1A. Each treatment was  
193 replicated in five flow-through circular tanks (diameter 90 cm), and juveniles of each family  
194 were allocated to their respective replicate treatment tanks in roughly equal numbers and  
195 subsequently reared under a controlled photoperiod set to the local latitude \*(coordinates).  
196 Water was sourced from a nearby lake, Lake Pääjärvi, and thus followed the natural  
197 annual water temperature cycle with the cold and warm water treatment maintained via a  
198 heat-exchange system ranging from 1.30-18.53°C and 1.35-19.04°C, respectively, with an  
199 average difference of 1.76°C (Figure 1B). Fish were fed *ad libitum* with commercial fish  
200 food, the pellet size of which matched the requirements set by the size distribution of the  
201 individuals (Raisio Baltic Blend; Raisio Oy) for the duration of the experiment. Wet mass ( $\pm$

202 0.01 g) and fork length ( $\pm 1$  mm) were measured, and a fin clip sampled for genetic  
203 analysis, for a sub-set of individuals at five timepoints (464-580 per time point), the first of  
204 which was eight months post-fertilization, and the last when the experiment was  
205 terminated at 24 months post-fertilization (Figure 1B). Sex was determined phenotypically  
206 following dissection, and maturation status was also assessed at the last two measuring  
207 timepoints through dissection and gonad assessment. In October 2018, an accident during  
208 cleaning resulted in the loss of one tank per treatment group, resulting in four replicate  
209 tanks per treatment group for sampling time points 2-5. Following DNA extraction, samples  
210 were genotyped with 141 SNPs and a sexing marker (Aykanat et al. 2016) to determine  
211 *vgll3* genotype and assign family of origin as outlined in Debes et al. (2021).



212

213 **Figure 1: A)** Experimental design for temperature treatments for larval and juvenile Atlantic salmon  
214 (red = warm temperature, blue = cold temperature). Each temperature group of individuals was  
215 split into two combinations as outlined above (WW, WC, CW, CC) presented as the proportion of  
216 total days post-fertilization across the duration of the experiment. **B)** Temperature curve for the  
217 larval and juvenile phases of the experiment with the warm temperature treatment water in red and  
218 the cold temperature treatment water in blue. 0.A and 0.B indicate the timing of transport of

219 juveniles to Lammi Biological station for the warm and cold larval treatment individuals,  
220 respectively. 1, 2 and 3 indicate the times of routine measurements for length and mass of 464-580  
221 individuals at the Summer0, Autumn0 and Spring1 time points, respectively. 4 and 5 indicate the  
222 final two time points with routine measurements of length and mass of 464 and ~1205 individuals,  
223 respectively, and maturation status checking in males.

## 224 **Statistical Analysis**

### 225 ***Sexual maturation***

226 We fitted a generalized animal model with probit-link function to maturation status at age 2  
227 years (coded as binaries) using Bayesian Markov chain Monte Carlo (MCMC) simulations  
228 implemented in MCMCglmm v. 2.32 (Hadfield 2010). We wanted to test whether  
229 maturation rates were affected by the larval and juvenile temperature treatments, their  
230 interaction, the maturation locus (*vgll3*), and whether the maturation locus (*vgll3*) effects  
231 interacted with the larval or juvenile temperature treatment effects or their interaction. We  
232 therefore specified the following model to test this and to reflect the mating and  
233 experimental designs:  $Y = \mu + \beta_1 \text{JuvenileTemperature} + \beta_2 \text{LarvalTemperature} +$   
234  $\beta_3 \text{JuvenileTemperature-By-LarvalTemperature} + \beta_4 \text{Vgll3} + \beta_5 \text{Vgll3-By-}$   
235  $\text{JuvenileTemperature} + \beta_6 \text{Vgll3-By-LarvalTemperature} + \beta_7 \text{Vgll3-By-JuvenileTemperature-}$   
236  $\text{By-larvalTemperature} + \text{animal-By-JuvenileTemperature} + \text{tank-By-JuvenileTemperature} +$   
237  $\text{error-By-JuvenileTemperature}$  (1), where *JuvenileTemperature* refers to the juvenile stage  
238 rearing temperature, *LarvalTemperature* refers to the larval incubation temperature, and  
239 the  $\beta_3 \text{JuvenileTemperature-By-LarvalTemperature}$  interaction refers to their interaction.  
240 The major locus term *Vgll3* refers to a continuous additive effect of *vgll3* genotype (LL = -1,  
241 EL or LE = 0, EE = 1, i.e., the additive effect of adding one E allele) and this effect was  
242 interacted with all temperature treatment terms. The random terms *animal*, *tank*, and *error*,  
243 refer to additive genetic, tank, and residual effects, respectively. The covariance structure  
244 for animal was specified as unstructured across the two feeding temperatures and as  
245 diagonal for tank and residual effects across the two juvenile rearing temperatures  
246 (because their covariance could not be estimated). We fitted variances conditionally on  
247 juvenile temperature because we expected larger effects of the juvenile than the larval  
248 temperatures. We ran the model with four chains for 1,009,900 iterations each and  
249 sampled every 100 iterations. We then ensured that i) sampling convergence was  
250 indicated by a scale reduction factor around 1 per chain (Brooks and Gelman 1998), ii) the  
251 number of samples to discard ("burn-in", determined = 100,000) led to consistently



