

1 Life history genomic regions explain differences in Atlantic salmon marine diet specialization

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10 Abstract

11 1. Animals employ various foraging strategies along their ontogeny to acquire energy, and with
12 varying degree of efficiencies, to support growth, maturation and subsequent reproduction events.
13 Individuals that can efficiently acquire energy early are more likely to mature at an earlier age, as a
14 result of faster energy gain which can fuel maturation and reproduction.

15 2. We aimed to test the hypothesis that heritable resource acquisition variation that co-varies with
16 efficiency along the ontogeny would influence maturation timing of individuals.

17 3. To test this hypothesis, we utilized Atlantic salmon as a model which exhibit a simple, hence
18 trackable, genetic control of maturation age. We then monitored the variation in diet acquisition
19 (quantified as stomach fullness and composition) of individuals with different ages, and linked it
20 with genomic regions (haploblocks) that were previously identified to be associated with age-at-
21 maturity.

22 4. Consistent with the hypothesis, we demonstrated that one of the life history genomic regions tested
23 (*six6*) was indeed associated with age-dependent differences in stomach fullness. Prey composition was
24 marginally linked to *six6* and suggestively but non-significantly to *vgl3* genomic regions. We further

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25 showed Atlantic salmon switched to the so-called “feast and famine” strategy along the ontogeny, where
26 older age groups exhibited heavier stomach content, but that came at the expense of running on empty
27 more often.

28 **5.** These results suggest genetic variation underlying resource utilization may explain the genetic basis of
29 age structure in Atlantic salmon. Given that ontogenetic diet has a genetic component and the strong
30 spatial diversity associated with these genomic regions, we predict populations with diverse maturation
31 age will have diverse evolutionary responses to future changes in marine food-web structures.

32

33 **Keywords:** *Diet specialization, ontogenetic diet shift, life history evolution, ontogenetic foraging variation,*
34 *Atlantic salmon.*

35

36 **Introduction**

37 Diet acquisition is a strong evolutionary force that can shape population demography and abundance,
38 and is an integral determinant of ecosystem functions (Engen and Stenseth 1989, Svanback and
39 Persson 2004, Bolnick and Araujo 2011). Individuals exhibit differences in prey preference and prey
40 acquisition efficiency, which, if heritable, may be a target of selection and ultimately promote
41 ecological specialization (Fox and Morrow 1981, Smith and Skulason 1996, Devictor et al. 2010).
42 Large-scale disturbances in community structure, e.g., as a result of climate change (Sydeman et al.
43 2015) alter food web structures and the composition of available resources (Daufresne et al. 2009,
44 Pershing et al. 2015, Bentley et al. 2017), forcing species to rapidly adapt to new diet landscapes.
45 Therefore, understanding the underlying mechanisms shaping food acquisition strategies is
46 fundamental to evolutionary biology and vital for predicting species survival in a changing world.

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47 If heritable, inter-individual variation in resource acquisition strategies may have complex
48 evolutionary consequences mediated by trade-offs between energy gain and survival across density-
49 and frequency-dependent fitness landscapes (Mousseau et al. 2000, Reznick and Ghalambor 2001,
50 Reznick 2016, Sexton et al. 2017). For example, increased boldness to improve resource acquisition
51 success may come at the expense of higher predation risk, the fitness costs of which may be linked
52 to predator densities (Gotthard 2000, Carter et al. 2010, Bolnick et al. 2011). Likewise, the
53 composition and abundance of available resources may alter the demographic structure of a
54 population (e.g., Heino and Kaitala 1999, Enberg et al. 2012). For example, fast growth at an early
55 age, e.g. as a result of abundant food sources during the initial stages of life, may result in early
56 maturation and hence a younger age at reproduction. In contrast, resource limitation due to high
57 population densities results in increased allocation to somatic growth to improve size-dependent
58 intraspecific competition (e.g., Reznick and Endler 1982).

59 Ontogenetic diet shifts in organisms may be viewed as a special type of resource acquisition strategy
60 in which diet variation is expressed as a function of age. Ontogenetic diet shift is a significant source
61 of variation in species' diet breadth, especially among size- and age-structured organisms, such as
62 fishes. In general, relatively large and/or old individuals shift towards feeding at higher trophic levels
63 and/or on larger prey items to maintain a positive energy balance (Werner and Gilliam 1984,
64 Mittelbach and Persson 1998, Jensen et al. 2012). Under changing food-web dynamics, diet
65 specialization among different age groups may substantially influence the demographic structure and
66 life history diversity (Sanchez-Hernandez et al. 2019). For example, changes in resource composition
67 that favour younger age groups would improve growth and subsequently increase the rate of
68 maturation and the probability of survival at early ages. Ontogenetic diet shift is associated with a

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69 suite of changes in an individual's morphology, physiology and behaviour to maximize the efficiency
70 of particular resources at a given ontogenic stage, perhaps at the expense of reduced efficiency at
71 other stages (Claessen and Dieckmann 2002).

72 If ontogenetic diet variation has a genetic basis, then some individuals in a population may be selected
73 for high prey acquisition efficiency early in their life history (via physiological or morphological
74 trade-offs towards efficient exploitation at earlier stages), even if this may come at a cost of
75 compromised energy acquisition at later stages in life (Claessen and Dieckmann 2002). We predict
76 that such genetically driven trade-offs in resource acquisition efficiency between early and late stages
77 mediate the age structure (i.e. maturation timing) and abundance within and among populations and
78 maintain genetic variation in resource acquisition strategies, but such examples in the wild are rare.

79 Atlantic salmon (*Salmo salar*) is a fish species recognized as a diet generalist and an opportunistic
80 feeder with extensive ontogenetic and stage- and space-structured individual variation in diet breadth
81 (Erkinaro et al. 1997, Jacobsen and Hansen 2001, Haugland et al. 2006, Hvidsten et al. 2009,
82 Rikardsen and Dempson 2010, MacKenzie et al. 2012). At sea, where most growth occurs, salmon
83 increasingly feed on prey at higher trophic levels as they grow and age (Jacobsen and Hansen 2001,
84 Rikardsen and Dempson 2010). The time salmon spend at sea prior to maturation (sea age at maturity)
85 also varies greatly within and among populations (Friedland and Haas 1996). Although the functional
86 and physiological basis underlying age at maturity is not entirely known, it is considered to be a
87 threshold trait, whereby higher lipid deposition is associated with early maturation (Friedland and
88 Haas 1996, Jonsson et al. 1997, Thorpe et al. 1998, Taranger et al. 2010, Jonsson and Jonsson 2011).
89 Therefore, variation in resource acquisition may be a strong determinant of the life history variation

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90 in salmon and a trait via which natural selection can act and result in adaptive genetic changes in
91 populations.

