Ontogenetic variation in the marine foraging of Atlantic salmon functionally links genomic diversity with a major life history polymorphism

Running title: Functional studies of the genotype-phenotype map of Atlantic salmon

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Abstract

The ecological role of heritable phenotypic variation in free-living populations remains largely unknown. Knowledge of the genetic basis of functional ecological processes can link genomic and phenotypic diversity, providing insight into polymorphism evolution and how populations respond to environmental change. By quantifying the marine diet, of sub-adult Atlantic salmon, we assessed how foraging behavior changes along the ontogeny, and in relation to genetic variation in two loci with major effect on age-at-maturity (*six6* and *vgll3*). We used a two-component, zero-inflated negative binomial model to simultaneously quantify foraging frequency (zero-inflation components) and foraging outcome (count component), separately for fish and crustaceans in the diet. We found that older salmon forage for both prey types more actively (as evidenced by increased foraging frequency), but with a decreased efficiency (as evidenced by fewer prey items in the diet), suggesting an age-dependent shift in foraging dynamics. The *vgll3* locus was linked to age-dependent changes in foraging behavior: younger salmon with $vgll3^{LL}$ (the genotype associated with late maturation) tend to forage crustaceans more often than those with $vgll3^{EE}$ (the genotype associated with early maturation), while the pattern was reversed in older salmon. $Vgll3^{LL}$ genotype was also linked to marginal increase in fish acquisition especially in younger salmon, while *six6* was not a factor explaining the diet variation. Our results suggest a functional role for variation in marine feeding behavior linking genomic diversity at *vgll3* with age-at-maturity among salmon, with potential age-dependent trade-offs maintaining the genetic variation. A shared genetic basis between dietary ecology and age-at-maturity likely subjects Atlantic salmon populations to evolution induced by bottom-up changes in marine productivity.

Introduction

Phenotypic polymorphisms are ubiquitous, discrete trait morphs (e.g., (Bataillon et al., 2022; Funk et al., 2021; Janssen, Bustnes, & Mundy, 2021; Johnston et al., 2013), the genetic basis of which are maintained at higher frequencies than what would be expected under mutation-selection balance (Ford, 1945). Much of the research on phenotypic polymorphism focuses on determining which selective landscapes generate and maintain heritable polymorphisms, such as negative frequency-dependence (Chouteau, Arias, & Joron, 2016; Goldberg et al., 2020; Gross, 1985; Svensson, Willink, Duryea, & Lancaster, 2020), antagonistic pleiotropy (Charmantier, Perrins, McCleery, & Sheldon, 2006; Marden, Langford, Robertson, & Fescemyer, 2021), fluctuating selection (Bonnet & Postma, 2018; Grant & Grant, 2002) and, heterozygote advantage (Coulson et al., 2011; Hedrick, 2012). Furthermore, by the advent of next-generation sequencing, an increasing number of studies report associations between discrete chromosomal elements (large-effect loci, inversions, supergenes) and phenotypic polymorphisms (Barson et al., 2015; Funk et al., 2021; Johnston et al., 2013; Matschiner et al., 2022). Such an intense research focus is unsurprising given that studying polymorphisms provides insight into speciation (Jamie & Meier, 2020), one of the cornerstones of biology since Darwin. Despite the increasing number of known genotype-phenotype associations, how such genomic diversity is functionally translated into phenotypic diversity within wild populations is mostly unresolved. This is likely due to the experimental studies and sampling designs required for monitoring wild individuals being financially and logistically unfeasible without applying various simplifying assumptions (Mousseau, Sinervo, & Endler, 2000; Reznick, 2016). As such, our understanding of how genomic

variation influences individual-level differences in ecology, and how such ecological differences might covary with polymorphic trait states, is incomplete.