252 reaching a scale reduction factor  $< 1.1$  across chains (Brooks and Gelman 1998), and iii)  
253 the thinning per chain resulted in autocorrelations at lag 2  $< 0.1$  (determined thinning =  
254 500). We also checked for sufficient mixing via MCMC per chain by visually examining the  
255 trace plots. These criteria resulted in combined posteriors across chains totaling 7,280  
256 iterations.

### 257 ***Growth and condition models***

258 We recorded length and mass data at altogether five time points. Because we lethally  
259 sampled individuals, we only hold cross-sectional data at the individual level, but obtained  
260 longitudinal data (i.e., for several time points) at the biological levels of *vgll3*, sex and  
261 family and experimental levels of temperature treatments and tanks. We defined individual  
262 body condition as the deviation of the individual mass at the average length as predicted  
263 from a regression model of log of mass on log of length. The average length was 10.98 cm  
264 so that individual condition is defined as the mass standardized to this length. We fitted  
265 general animal models with normally distributed residuals for condition or length records  
266 using residual maximum likelihood (REML) as implemented in ASReml-R v. 4.1.0.176  
267 (Butler et al. 2018). We fitted models to the responses of either length or condition that  
268 were similar to the model for maturation probability in respect to the two temperature  
269 treatments and the major locus, but included additional temporal terms the five time points  
270 and SexMat, which characterized a 3-level factor for the combination of sex (female, male)  
271 and maturation status (immature, mature, conditional for males because all females were  
272 immature).

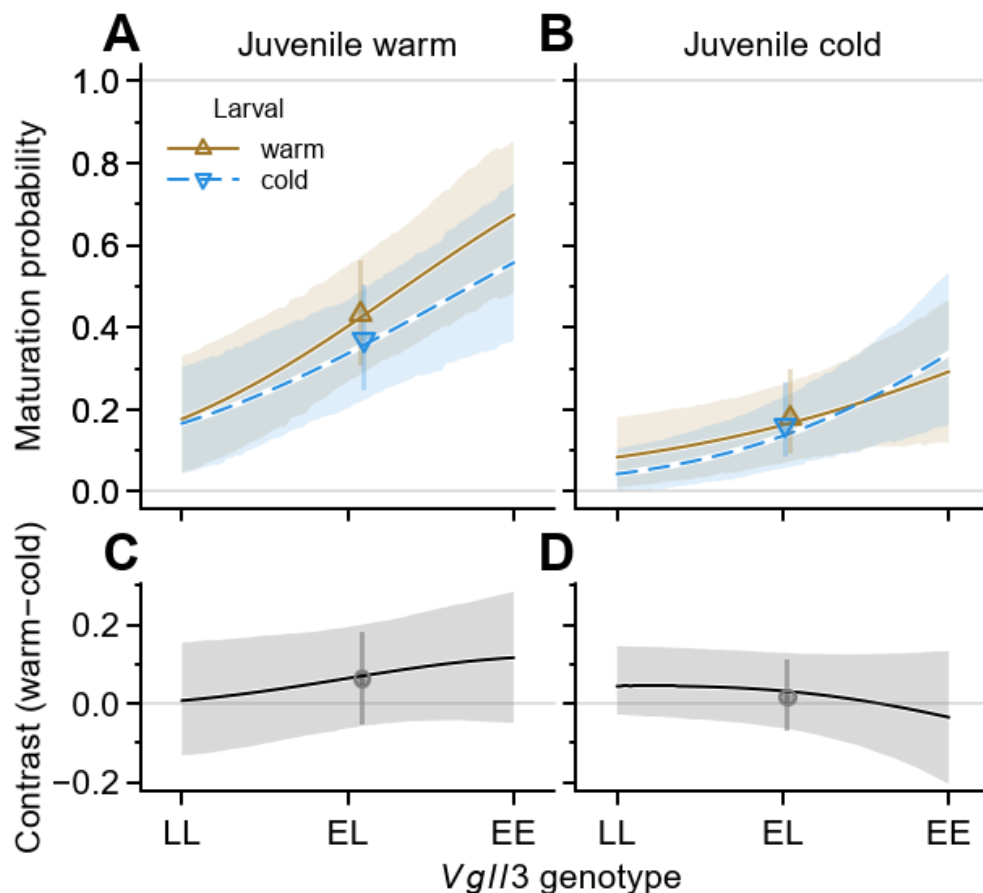
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## 274 **Results**