92 In Atlantic salmon, two genomic regions on chromosomes 9 and 25 have been identified to have a
93 disproportionate influence on life history strategy and population differentiation within and among
94 populations (Ayllon et al. 2015, Barson et al. 2015, Czorlich et al. 2018, Pritchard et al. 2018, Aykanat
95 et al. 2019). The so-called *vgll3* and *six6* genomic regions are named after the most prominent genes
96 in their respective haploblocks on chromosomes 25 and 9, respectively. The *vgll3* genomic region on
97 chromosome 25 has been shown to be associated with age at maturity (initially by GWAS, see: Ayllon
98 et al. 2015, Barson et al. 2015), iteroparity (Aykanat et al. 2019), and precocious male maturation in
99 Atlantic salmon (Lepais et al. 2017, Debes et al. 2019). This genomic region also exhibits strong
100 spatial divergence (Barson et al. 2015, Pritchard et al. 2018), and it has recently been shown to have
101 been affected by natural selection over the last 36 years (equivalent to 4-6 salmon generations) in
102 parallel to the changing age structure in a large salmon population (Czorlich et al. 2018). The *six6*
103 region on chromosome 9 is associated with sea age at maturity at the population level as a result of
104 the strong correlation between the average allele frequency and average maturation age of populations
105 (Barson et al. 2015). This region also exhibits the strongest signal of differentiation among European
106 populations (Barson et al. 2015) and Tana/Teno River populations (Pritchard et al. 2018) and is hence
107 distinguished as a critical genomic region for local adaptation. Genes found in these haploblocks
108 appear to have a role in adipose or energy metabolism regulation in other organisms. The *vgll3* gene
109 is an adipocyte inhibitor, the expression of which is correlated with body weight and gonadal adipose
110 content in mice (Halperin et al. 2013). Recently, a strong selective sweep near the *vgll3* gene was
111 postulated to be due to energy metabolism effects in humans in Mongolia (Nakayama et al. 2017). In

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112 turn, genes in the *six6* genomic region are involved in cell growth, cell differentiation, apoptosis in
113 human cell lines (*PPM1A*, Lin et al. 2006), and myogenesis and skeletal muscle cell proliferation in
114 zebrafish (*six1b*, Ridgeway and Skerjanc 2001, Bessarab et al. 2004, O'Brien et al. 2014) and act as
115 an evolutionarily conserved regulator of eye development and the pituitary–hypothalamic axis (*six6*,
116 Serikaku and Otousa 1994, Toy et al. 1998, Gallardo et al. 1999). Collectively, this suggests that the
117 *vgll3* and *six6* haploblocks might have broad-scale roles in reproductive and life-history strategies in
118 Atlantic salmon. However, how polymorphism in these regions may be translated to functional
119 differences expressed in the wild is unclear.

120 Here, our objective was to test whether age-dependent differences in food acquisition efficiency are
121 associated with the *vgll3* and *six6* genomic regions and discuss their role in explaining the genetic
122 variation in age structure. We achieved this goal by assessing stomach content data from adult
123 Atlantic salmon sampled along the coast during spawning migration and genotyping the same
124 individuals for the *vgll3* and *six6* genomic regions using a targeted sequencing approach. Using a
125 modelling framework that accounted for potentially confounding environmental and phenotypic
126 variables, we tested whether variation in diet and resource acquisition strategies had a genetic
127 component explained by the age at maturity-linked genomic regions. Elucidating the genetic interplay
128 between age at maturity and diet breadth is crucial to better understand the dynamics and evolution
129 of ecological specialization and to better predict future demographic changes in Atlantic salmon
130 populations under climate change.

131 **Materials and Methods**

132 *Sample collection*

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133 As part of a larger effort within the project “Sea salmon fishery, resource and potential (KOLARCTIC)”,
134 Atlantic salmon (*Salmo salar*), on their return migration to spawning grounds, were sampled and
135 stomachs were collected between mid-May and late July in 2008 by local sea fishers with bend nets
136 or bag nets along the Finnmark coast, northern Norway (Svenning et al. 2019, Figure 1). Sampled
137 fish were measured (fork length, cm) and weighed (g); their sex and maturity were identified, and
138 stomachs were frozen for later diet analysis. In addition, scales were sampled from all fish for sea age
139 determination, categorization as wild or farmed fish according to ICES guidelines (ICES 2011,
140 Svenning et al. 2019), and genetic analysis. The species composition of the diet was then identified
141 to species by visual inspection of the morphology of prey remains and otoliths which were compared
142 to a reference collection with known species identity, with uncertain cases further inspected using
143 keys (Härkönen 1986, Pethon and Nyström 2005). All prey items, including unidentified digested
144 remains were weighted (wet mass at a precision of 0.1 g). The identifiable portion of the diet in the
145 dataset was overwhelmingly comprised of four fish species: sand eel (*Ammodytes* spp.), capelin
146 (*Mallotus villosus*), herring (*Clupea harengus*), and haddock (*Melanogrammus aeglefinus*, see
147 Results section for details). In the interest of analytical brevity, a few rare prey species were handled
148 as follows: one gadoid fish was grouped with haddocks, both of which belong to the Gadiformes
149 order, and negligible amounts of krill, other crustaceans, and Liparidae (0.2% of the total stomach
150 weight) were categorized together with the unidentified material.

151

152 *DNA extraction, microsatellite genotyping, and SNP genotyping by targeted sequencing*

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153 DNA was extracted from scales either using a QIAamp 96 DNA QIAcube HT Kit (Qiagen) following
154 the manufacturer's protocol or according to Elphinstone et al. (2003). Microsatellite genotyping of 31
155 markers was performed as outlined in Ozerov et al. (2017). Samples were further genotyped by
156 targeted sequencing at 173 SNP markers and the sex determination locus (sdy) using a GTSeq
157 approach (Campbell et al. 2015) as outlined in Aykanat et al. (2016), with some modifications so the
158 genotyping panel was compatible with the Illumina platform. More specifically, 174 genomic regions
159 were first amplified in one multiplex PCR using locus-specific primers with truncated Illumina
160 adapter sequences and using primer concentrations re-optimized for the Illumina platform (Supp.
161 Table 1). The PCR products were then treated with Exonuclease I and FastAP Thermosensitive
162 Alkaline Phosphatase (Thermo Fisher) to remove unused primers and nucleotides. After the
163 treatment, the products were re-amplified with adapter-specific primers containing Illumina and
164 sample-specific dual-indexes. The index set was optimized using the BARCOSEL software
165 (Somervuo et al. 2018). The PCR products were then pooled, purified and quantified with a Qubit 2.0
166 fluorimeter (Thermo Fisher) and analysed on a fragment analyser (Agilent Technologies). The pooled
167 library was then size selected using BluePippin (Sage Sciences) to remove short unspecific products
168 and checked on a fragment analyser. Finally, samples were single-end sequenced using a 150-cycle
169 high-output sequencing kit on a NextSeq 500 Illumina Sequencer following the manufacturer's
170 guidelines. Loci with coverage over 12x were scored as in Aykanat et al. (2016). To calculate
171 coverage for each SNP, raw genotype files (fastq) were scanned for every SNP, and the coverage was
172 determined by counting sequences that matched SNP's forward and reverse primer sequences, and
173 the 9 bp region around the SNP site. Finally, genotypes were scored based on coverage ratios between
174 alleles: $\text{Ratio}_{\text{Cov}(\text{allele1}/\text{allele2})} > 10$ was assigned as homozygous for allele 1, $\text{Ratio}_{\text{Cov}(\text{allele1}/\text{allele2})} < 0.1$ was

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175 assigned as homozygous for allele 2, $\text{Ratio}_{\text{Cov}(\text{allele1}/\text{allele2})}$ between 0.2 and 5 was assigned as
176 heterozygous and any proportion in between was discarded (see also, Campbell et al. 2015).