### 275 **Sexual maturation**

276 No female sampled throughout the study and no male sampled prior to autumn of their  
277 second year in fresh water had matured. However, 227 of the 615 males (37%) sampled in  
278 autumn of their second year were mature. Results by the generalized mixed model  
279 indicated that maturation rates did not differ between the larval temperature treatments  
280 reared within each juvenile temperature treatment (Table 1, Figure 2). However,  
281 maturation rates did differ between the juvenile temperature treatments with a 2.3 times  
282 higher maturation rate in the warm vs. the cold juvenile temperature. Specifically, the back-  
283 transformed maturation rate predicted by the generalized mixed model across major locus

284 genotypes and larval rearing temperatures was 0.40 (95% CI: 0.29-0.52) in the warm  
285 juvenile rearing treatment and 0.17 (95% CI: 0.10-0.27) in the cold juvenile rearing  
286 treatment (warm-cold contrast: 0.23; 0.13-0.32).  
287 The major locus (*vgll3*) affected male maturation rate according to expectations, i.e.,  
288 adding one or two E alleles dramatically increased the probability to mature from 0.06 to  
289 0.15 and 0.31 in the cold juvenile treatment and from 0.17 to 0.37 and 0.62 in the warm  
290 juvenile treatment, respectively (Figure 2, Table 1). In contrast to the average maturation  
291 rate, the additive major locus effect did not differ significantly between the larval or juvenile  
292 temperatures, or their interaction (Figure 2, Table 1 - model coefficients). In other words,  
293 juvenile, but not larval rearing temperature, significantly affected the overall maturation  
294 rate and the major locus effect on maturation probability remained consistent regardless of  
295 larval temperature rearing treatment.  
296



297

298

299 **Figure 2.** Model predicted, back-transformed male maturation probability for each *vgll3* genotype,  
 300 and for the overall mean across genotypes, at either a warm (A) or 2°C colder (B) juvenile  
 301 temperature. The predicted average maturation rates are depicted by larval-temperature-specific  
 302 symbols with 95% credible intervals and have been plotted at each average *vgll3* allele frequency.  
 303 The predicted additive major locus (*vgll3*) effects are depicted by larval-temperature-specific lines  
 304 with 95% credible bands. The corresponding larval-temperature contrasts for both the means and  
 305 the additive major locus effects are shown in the lower panels (C, D).

306

307 **Table 1.** Model coefficient estimates with lower and upper 95% credible intervals for the response  
 308 of male maturation status (mature, immature). Estimates are on the probit scale.

<i>Term</i>	<i>estimate</i>	<i>lower</i>	<i>upper</i>
<i>Intercept</i>	-1.71	-2.39	-1.01
<i>Larval.warm</i>	0.18	-0.43	0.79
<i>Juvenile.warm</i>	1.04	0.21	1.73
<i>Vgll3</i>	1.04	0.40	1.71
<i>Larval.warm:Juvenile.warm</i>	0.10	-0.73	0.94
<i>Larval.warm: Vgll3</i>	-0.37	-1.02	0.26
<i>Juvenile.warm: Vgll3</i>	-0.15	-0.90	0.52
<i>Larval.warm:Juvenile.warm: Vgll3</i>	0.58	-0.31	1.41

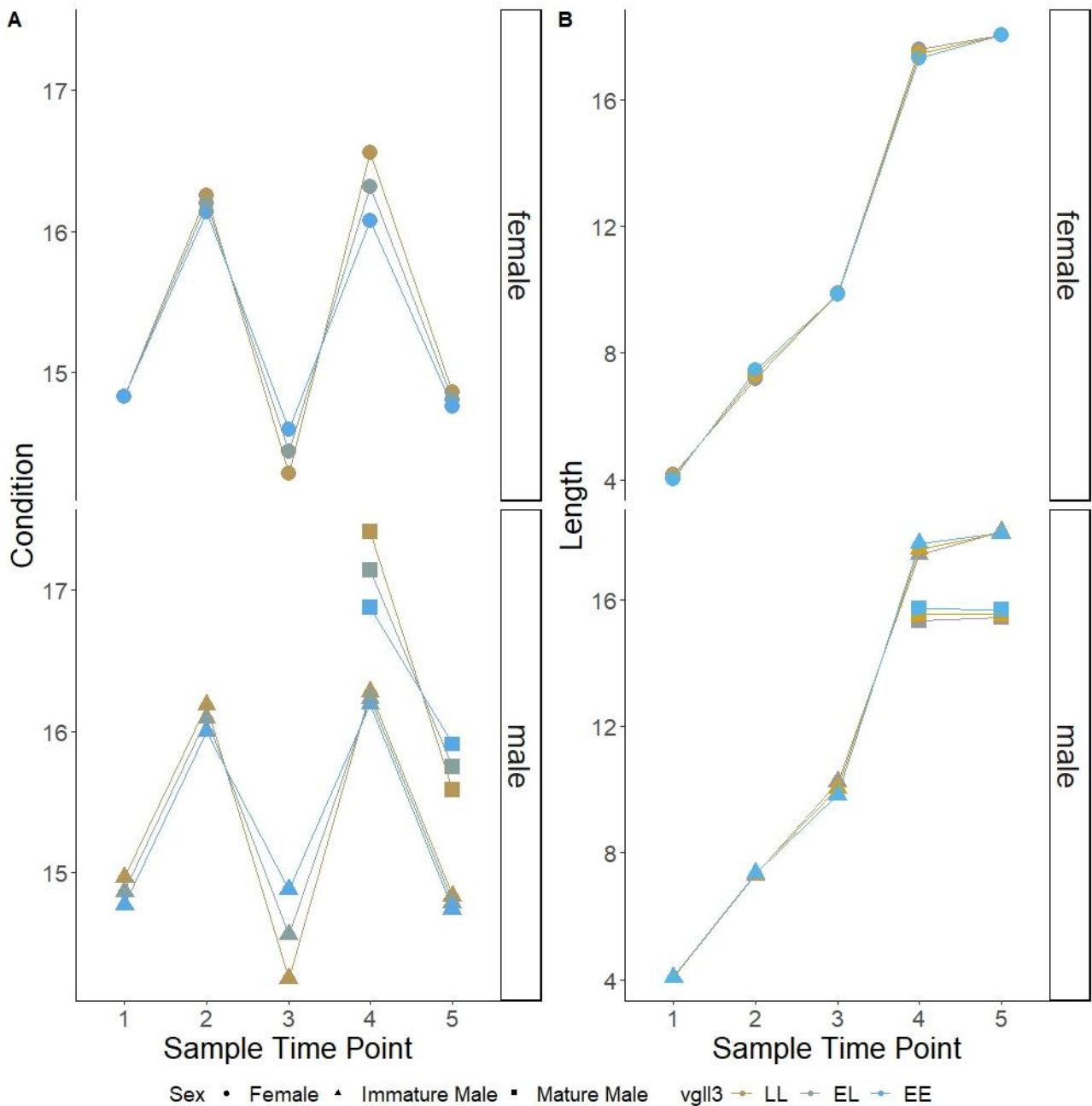
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### 311 ***vgll3* genotype effects on condition and length**

312 By predicting results based on a general animal model, it appeared evident that body  
 313 condition changes between seasons were stronger in *vgll3*\*LL individuals than in *vgll3*\*EE  
 314 individuals in both sexes: *vgll3*\*LL individuals had lower body condition than *vgll3*\*EE  
 315 individuals in the spring prior to the breeding season, but higher body condition in the  
 316 autumn, and *vgll3*\*EL individuals fell in between (Figure 3 A). The estimates of *vgll3*  
 317 additive effects for condition and length enabled a formal assessment of these time-  
 318 specific *vgll3* effects on body condition and the temporal changes of these effects during  
 319 our experiment. This assessment indicated that body condition is generally affected by  
 320 *vgll3* in both sexes (Table 2) with the *vgll3* effect during the spring receiving the strongest  
 321 statistical support, although statistical support was not given once accounted for the false  
 322 discovery rate (Table 3). However, the change of the *vgll3* effect on condition across time  
 323 was significant (Table 4). The spring timepoint also had the strongest *vgll3* additive effect  
 324 contrast between all three other seasons measured in the experiment (Table 4). Thus,  
 325 even though there was only limited statistical support for time-specific differences in

326 condition among *vgll3* genotypes, the difference in condition change across seasons  
327 between *vgll3* genotypes received sufficient statistical support (Table 4).  
328 In contrast to condition, length was not affected by *vgll3* (Table 5). However, mature  
329 *vgll3*\*LL males in CC were fatter but shorter than *vgll3*\*EE males, whereas mature *vgll3*\*LL  
330 males in WW were thinner but longer than *vgll3*\*EE males, but only at the first time point in  
331 autumn as shown above in Figure 3.  
332