177 Two focal SNPs used in the analyses were $vgll3_{\text{TOP}}$, which exhibits the strongest signal of association
178 with age at maturity in the $vgll3$ genomic region, and $six6_{\text{TOP.LD}}$ in the $six6$ haploblock on chromosome
179 9, the region that exhibited the second strongest association with sea age at maturity prior to
180 population structure correction and is 34.5 kb away from and in complete linkage disequilibrium with
181 the $six6_{\text{TOP}}$ SNP reported in Barson et al. (2015).

182 *Genetic stock identification (GSI)*

183 In total, 2023 samples that had greater than 80% success in regard to microsatellite genotyping were
184 assigned to their population of origin with 31 microsatellite markers as described in Svenning et al.
185 (2019) using the Bayesian GSI methodology described in Pella and Masuda (2001) and implemented
186 in cBayes 5.0.1 (Neaves et al. 2005). In brief, the samples were allocated into 18 analysis groups, that
187 is, the combination of two time periods (May-June and July) and 10 fisheries regions, with each group
188 consisting of 30 to 288 samples for analysis. The GSI analyses were performed using five independent
189 Monte Carlo Markov chains of 100K iterations starting from three random stocks (StartStock
190 parameter), and the last 10K iterations of each chain were combined and used to assign individuals
191 to their population of origin to remove the influence of initial starting values. The baseline population
192 data for the GSI analysis included genetic information on 185 Atlantic salmon populations spanning
193 from the Pechora River (Russia) in the east to the Beiarelva River (Norway) in the west (see details
194 in Ozerov et al. 2017).

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195 The probability (p) threshold for assignment of an individual to a population was set at ≥ 0.7 following
196 Vähä et al. (2011, 2014) and Bradbury et al. (2015). The 30% of individuals assigned to a population
197 with lower confidence were kept in the dataset with the highest ranked population assigned as the
198 population of origin. Samples with no assignment due to low genotyping success with microsatellites
199 (4%) were assigned a population of origin using genotype information from the SNP panel. In such
200 cases, individuals were assigned to the population in which they exhibited the highest genetic
201 similarity. This was measured according to the average genetic similarity of focal individuals to the
202 individuals in each population (as inferred with the GSI analysis in the previous step) using the *A.mat*
203 function in the rrBLUP package (Endelman 2011) A small subset of individuals (N=16, < 1%) with
204 poor genotyping success with SNPs (less than 50 SNPs with high quality genotypes) was randomly
205 assigned to a population, in which population assignment probability is weighted over the total
206 number of individuals that were assigned by GSI. The effect of including incomplete population
207 assignment was assessed for the main analysis by repeating the analysis but only including
208 confidently assigned individuals.

209 Missing data points for some variables were inferred from highly correlated variables. In that regard,
210 missing sea age information (i.e., due to unclear formation of sea annulus for detecting the correct
211 sea-age for some first time spawners) was inferred from length data for 15 (0.7%) individuals, where
212 the likelihood of age, given the length, was substantially higher (>20 times) for the inferred age group
213 than for other age groups. Additionally, for 21 (1.0%) individuals with missing length data, fit using
214 coefficients of log(weight) to log(length) regression (adjusted $R^2 = 0.94$) was used to estimate the
215 length information from the weight data. Finally, data for 33 (1.6%) individuals with missing *vgll3*_{TOP}
216 genotype scores were inferred from the genotype score of an adjacent SNP marker in the genotyping

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217 panel, *vgll3*_{Met54Thr}, which is in close physical proximity to *vgll3*_{TOP} with high linkage disequilibrium
218 ($r^2 = 0.79$).

219 *Genetic and ecological basis of the diet scope*

220 Unless otherwise noted, all statistical analyses were performed in R software v.3.2.5 (R Core Team,
221 2018). Either a two-component hurdle model (with binomial and the conditional negative binomial
222 components) using the *glmmTMB* package (Brooks et al. 2017) or a binomial model (with a log link
223 function) using the *gamm* function in the *mgcv* package (Wood 2011) was employed as the statistical
224 model. In all models, population of origin was included as a random term to account for background
225 population effects. To control for spatio-temporal variation, sampling location (longitude) and the
226 day of sampling (Julian day, zero centred, and scaled to one standard deviation) were included as
227 smoother terms. Longitude, which explained 90.7% of the spatial variation (i.e., sampling locations
228 mostly occurred along a longitudinal axis (see Figure 1) and were included in the models as a
229 surrogate for the two-dimensional spatial distribution to decrease the parametrization of the model.
230 In addition to including the genetic variation in the *six6* and *vgll3* genomic regions additively in the
231 model (i.e., genotypes coded as a continuous factor with heterozygotes coded as the average of two
232 homozygotes), age at maturity (e.g. Fleming 1996) and residual length (log transformed total length
233 after controlling for age at maturity) were also included in the model as categorical and continuous
234 variables, respectively. All numeric variables were centred and scaled. For both genomic regions
235 (*six6* and *vgll3*), alleles associated with late and early age at maturity were labelled as *L* and *E*,
236 respectively.

237 The general model structure was as follows:

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238 $Z = SA + \text{resL}_{SA} + V_{SA} + S_{SA} + s(D) + s(L) + p + e$

239 where Z is the vector of response variables given as a function of sea age (SA), scaled residual length
240 and *vgl3* and *six6* genotypes nested within sea age (resL_{SA} , V_{SA} and S_{SA} , respectively), the smoother
241 functions of sampling day (D) and location (L), and normally distributed random variance due to the
242 population (p) and individual (residual) effects. The genotypes were coded additively as 1, 2, and 3
243 (for *EE*, *EL* and *LL*, respectively). In the model, the scaled genotypes and residual length were
244 analysed independently within sea age group (i.e., nested model), which provided a statistical
245 framework suitable for testing hypotheses related to ontogenetic diet structure. In this model, a small
246 number of 4SW individuals ($N = 15$, 0.7%, SW denotes number of winters salmon spent at sea prior
247 to sampling.) was grouped and analysed within the 3SW for statistical coherence of the nested model.
248 Models also accounted for spatio-temporal variation in the diet with smoothing spline functions.
249 When using the *gamm* package, which provides a platform for generalized additive models, days and
250 location were modelled with a smooth function ($s()$). When using *glmmTMB* package, which provides
251 a platform for hurdle models but cannot directly model the smoother functions, an orthogonal spline
252 design matrix with a low-rank thin-plate function was generated using the *spl* function in the
253 *MCMCglmm* package (Hadfield 2010) in R and included in the model as fixed terms as a surrogate
254 for the spatio-temporal spline functions. The number of knot points (k , which defines the curvature
255 of the spline function) was set to five for both variables, but the results were robust to an increase in
256 the k value, which did not qualitatively change the results (data not shown).