333

334 **Figure 3.** Model-predicted body condition and length values of the large effect maturation locus  
335 (*vgll3*) in Atlantic salmon juveniles across 1.5-years (N = 3177). Sample time point numbers 1, 2,  
336 3, 4 and 5 represent 1 – Summer age 0, 2 – Autumn age 0, 3 - Spring age 1, 4 - Autumn age 1 and

337 5 – Autumn age 1, respectively. The colors represent *vgll3* genotypes (gold = LL, gray = EL, blue =  
 338 EE) and the shapes represent sex/maturation status (circle = female, triangle = immature male,  
 339 square = mature male). All females were immature.  
 340

341 **Table 2:** *F*-test results based on the mixed model for body condition.

	<i>DF</i>	<i>DDF</i>	<i>F</i>	<i>P</i>
<i>Intercept</i>	1	18.3	0.01	0.9398
<i>Vgll3</i>	1	16.1	0.22	0.6434
<i>JuvenileTemp</i>	1	17	0.18	0.6728
<i>LarvalTemp</i>	1	20.9	0.72	0.4066
<i>TimePoint</i>	4	29.5	172.3	<0.001
<i>Sex.MAT</i>	2	2015.2	150.6	<0.001
<i>Vgll3:JuvenileTemp</i>	1	23.3	0.37	0.5469
<i>Vgll3:LarvalTemp</i>	1	2795.5	2.36	0.1248
<i>JuvenileTemp:LarvalTemp</i>	1	12.4	0.00	0.9819
<i>Vgll3:TimePoint</i>	4	1139.8	5.84	0.0001
<i>JuvenileTemp:TimePoint</i>	4	19.7	11.95	<0.001
<i>LarvalTemp:TimePoint</i>	4	29.8	0.31	0.8703
<i>Vgll3:Sex.MAT</i>	2	1960.7	2.38	0.0929
<i>JuvenileTemp:Sex.MAT</i>	2	2023.5	0.06	0.9372
<i>LarvalTemp:Sex.MAT</i>	2	1993.9	4.86	0.0079
<i>TimePoint:Sex.MAT</i>	5	1179.7	1.52	0.1792
<i>Vgll3:Juvenile:LarvalTemp</i>	1	2562.3	1.13	0.2877
<i>Vgll3:Juvenile:TimePoint</i>	4	1123.4	0.66	0.6176
<i>Vgll3:LarvalTemp:TimePoint</i>	4	1133.9	1.66	0.1559
<i>Juevenile:LarvalTemp:TimePoint</i>	4	19.9	1.45	0.2549
<i>Vgll3:JuvenileTemp:Sex.MAT</i>	2	2006.2	0.44	0.6456
<i>Vgll3:LarvalTemp:Sex.MAT</i>	2	1929.9	2.89	0.0557
<i>JuvenileTemp:LarvalTemp:Sex.MAT</i>	2	2015.8	6.62	0.0014
<i>Vgll3:TimePoint:Sex.MAT</i>	5	1157.9	0.68	0.6395
<i>JuvenileTemp:TimePoint:Sex.MAT</i>	5	1157.8	0.46	0.8063
<i>LarvalTemp:TimePoint:Sex.MAT</i>	5	1172.4	1.85	0.1011
<i>Vgll3:JuvenileTemp:LarvalTemp:TimePoint</i>	4	1119.1	1.17	0.3215
<i>Vgll3:JuvenileTemp:LarvalTemp:Sex.MAT</i>	2	1990.8	0.98	0.3739
<i>Vgll3:JuvenileTemp:TimePoint:Sex.MAT</i>	5	1109.1	1.39	0.2253
<i>Vgll3:LarvalTemp:TimePoint:Sex.MAT</i>	5	1150	1.23	0.2908
<i>Juvenile:LarvalTemp:TimePoint:Sex.MAT</i>	5	1139.9	1.26	0.2804
<i>Vgll3:JuvenileTemp:LarvalTemp:TimePoint:Sex.MAT</i>	5	1082.2	1.77	0.1152

342

343

344 **Table 3.** Time-point specific estimates of the *vgll3* additive effect (effect of adding one E allele) on  
 345 body condition.

346

*TimePoint* *diff* *sed* *t* *p* *fdr*

1Summer0	0.00442	0.006263	0.72	0.490474	0.613
2Autumn0	0.006389	0.006009	1.06	0.303397	0.506
3Spring1	-0.01447	0.006415	-2.26	<b>0.038369</b>	0.192
4Autumn1	0.010562	0.006085	1.74	0.101708	0.254
5Autumn1	0.002602	0.005175	0.50	0.621928	0.622

347

348 **Table 4.** Between-time point contrasts of the *vgll3* additive effect (effect of adding one E allele) on  
349 body condition.

350

<i>TimePoint</i>	<i>Contrast terms</i>	<i>diff</i>	<i>sed</i>	<i>t</i>	<i>p</i>	<i>fdr</i>
1Summer0	Vgll3.ADD:2Autumn0	-0.00197	0.005271	-0.37	0.70872	0.709
	Vgll3.ADD:3Spring1	0.018888	0.005763	3.28	<b>0.00108</b>	<b>0.002</b>
	Vgll3.ADD:4Autumn1	-0.00614	0.005402	-1.14	0.25567	0.384
2Autumn0	Vgll3.ADD:3Spring1	0.020858	0.005549	3.76	<b>0.00018</b>	0.001
	Vgll3.ADD:4Autumn1	-0.00417	0.005167	-0.81	0.41943	<b>0.503</b>
	Vgll3.ADD:1Summer0	0.00197	0.005271	0.37	0.70872	0.709
3Spring1	Vgll3.ADD:4Autumn1	-0.02503	0.005651	-4.43	<b>0.00001</b>	0.000
	Vgll3.ADD:1Summer0	-0.01889	0.005763	-3.28	<b>0.00108</b>	<b>0.002</b>
	Vgll3.ADD:2Autumn0	-0.02086	0.005549	-3.76	<b>0.00018</b>	<b>0.001</b>
4Autumn1	Vgll3.ADD:1Summer0	0.006143	0.005402	1.14	0.25567	0.384
	Vgll3.ADD:2Autumn0	0.004174	0.005167	0.81	0.41943	0.503
	Vgll3.ADD:3Spring1	0.025031	0.005651	4.43	<b>0.00001</b>	<b>0.000</b>

351

352

353 **Table 5:** *F*-test results based on the mixed model for length.

	<i>DF</i>	<i>DDF</i>	<i>F</i>	<i>P</i>
(Intercept)	1	16.7	13190	<0.001
Vgll3	1	16.8	0.8	0.380
JuvenileTemp	1	23.5	224.3	<0.001
LarvalTemp	1	22	42	<0.001
TimePoint	4	28.1	12230	<0.001
Sex.MAT	2	2134.5	108.6	<0.001
Vgll3: Juvenile Temp	1	19.9	2.4	0.1396
Vgll3:LarvalTemp	1	2329.6	2.5	0.1113

<i>JuvenileTemp:LarvalTemp</i>	1	31.3	0.7	0.3954
<i>Vgll3:TimePoint</i>	4	1140.1	1.8	0.119
<i>Juvenile Temp:TimePoint</i>	4	22.6	14.7	<0.001
<i>Larval Temp:TimePoint</i>	4	28.4	7.9	0.0002
<i>Vgll3:Sex.MAT</i>	2	2103.9	0.2	0.8001
<i>JuvenileTemp:Sex.MAT</i>	2	1942.4	3.2	0.0409
<i>LarvalTemp:Sex.MAT</i>	2	2118.8	0.2	0.8277
<i>TimePoint:Sex.MAT</i>	5	1238.1	1.1	0.3331
<i>Vgll3: JuvenileTemp:LarvalTemp</i>	1	2099.5	0.2	0.6826
<i>Vgll3: JuvenileTemp:TimePoint</i>	4	1108.7	0.7	0.5683
<i>Vgll3: LarvalTemp:TimePoint</i>	4	1136.5	2.1	0.0759
<i>JuvenileTemp: Larval Temp:TimePoint</i>	4	22.9	0.4	0.7956
<i>Vgll3: Juvenile Temp:Sex.MAT</i>	2	1968.1	1.3	0.275
<i>Vgll3: Larval Temp:Sex.MAT</i>	2	2083.3	0.7	0.4977
<i>Juvenile Temp: Larval Temp:Sex.MAT</i>	2	1935.4	4	0.0179
<i>Vgll3:TimePoint:Sex.MAT</i>	5	1224.9	2	0.0812
<i>Juvenile Temp:TimePoint:Sex.MAT</i>	5	1202.9	1.9	0.0848
<i>Larval Temp:TimePoint:Sex.MAT</i>	5	1231.9	1.4	0.2134
<i>Vgll3: Juvenile Temp:LarvalTemp:TimePoint</i>	4	1104	0.8	0.5358
<i>Vgll3: JuvenileTemp:Larval Temp:Sex.MAT</i>	2	1943.6	1.3	0.2761
<i>Vgll3: JuvenileTemp:TimePoint:Sex.MAT</i>	5	1163.1	2	0.0782
<i>Vgll3: LarvalTemp:TimePoint:Sex.MAT</i>	5	1214.9	1.7	0.1219
<i>JuvenileTemp: Larval Temp:TimePoint:Sex.MAT</i>	5	1194.1	1.5	0.1883
<i>Vgll3:</i>	5	1143.9	0.9	0.4868
<i>JuvenileTemp:LarvalTemp:TimePoint:Sex.MAT</i>				