257 A number of variables pertaining to the diet content data were used as response variables in this study.

258 Conceptually, these variables are linked to different aspects of diet acquisition mechanisms of this

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259 species (e.g., Arrington et al. 2002) and may indicate different functional aspects associated with
260 performance and life history variation among individuals.

261 1) *The presence and amount of total diet content in the stomach:* We used a two-component
262 hurdle model to simultaneously account for stomach content quantity and empty stomach probability.
263 By this, we tested for the prevalence of the “feast and famine” diet acquisition strategy in Atlantic
264 salmon as a function of ontogeny and genotype, whereby large piscivorous fish species are predicted
265 to experience prolonged periods with empty stomachs in the interest of acquiring a high quantity of
266 food (Arrington et al. 2002, Armstrong and Schindler 2011). Both components in the hurdle model
267 included the same set of covariates (as described above). A logistic model with a log link was used
268 to model the probability of the presence of a prey item, whereas a zero truncated negative binomial
269 model with a log link was utilized as the conditional component. In this analysis, the total stomach
270 weight, which had excess zero elements and a right-tailed continuous distribution (ranging from 0.5
271 to 393.3 g), was transformed to a discrete distribution by arbitrarily binning the total weight in 10 g
272 increments, with zero stomach content set as the first bin at a value of zero (Supp. Figure 1). This
273 transformation provided a distribution that can be modelled with the hurdle framework in the
274 *glmmTMB* package (Brooks et al. 2017). Finally, we also repeated the analysis by only including
275 confidently assigned individuals in order to assess the robustness of model to incomplete population
276 assignment.

277 2) *Total number and average weight of prey items in the stomach:* An increase in the total prey
278 weight in the stomach can be explained either by an increase in prey number or an increase in the
279 average prey weight. Therefore, we next investigated the contribution of these two components in
280 terms of explaining the model using the same statistical framework as above. Similar to the total prey

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281 weight, the average prey item weight (ranging between 0.2 and 300.2 g) was also transformed to
282 discrete units by arbitrarily binning the data at 5 g intervals, with zero stomach content set as the first
283 bin (Supp. Figure 1).

284 3) *Relative prey composition*: Finally, to test whether sea age, size at age, or genotype is
285 associated with specific prey species, we modelled the prey composition, measured as the proportion
286 of a specific prey species contributing to the stomach content weight. The proportion of each of the
287 four prey species in the total prey weight was modelled as a response variable using binomial
288 regression in the mgcv package (Wood 2011)

289 Extensively digested, unidentified content in the stomach (4.5% of the total stomach weight) was not
290 treated as diet material in order to accurately reflect the recent feeding activity (e.g., Jacobsen and
291 Hansen 2001). For all models, the effect size and confidence intervals were calculated with 10,000
292 parametric permutations of the model coefficients. To account for potential spurious inflation
293 associated with genotype, i.e. due to cryptic family structure, the analytical pathway was repeated
294 using 168 independent and putatively neutral markers that are present in the SNP panel, and focal
295 SNPs were ranked across the background genetic effect (by comparing the genetic model and the null
296 model at each SNP marker). Throughout the MS, for values < 0.1 and > 0.001 , we reported exact p-
297 values and provided 95% confidence intervals with the estimates. Understanding the genetic
298 association between diet and life history variation in the wild is rather unexplored. This coupled with
299 noisy nature of diet studies, we also highlighted alpha value 0.1 as a non-significant but suggestive
300 cut-off value to facilitate future research direction and encourage replications.

301 **Results**

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302 The final dataset contained 2121 individuals after excluding previously spawned and escaped farmed
303 salmon. In the final dataset, 93.3% of the samples had visibly detectable developing gonads,
304 confirming concordance between sea age and sea age at maturity. A total of 1372 (64.7%) individuals
305 were confidently assigned to a population of origin ($p > 0.7$), and (N=651) Individuals assigned to a
306 population with lower confidence ($p < 0.7$, 30.7%). A further 82 individuals (3.9%) with low
307 genotyping success with microsatellites were assigned a population of origin using SNP data and 16
308 individuals (< 1%) lacking reliable genotypes with either set of genetic markers were randomly
309 assigned to a population (see Materials and Methods for details).

310 *Stomach content analysis*

311 Out of the 2121 individuals examined in the final dataset, 992 individuals had identifiable prey items
312 in their stomachs (46.8%). Four fish species, sand eel (*Ammodytes* spp.), capelin (*Mallotus villosus*),
313 herring (*Clupea harengus*), and haddock (*Melanogrammus aeglefinus*), comprised the bulk of the diet
314 content, representing 42.2 kg of the 44.2 kg quantified diet content (95.5%). In total, there were 2843
315 identifiable prey items in the datasets, with sand eel being the most abundant and herring being the
316 largest percentage by weight (Supp. Figure 2). On average, prey weight significantly differed among
317 species, with haddock being the heaviest, followed by herring, capelin, and sand eel (Supp. Figure
318 2).

319 *Prey probability and weight in the stomach as a function of sea age, size at age, and genetic variation*

320 The two-component hurdle model revealed a striking negative relationship between the probability
321 of non-empty stomach (e.g. presence of identifiable prey item in the stomach) and prey weight (g) in
322 the stomachs of Atlantic salmon as a function of sea age (Figure 2a-b, Supp. Table 2). Young age

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323 groups were more likely than older age groups to have prey in their stomach. 1SW individuals were
324 1.45 (1.02 - 2.07, 95% CI, $p = 0.020$) and 2.39 (1.62 - 3.51, 95% CI, $p < 0.001$) times more likely to
325 have any prey item in their stomachs than 2SW and 3SW individuals, respectively, and 2SW
326 individuals were 1.65 times more likely to have a prey item in their stomachs than 3SW fish (1.30 -
327 2.08, 95% CI, $p < 0.001$). The decrease in non-empty stomach was significantly associated with
328 residual size variation within the 2SW age group ($p = 0.027$, Figure 2e), with larger individuals having
329 empty stomachs more often than the smaller-sized fish in the same age group.

330 The conditional truncated negative binomial model suggested that young age groups had significantly
331 less prey in their stomachs than older age groups despite a higher likelihood of having non-empty
332 stomachs (Figure 2b). The contrasting results between the zero-inflated and truncated negative
333 binomial components suggested that resource acquisition strategies differed among age groups. The
334 model estimated, on average, 9.9 g (6.5 - 14.9, 95% CI), 24.8 g (20.8 - 29.5, 95% CI), and 41.5 g
335 (32.5 - 53.0, 95% CI) of prey items in the stomachs of 1SW, 2SW and 3SW fish, respectively, all of
336 which were highly significantly different from one another ($p < 0.001$). Residual length at age also

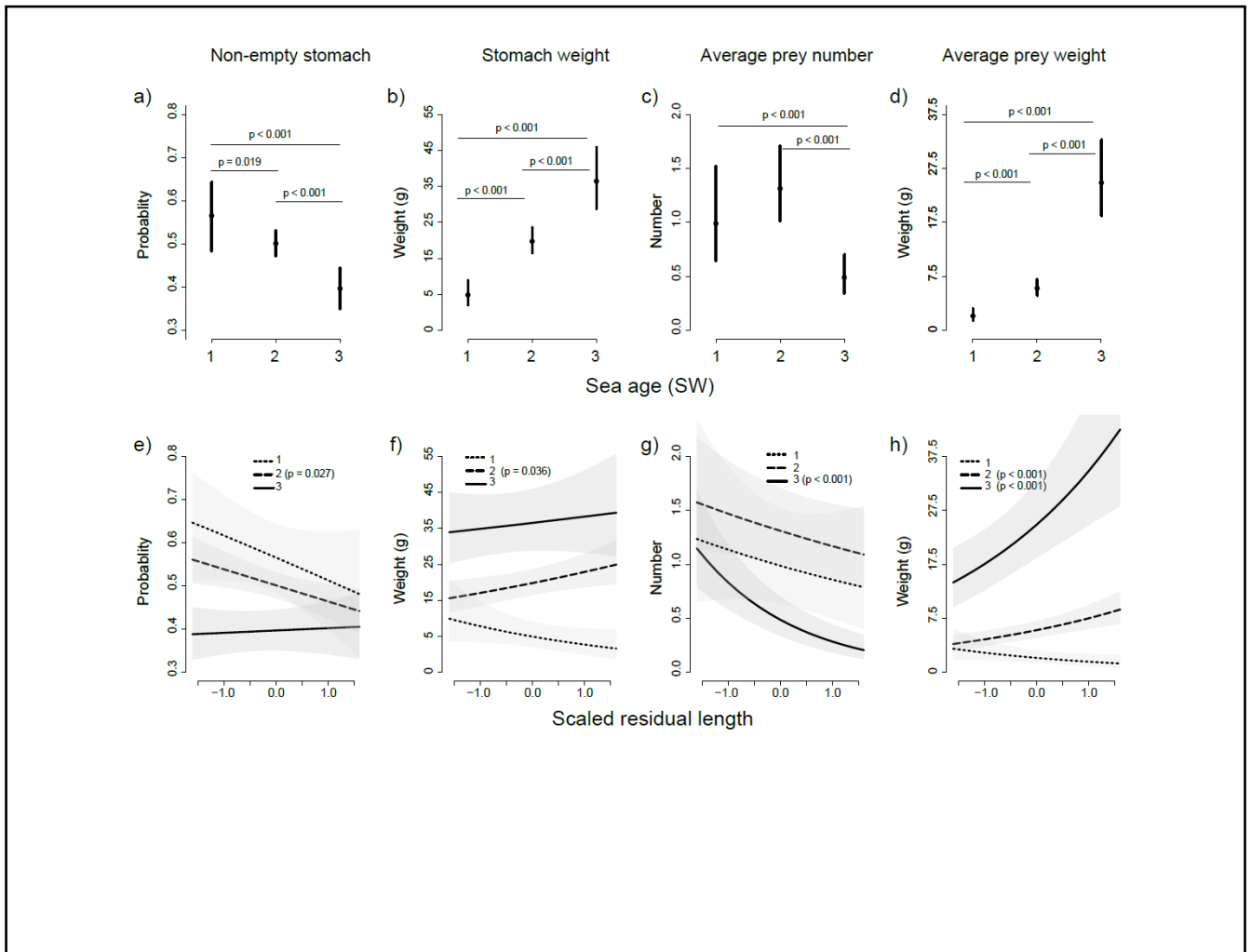
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337 appeared to be a predictor of prey content, but only significantly so in the 2SW age group ($p = 0.036$,



338 Figure 2b).

339 The *six6***L* allele, which has a higher frequency in populations with an older sea age at maturity
340 (Barson et al. 2015), was associated with an increase in the probability of non-empty stomach in an
341 age-dependent order, with a more pronounced effect in younger age groups (Figure 3a). Allelic
342 substitution from *E* to *L* in the *six6* genomic region (i.e. change in effect size by changing one allele
343 of the genotype) increased the probability of prey occurring in the stomach by 1.56 (0.98 – 2.48, 95%

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344 CI, $p = 0.057$) and 1.25 times (1.05 - 1.49, 95% CI, $p < 0.014$) in the 1SW and 2SW groups,
345 respectively (Figure 3a). Both age groups exhibited significant or suggestive age-dependent genotype
346 effects relative to the 3SW group ($p = 0.036$ and 0.051 , respectively, Figure 3b). Strikingly, the
347 probability of prey in the stomach in relation to size at age (Figure 2e) was in the opposite direction
348 to the *six6***L* effect (Figure 3a) despite the two (*six6* and size at age) exhibiting a significant positive
349 correlation (Supp. Table 3), suggesting the occurrence of complex, contrasting effects of *six6* genetic
350 variation across different phenotypic classes.

351 The conditional model suggested that the *six6***L* allele was also associated with increased total
352 stomach weight in the young age groups (1SW and 2SW) but not in the 3SW group (Figure 3b). The
353 allelic substitution effect from *E* to *L* was significant and associated with a 1.87-fold (1.20-2.94, 95%
354 CI, $p = 0.006$) increase in prey weight in the 1SW group and was suggestive in the 2SW group,
355 associated with a 1.14 (0.98-1.34, 95% CI, $p = 0.099$) increase in prey weight (Figure 3b).

356 The *vgll3* genomic region was not associated with diet content variation, suggesting no causal link
357 between the two (Figure 3e-h). However, selection on diet may still exert evolutionary change in the
358 *vgll3* genomic region, via correlated response to selection (Lande and Arnold 1983), as a result of
359 phenotypic covariation between diet and age at maturity and length at age. Accordingly, the effect of
360 *vgll3* was significant when these co-varying phenotypes were not accounted for in the model (Supp.
361 Table 4). Spatio-temporal variance in the dataset was substantial in explaining diet variation in both
362 components of the hurdle model (Supp. Table 2, see also Supp. Figure 3). In general, diet presence
363 and quantity were the highest at the westerly end of the distribution, with a gradual decrease towards
364 the east. At the temporal scale, sampling days in the middle of the sampling period were associated
365 with a higher presence and quantity of diet in the stomach (Supp. Figure 3).