354

355

### 356 Larval temperature effects on body condition, length, and interaction with *vgll3* 357 genotypes

358 Body condition showed only one significant (FDR < 0.05) effect on means between larval  
359 temperatures (ignoring *vgll3*): in mature males at the last time point and at the warm  
360 feeding temperature with WW males being 0.6 g (0.3-0.9 g) smaller for the same length as  
361 CW males. With length, there were several significant (FDR < 0.05) effects on means  
362 between larval temperatures. However, no differences for any *vgll3* effects with larval  
363 temperatures were detected for either condition or length, only the abovementioned *vgll3*  
364 effects on condition change.

365

### 366 Discussion

367 It has previously been shown that temperature experienced at an early point in life can  
368 have lasting effects in later life stages (Macqueen et al. 2008; Nord and Nilsson 2016;  
369 While et al. 2018; reviewed in Jonsson and Jonsson 2019) We aimed to experimentally

370 test for the occurrence of such effects during the freshwater phase in Atlantic salmon as  
371 water temperature has been earlier shown known to influence behavior, food availability  
372 and metabolic rate (Morash et al. 2021; Jutfelt et al. 2021). We present two key findings  
373 that contribute to our understanding how temperature differences experienced during early  
374 life affect (life-history) traits later in life. The first finding that a 2°C difference in rearing  
375 temperature during the larval phase, the 4.5- to 6-month period from fertilization to first  
376 exogenous feeding, did not significantly affect maturation rate, is of relevance for  
377 considering the fate of wild populations experiencing environmental change, but also to  
378 aquaculture production where early sexual maturation is an undesired event. Juveniles of  
379 most wild Atlantic salmon populations spend at least two, and sometimes more, years in  
380 riverine environments where water temperatures can vary considerably between larval and  
381 juvenile phases. Our results suggest that populations may be resilient to temperature  
382 differences of up to 2°C during the larval phase when considering future effects on  
383 maturation age, at least at the age of two years as mature parr as studied here. Our  
384 second finding of relevance is that differing larval or juvenile temperature did not appear to  
385 alter the *vgll3* locus effects on maturation, nor on growth, length, or body condition.  
386 Interestingly, no differences for any sex in any feeding temperature exist thereafter which  
387 meant the individuals in the colder temperature during larval phase had full growth  
388 compensation during the length of the experiment.  
389 This second finding of no larval or juvenile temperature effect with *vgll3* leads us to expect  
390 a temperature consistency in *vgll3* effects on maturation and other affected traits, and thus  
391 also to a *vgll3*-effect consistency in response to either natural or artificial selection. This is  
392 an important finding with respect to modelling the effects of temperature change across  
393 thermal environments as the predicted effects of *vgll3* on maturation probability can be  
394 assumed stable across temperatures. That said, it should be noted that a relatively narrow  
395 range of temperatures were explored here, so future research across a broader  
396 temperature range may be useful. Lastly, the overall higher maturation probability in the  
397 warmer juvenile treatment observed in controlled conditions in our study is consistent with  
398 previous reports in wild populations (Martinez et al. 2000) and controlled conditions (Rowe  
399 and Thorpe 1990a; Åsheim et al. 2022) showing higher rates of early maturation in certain  
400 populations with warmer temperatures (Jonsson and Jonsson 2013). We found *vgll3*  
401 genotype was correlated with higher maturation probability with each addition of a *vgll3*\*E  
402 allele increasing the observed maturation probability. This was also found in a recent study  
403 by Debes et al. (2021) which found the additive effect of one *vgll3*\*E allele probability