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366 Population of origin was not a significant source of diet variation and explained only a fraction of the
367 total variation in diet content (Supp. Table 2, $\Delta\text{AIC} = 3.91$, $\text{LRT}_{2,2057} = 0.09$, $p = 0.96$). When the
368 analysis was performed with samples assigned to a population of origin with high confidence ($N =$
369 1372), the variance due to population was similarly small (see Supp. Table 5 for total stomach weight
370 as the response variable) and the model was also less parsimonious than a model without the
371 population effect, as assessed by comparing the model fit by difference in their Akaike information
372 criterion and likelihood ratio test ($\Delta\text{AIC} = 3.42$, $\text{LRT}_{2,1340} = 0.58$, $p = 0.75$). Likewise, the relation
373 between total stomach weight and *six6* genetic variation was relatively robust for the full dataset
374 ($N=2057$, Supp. table 2) and dataset only including individuals with high population assignment
375 confidence ($N=1372$, Supp. table 5).

376 In our framework, digested, unidentified material in the stomach was not included in the analysis
377 (e.g., Jacobsen and Hansen 2001). However, the results were qualitatively similar when digested
378 material was included in the analysis (Supp. Table 6). A model including sex was less parsimonious
379 and the term was not included as a parameter in the model ($\Delta\text{AIC} = 0.75$). Finally, when the fit of the
380 genetic models (*six6* and *vgl3*) was compared to the putatively neutral SNPs in the panel, *six6* ranked
381 first out 167, confirming its significance, while *vgl3* was only ranked 123rd (Supp. Figure 4).

382 In general, both the number of prey items and the increase in the individual prey weight contributed
383 to the variation in the total stomach weight (Figures 2c-d & 3c-d, Supp. Tables 7 & 8). The 3SW age
384 group was associated with significantly fewer prey items (0.49 prey items, 0.32-0.76, 95% CI) than
385 the 1SW (0.99 prey items, 0.60-1.65, 95% CI, $p = 0.004$) and 2SW age groups (1.32 prey items, 0.96-
386 1.80, 95% CI, $p < 0.001$), but the average prey weight was significantly heavier (27.40 g, 21.19-
387 37.20, 95% CI) than that in the 1SW (2.68 g, 1.65-4.37, 95% CI, $p < 0.001$) and 2SW (7.83 g, 6.20-

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388 9.88, 95% CI, $p < 0.001$) salmon. The average prey weight, but not the prey number, was also
389 significantly different between the 2SW and 1SW age groups ($p < 0.001$, Figure 2c-d). Size within
390 age group also significantly influenced the number and size of prey. Larger fish within the 3SW age
391 group had fewer ($p < 0.001$) but heavier ($p < 0.001$) prey items in the diet than smaller fish, and larger
392 2SW individuals consumed smaller prey items ($p < 0.001$, Figure 2g-h, Supp. Tables 7 & 8).

393 The number and size of prey items was also explained by the *six6* genotype in an age-dependent
394 manner, with a more pronounced effect in the relatively young age groups. The *E* to *L* substitution in
395 *six6* was associated with a 1.60-fold (1.01-2.56, 95% CI, $p = 0.048$) increase in prey number in the
396 1SW age group (Figure 3c). The allelic substitution was also associated with 1.65-fold (0.99-2.77,
397 95% CI, $p = 0.056$) and 1.22-fold (1.01-1.47, 95% CI, $p = 0.040$) increases in average prey weight in
398 the 1SW and 2SW age groups, respectively, which was significant compared to that observed in the
399 3SW age group ($p = 0.018$ and 0.030 , respectively, Figure 3d). Genetic variation in *vgll3* was not
400 significantly associated with average individual prey weight or prey number after controlling for age
401 at maturity (Figure 3e-h).

402 *Relative prey composition as a function of sea age, size, and genetic variation*

403 Prey composition varied substantially across different age groups, suggesting a change in prey
404 composition as the fish grow older (Figure 4). In general, older age groups were more likely to prey
405 on herring and haddock (Figure 4a-b), while younger age groups preyed on capelin and sand eel
406 (Figure 4c-d). The same pattern was observed within age groups, (e.g. larger fish within an age group
407 had proportionally more herring and haddock than smaller fish in the same age group) albeit generally
408 not significantly (Supp. Figure 5), suggesting that size may be a contributing factor explaining prey

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409 composition. In all analyses, spatio-temporal variation was a significant component explaining the
410 prey composition (Supp. Table 9).

411 Genetic variation in *six6* and *vgll3* did not appear to be a strong predictor of prey composition, but
412 some notable associational trends existed for the two genomic regions (Supp. Figure 6, Supp. Table
413 9). Particularly, *E* to *L* substitution in *vgll3* is associated with 1.31 times (0.96-1.79, 95% CI, $p =$
414 0.089) and 1.49 times (0.96-2.33, 95% CI, $p = 0.076$) fewer capelin in the stomach relative to other
415 prey species in the 2SW and 3SW age groups, respectively (Supp. Figure 6). Additionally, there was
416 a significant age-dependent preference for capelin over herring associated with the *E* to *L* substitution
417 in the *six6* genomic region (Supp. Figure 6). When compared to putatively neutral SNPs in the
418 genotyping panel, capelin composition modelled with *vgll3* ranked 12th out of 164 SNPs (0.073, Supp.
419 Figure 7), a value that is consistent with the analytically inferred p -value. Finally, when sea age and
420 size at age were not controlled for, as expected, genetic variation in both the *vgll3* and *six6* genomic
421 regions explained a substantial portion of the variation also in the relative prey composition (Supp.
422 Table 10). This suggests the phenotypic covariance between diet composition and age at maturity
423 may exert a correlated response to selection at the life history genomic region (i.e. *vgll3*), despite not
424 being causally linked to diet (i.e. Lande and Arnold 1983).

425 **Discussion**

426 Quantifying resource acquisition via stomach content analysis has been an integral component of
427 ecology and evolution for long, es early as on Darwin's Galápagos finches in 1900s (Snodgrass 1902).
428 In this study, we used stomach content from a single time point as a proxy for diet in Atlantic salmon.
429 Diet analysis may be difficult for a number of reasons, such as the challenges in accounting for the

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430 diverse nature of diet content data, high percentage of digested food items, difficulty of knowing what
431 is accessible, and the diversity of metrics for statistical analysis (e.g., Rice 1988, Cortés 1997, de
432 Crespin de Billy 2000, Baker et al. 2014, Amundsen and Sánchez-Hernández 2019). Recently, dietary
433 studies have received renewed interest with methodological development in trophic ecology using
434 stable isotopes (MacKenzie et al. 2012, Kawakami et al. 2019), environmental DNA (Taberlet et al.
435 2018), and in the quantitative analyses of stomach contents (Amundsen and Sánchez-Hernández
436 2019). In our study, the focus was on diet specialization and evolution, where we tested if ontogenetic
437 variation in feeding strategies could be associated with variation in major life history genes. The
438 relatively small number of prey species in our dataset, all fishes, and the small proportion of
439 undigested material provided us with a robust quantification of the diet and a powerful statistical
440 framework with ecologically relevant response variables. The fact that three most common prey species
441 in our dataset (e.g., herring, capelin and sand eel) are from similar trophic levels (independent of size or
442 ontogeny Dommasnes et al. 2001, Bentley et al. 2017) makes stomach content analysis more suitable
443 alternative for diet assessment, as oppose to, e.g. stable isotopes analysis that is useful for detecting
444 long term trophic variation but insensitive to discern prey species from same trophic levels, nor to assess
445 diet quantity.

446 Our analyses indicate that diet acquisition strategies in the sea vary with sea age in Atlantic salmon
447 and that this variation is associated with genetic variation in key life history genomic regions,
448 particularly in the *six6* genomic region. The variation in diet explained by sea age and size at age was
449 mostly concordant, suggesting that size is the major driver of diet variation, influencing both the
450 quantity and species composition of prey (Figures 2 & 4). Atlantic salmon prey on heavier but fewer
451 prey as they grow older and larger, which seems to be a strategy that comes at the expense of a

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452 reduced prey acquisition probability (Figure 2a-d, Huey et al. 2001, Arrington et al. 2002). This
453 pattern is consistent with the so-called “feast and famine” strategy observed among large piscivorous
454 fish species (Arrington et al. 2002). The feast and famine feeding strategy is suggested to be an
455 adaptation to maintain a positive energy balance at a large body size, especially when the acquisition
456 of energy-rich food sources is unpredictable (Armstrong and Schindler 2011). Large Atlantic salmon
457 appear to adopt this strategy, which is likely beneficial in terms of balancing the increase in energy
458 costs associated with a large body size. A suite of physiological adaptations and metabolic
459 adjustments, such as increased digestion capacity (Armstrong and Schindler 2011) and fat storage
460 (Bustard 1967), may be associated with this strategy (Wang et al. 2006). For example, it has been
461 shown that piscivorous species that adopt a feast and famine strategy maintain a large digestive tract,
462 which allows rapid food utilization when abundant prey are encountered (Armstrong and Schindler
463 2011). This physiological trade-off seems to be evolutionarily favourable for large fish when the prey
464 distribution is stochastic despite the energetic costs of sustaining excess and energetically expensive
465 digestive tissue (Armstrong and Schindler 2011). The feast and famine strategy in large Atlantic
466 salmon may also be facilitated by other mechanistic processes, such as the trade-off of a lower success
467 rate linked to larger prey or a lower attack rate associated with increasing size. Nonetheless, variation
468 in foraging strategies among different age groups results in a large diet breadth, efficient resource
469 partitioning, and reduced intraspecific competition among age groups, which subsequently promotes
470 their co-existence (e.g., Polis 1984, Smith and Skulason 1996, Svanback and Bolnick 2007). It is
471 unclear what physiological or behavioural modifications are associated with the differential feeding
472 strategies among the various age groups in Atlantic salmon. Nonetheless, changes in marine food
473 webs may alter the density and composition of prey available to different age groups and hence alter
474 the age-dependent selection landscape, potentially leading to adaptive changes in age structure. Our

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475 results confirm the value of Atlantic salmon as a model species to study the evolutionary physiology
476 of starvation and feeding in response to environmental changes in the wild.

477 Salmon are generally considered to be diet generalists. However, the association between the life
478 history genomic region *six6* and diet acquisition (as well as the non-significant but suggestive
479 acquisition with capelin prey preference and *vgl3*, see, Supp. Table 6) indicates that genetically
480 controlled intraspecific diet specialization occurs in Atlantic salmon. This genetic variation may be
481 linked to specialized dietary adaptations (e.g., physiological, morphological or behavioural) allowing
482 the efficient utilization of diverse diet sources, resulting in increased niche breadth and reduced
483 intraspecific competition (Dalmo et al. 1997, Bolnick et al. 2003, Bolnick and Fitzpatrick 2007,
484 Svanback and Bolnick 2007). In particular, the *six6*L* allele was associated with increased content in
485 the stomach, especially in young age groups, which was explained by both an increase in the number
486 of prey items and an increase in the average prey weight in the stomach. Intriguingly, however, the
487 *six6*L* allele was associated with a larger fish size within all sea ages (Supp. Table 3, see also, Barson
488 et al. 2015). Given that larger size at a given sea age is indicative of higher performance and fitness
489 in adult salmon (e.g., Fleming 1996; Mobley et al. 2020), the *six6*L* allele (being linked to larger
490 size) may be expected to have a selective advantage over the *E* allele and is hence predicted to prevail
491 within and among populations as a result of directional selection. However, the *six6* genomic region
492 is highly variable within and among populations (Barson et al. 2015, Pritchard et al. 2018), and
493 balancing selection appears to be the pervasive mode of evolution, with both alleles exerting fitness
494 advantage with different life-history strategies (Barson et al. 2015). The results of this study suggest
495 that the genetic variation in *six6* locus could be explained by antagonistic pleiotropy along the life
496 cycle of an individual (i.e., fitness trade-offs within the lifetime of an individual associated with the

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497 *six6* region) or fluctuating selection across generations. For example, genetic variation in *six6* may
498 be under balancing selection via antagonistic genetic correlations in diet acquisition over the life
499 cycle. Indeed, some results indicate that individuals having high freshwater growth may show poor
500 seawater growth (Einum et al. 2002), prescribing further hypothesis linking it to genetic variation in
501 *six6* genomic region.

502 Although our results suggest superior performance of the *six6***L* allele at the adult stage, the opposite
503 may be true at earlier life stages, when the prey species composition is substantially different, with
504 significantly more invertebrates in the diet (Jacobsen and Hansen 2001, Rikardsen et al. 2004,
505 Haugland et al. 2006), and different ecological drivers affect performance (Mittelbach et al. 2014,
506 Sanchez-Hernandez et al. 2019). For example, if increased metabolic costs are linked with increased
507 prey content in the stomach, a trait associated with *six6***L*, this may not be an optimal acquisition
508 strategy in younger years (i.e. juveniles prior to, or in the early phases of marine migration) when the
509 energy density of available prey cannot compensate for the greater effort (McNamara and Houston
510 1996, Enberg et al. 2012). Such antagonistic genetic correlations between early and late life histories
511 (i.e. genotype-environment interactions) in diet acquisition may maintain polymorphism in the
512 region. Alternatively, year-to-year variation in population-specific (e.g., density dependent) or
513 ecosystem-level processes (i.e., prey composition, food-web dynamics) may alter the adaptive
514 landscape of diet acquisition (Smith and Skulason 1996), resulting in fluctuating selection and a
515 change in the direction of selection among alleles, which would maintain the genetic variation in the
516 region. Indeed, in the year 2008, returning salmon had a notably older sea age at maturity in northern
517 Norway than that observed in more recent years (i.e., the oldest in the last 20 years, see (Anon 2014)).
518 This is consistent with observed patterns that *six6***L* is linked with larger size, perhaps as a result of

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519 providing a selective advantage for that particular year class. However, more research is required to
520 explicitly test this possibility. The *six6* genomic region is highly spatially differentiated among
521 populations (Barson et al. 2015, Pritchard et al. 2018). This suggests that any selection acting on *six6*
522 as a result of selection on diet acquisition would influence the fitness of populations differentially,
523 correlated with their average allele frequency. Hence, genetic variation in *six6* may be linked to the
524 differential survival of populations at sea and should be closely monitored in population management.