404 estimate to be 0.94 compared to 1.04 in our study. In addition, this is the first time to our  
405 knowledge of *vgll3* interactions with different larval rearing temperatures being reported  
406 and with *vgll3* showing no effect with the warm and cold larval temperature treatments.  
407 The observed seasonal changes in body condition were as expected, with body condition  
408 being highest in the autumn, following the period of highest food consumption rate in the  
409 summer, and lowest in the spring following the over-wintering period at cold temperatures  
410 (Figure 3A). However, an unexpected, but nevertheless noteworthy, finding of this study  
411 was that *vgll3* genotype affected the level of seasonal change in body condition in both  
412 sexes whereby *vgll3\*LL* individuals had lower body condition than *vgll3\*EE* individuals in  
413 the spring prior to the breeding season, but then higher body condition in the autumn.  
414 These *vgll3* genotype specific seasonal changes in body condition over the 1.5-year study  
415 period add further nuance to previous studies that suggested a role of *vgll3* in the control  
416 of resource allocation (Debes et al. 2021; Halperin et al. 2013). *Vgll3* effects on body  
417 condition may express as effects on condition change and, and thus may or may not  
418 express as an effect on average condition at a given time point. Our findings suggest that  
419 the general assumption that individuals with higher body condition are more likely to  
420 mature earlier due to having higher lipid reserves (Andersson et al., 2018; Good &  
421 Davidson, 2016; Roff, 2002; Rowe et al., 1991; Stearns, 1992; Taranger et al., 2010; Wells  
422 et al., 2017) may be too simplistic. Rather, backing up previous statements that it may be  
423 that having an adequate storage of energy at critical life history timepoints, which for  
424 salmon is thought to be in the spring prior to maturation, is key (Rowe et al, 1991). This is  
425 indeed the timepoint at which juveniles carrying the *vgll3\*EE* genotype exhibited higher  
426 body condition than individuals carrying other *vgll3* genotypes (Figure 3a), even though  
427 body condition was recorded at its lowest point for all genotypes of the five timepoints  
428 measured.

429 Our observation that the body condition of *vgll3\*EE* individuals was more stable across  
430 seasons than that of *vgll3\*LL* individuals is in line with recent studies investigating links  
431 between *vgll3* genotypes and other juvenile phenotypes including aggressive behavior and  
432 aerobic scope, both of which could perceivably have an effect on condition factor in  
433 Atlantic salmon. It was earlier found that *vgll3\*LL* juveniles were more aggressive  
434 compared to *vgll3\*EE* individuals (Bangura et al. 2022). Such a behavioral difference could  
435 result in *vgll3\*LL* individuals allocating energy for aggressive behavior, which otherwise  
436 could have been allocated to lipid storage. Considering aerobic scope, it was found that  
437 *vgll3\*EE* individuals had higher aerobic scope than *vgll3\*LL* individuals. Thus, superior

438 resource acquisition or assimilation via higher aerobic scope was suggested as a potential  
439 mechanism by which an increased condition factor in *vgll3\*EE* individuals could be  
440 achieved (Prokkola et al. 2022). Our finding here suggest that these qualities may be  
441 particularly important during the winter months, when *vgll3\*LL* individuals lost body  
442 condition much faster than *vgll3\*EE* individuals, the result being that *vgll3\*EE* individuals  
443 had higher condition factor at the critical point in the spring when physiological processes  
444 related to maturation are being determined.

445 One potential caveat for interpreting these results is the strong decline in body condition  
446 observed between the last two measuring time points just several weeks apart with mature  
447 individuals included in this calculation. One potential explanation for this is the prolonged  
448 sampling from time point 4 to 5, resulting from the large number of individuals being  
449 measured, may have resulted in the longer period of fasting resulting in lower condition in  
450 individual sampled during the fifth time point. This pattern could also simply be due to  
451 routine sampling involving dissection and growth measurements over a prolonged period  
452 of time e.g. one month, which is indicated by a decreasing *vgll3\*LL* mature male length  
453 with time (Figure 3B, male panel), which is unexpected over such a short time period, but  
454 could be explained by random sampling from tanks. Alternatively, males may need  
455 different cues (high condition vs. high length) to become mature in the different  
456 temperature environments of WW vs. CC as we see the average length to be the same at  
457 the first time point for both sexes and in both feeding temperatures. These results may  
458 simply reflect the later initiated feeding of the cold incubated fish.

459 To conclude, our study provides details of how genetic (the *vgll3* locus) and environmental  
460 (seasonal temperature) effects contribute to maturation probability, with seasonal body  
461 condition being a central phenotype. Importantly, the seasonal context in which condition  
462 factor is measured needs to be considered when interpreting results, as the relative  
463 condition factors of individuals with differing *vgll3* genotypes was completely reversed in  
464 autumn vs. spring. Future work to better understand energy allocation processes e.g., via  
465 lipidomics or functional genomics could help to shed more light on the mechanisms by  
466 which the large-effect *vgll3* locus influences maturation and exploring a broader range of  
467 temperature differences could aide understanding the absence of an effect of larval  
468 temperature on maturation.

469

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