525 The genetic variation in the *vgll3* genomic region had no clear effect on diet quantity overall, but
526 there was a marginal ($p = 0.073$), albeit consistent, association with higher capelin content in the
527 stomach (Supp. Figures 6 & 7). Capelin is a key component in the Barents Sea ecosystem with critical
528 bottom-up effect (Gjørseter et al. 2016), and both salmon post-smolts and returning adults utilize them
529 as a food resource (Rikardsen and Dempson 2010, this study) when they migrate through the coastal
530 regions (Gjørseter et al. 2016). Individuals with the *vgll3*L* allele, which is associated with a later
531 sea-age at maturity (Barson et al. 2015), were marginally less likely to feed on capelin, particularly
532 in older age groups (2SW and 3SW). In addition, in contrast to herring, which was the most common
533 prey item in the stomachs of the individuals in the 2SW and 3SW age groups (Figure 4c), capelin is
534 likely a lower-energy prey item for Atlantic salmon (Elliott and Gaston 2008, Hedeholm et al. 2011,
535 Renkawitz et al. 2015). This supports the notion that *vgll3*L* may contribute to foraging adaptations
536 to support the high-energy demands associated with the larger body size of late maturing fish.
537 However, further research is needed to substantiate our suggestive link and to identify mechanisms
538 driving such a compositional difference.

539 Overall, genetic variation in both life history genomic regions appears to have a role in intraspecific
540 diet specialization, but the mechanisms remain to be clarified. Although the underlying mechanism

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541 of diet specialization is complex (e.g., Mittelbach et al. 2014) and challenging to disentangle,
542 performance trade-offs across different ecological settings and the life cycle are likely driving the
543 life-history variation associated with these genomic regions. Analyses of datasets collected in the
544 wild may suffer from confounding effects that co-vary with both the response variable and parameters
545 of interest and generate spurious associations if they are not accounted for. In this study, a highly
546 controlled linear model was employed to account for environmental and intrinsic parameters with
547 potential confounding effects. First, resource availability at sea, e.g., the prey species density and
548 distribution, is highly variable across time and space, even at small scales. Likewise, during their
549 return migration, Atlantic salmon may be non-randomly distributed in relation to their life history,
550 genotype, and population of origin (Svenning et al. 2019). For example, relatively early run timing is
551 linked to both later maturation (Jonsson and Jonsson 2011) and *six6***L* (Cauwelier et al. 2018,
552 Pritchard et al. 2018), a pattern that concordantly holds in our dataset (Supp. Table 11). Hence, the
553 analytical framework controlled for spatio-temporal variation and also accounted for non-linear
554 changes through space and time (Supp. Figure 3). Similarly, sea age at maturity and size within an
555 age group exhibited strong links with both diet and genetic variation in the life history genomic
556 regions. By accounting for these phenotypes in the model, we were able to exclude the possibility of
557 modelling the genetic variation via the effects of these intermediate phenotypes. Therefore, our
558 framework was rather robust to drawbacks related to confounding factors observed in wild settings.
559 Finally, variation in diet due to the population of origin was also accounted for in the model as a
560 random intercept but did not explain significant diet variation at sea (Supp. Tables 2 & 5).

561 On the other hand, evidence for association between diet variation and life history genomic regions
562 had relatively low statistical support. Therefore, further research is warranted to validate these results.

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563 Further, genetic variation outside these two major maturation-timing loci and potential pleiotropic
564 effects remain unexplained, which could be explored with a genome wide approach in future studies.
565 Likewise, similar set-ups at different life history stages, under different feeding regimes, or in
566 common garden conditions, would help to elucidate the effect of genotype-environment interactions
567 that may have been overlooked in this dataset.

568 Marine ecosystems, which are composed of mostly poikilothermic species, are sensitive and highly
569 responsive to temperature-driven changes (e.g., Clarke 2003, Sydeman et al. 2015). The Arctic region
570 is particularly sensitive to global climate change (Polyakov et al. 2010), with significant
571 anthropogenic effects further shaping the marine food webs in the region. Over the last 40 years, the
572 abundance of Atlantic salmon has been declining, and the age structure has been shifting towards a
573 younger age at maturity (Chaput 2012, Czorlich et al. 2018, Erkinaro et al. 2018). Such changes in
574 demography are likely the result of bottom-up changes in prey community structure, likely fuelled by
575 climate-induced changes to the ecosystem (Frederiksen et al. 2006, Todd et al. 2008). In this study,
576 we demonstrated that the inter-individual variation in diet specialization is linked with age structure
577 as well as the genetic variation in *six6* and *vgl3*, two genomic regions with substantial influence on
578 life history variation and population divergence. This heritable intraspecific variation in diet
579 specialization likely plays an important role in salmon life history by both promoting the niche
580 breadth of species and enabling evolutionary responses in populations to changes in food
581 composition. Given that both genomic regions are highly differentiated among populations,
582 evolutionary response and the resulting demographic trajectories likely differ among populations,
583 concordantly. Future work should focus on characterizing the underlying physiological and/or

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584 behavioural mechanisms linking genetic variation with salmon diet acquisition to better predict the
585 evolutionary response of populations to changing environments.

586 **Authors' contributions**

587 TA conceived the study; MR, MAS, and TP collected the stomach content data and performed the
588 diet analysis; TA and MO analysed the data; EN, MAS, VW, MO, JPV took part in Kolarctic ENPI
589 CBC project (KO197) sample collection, and microsatellite genetic analysis; LP, TA, and CRP
590 optimised and coordinated the targeted SNP genotyping assays. KH initiated the collaboration and
591 co-ordinated sample transfer. TA, CRP, and MAS led the writing of the manuscript. All authors
592 contributed critically to the drafts and gave final approval for publication.

593 **Data Availability Statement**

594 Data and R codes for analyses are available from the Dryad Digital Repository: XXXX (will be
595 filled by upon acceptance)

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