One well studied genotype-polymorphism association is that between age-at-maturity and the *vgll3* and *six6* haploblocks in Atlantic salmon, *Salmo salar* (Ayllon et al., 2015; Barson et al., 2015). Atlantic salmon most often display an anadromous life history. They hatch in rivers where they can spend several years growing before migrating to the ocean. The marine environment is much more productive than fresh water (Gross, Coleman, & McDowall, 1988) and juvenile salmon undertake this costly migration in order to maximize growth and lipid storage. This, in turn, supports future reproductive efforts when they return to fresh water to spawn (Esteve, 2005; Ferguson, Reed, Cross, McGinnity, & Prodohl, 2019). Atlantic salmon most commonly stay at sea for one to three years prior to return to fresh water for reproduction, which is termed as sea-age at maturity. Atlantic salmon exhibit a high degree of divergence in this polymorphic phenotype within and among populations, the genetic variation of which is largely explained by two genomic regions, so called *vgll3* and *six6*, after the most prominent genes within the haploblock (Barson et al., 2015; Sinclair-Waters et al., 2022). The *vgll3* gene encodes for a functionally-conserved transcription co-factor that regulates adiposity in mice (Halperin, Pan, Lusis, & Tontonoz, 2013) and influences pubertal timing in vertebrates (Cousminer et al., 2013). The functional relationship between adiposity and maturation via *vgll3* haploblock likely operates also in Atlantic salmon since condition factor has been shown to drive *vgll3* dependent maturation response in the species (Debes et al., 2021). Salmon with the 'early' *EE* genotype are more likely to mature after one year at sea (one-sea-winter salmon, 1SW) than individuals with the 'late' *LL* genotype, which are more likely to spend multiple years at sea before maturing (multi-sea-winter, MSW, predominantly composed of 2SW and 3SW salmon). The second major

84 haploblock, *six6*, displays substantial population-level effects on sea-age at maturity among wild
85 salmon populations (Barson et al., 2015), and within aquaculture strains (Sinclair-Waters et al.,
86 2022). The *six6* haploblock contains genes with known functional roles in sensory and digestive
87 system development (Lee et al., 2012; Moustakas-Verho et al., 2020). The molecular functions
88 associated with *vgll3* (adiposity regulation) and *six6* (sensory and digestive system development)
89 suggest that dietary ecology may underpin processes by which genomic variation at the *vgll3* and
90 *six6* haploblocks is expressed as phenotypic variation in sea-age at maturity.

91 Variation in how food is acquired by organisms and how derived metabolic energy is invested
92 into different biological processes can be conceptualized using the resource acquisition-
93 allocation framework (Enberg et al., 2012). Briefly, individuals acquire a given amount of a
94 resource from which they service their basal metabolism. Any surplus resources are then
95 allocated to behavior, structural (skeletal/muscle) growth, or maturation/gonadal growth
96 (Enberg et al., 2012). A supposition arising from the resource acquisition-allocation framework is
97 that individuals vary in how much/which resources they acquire, and this may alter their
98 maturation trajectories. As such, variation in feeding opportunities and strategies may play a role
99 in survival and maturation of the organisms.

100 Atlantic salmon is recognized as an opportunistic feeder with extensive ontogenetic and
101 spatiotemporal variation in diet breadth (Rikardsen & Dempson, 2010). Salmon feed increasingly
102 on higher trophic levels as they age, which is strongly correlated to their size (Aykanat et al.,
103 2020; Jacobsen & Hansen, 2001; Salminen, Erkamo, & Salmi, 2001; Salminen, Kuikka, & Erkamo,
104 1995). The variation in available prey items, as well as preference for particular prey items, can
105 affect the net energy gain from foraging activities, and this may subsequently alter the sea-age at
106 which they mature (Czorlich, Aykanat, Erkinaro, Orell, & Primmer, 2022; Hvidsten et al., 2009;

Vollset et al., 2022). For example, Vollset et al. (2022) showed that the reduced marine growth of Atlantic salmon (and subsequent decrease in maturation age) was linked to reduction in the Arctic cold water flux to the Northeast Atlantic Ocean and the subsequent decrease in the plankton biomass in the feeding grounds in the Northeast Atlantic Ocean. Similarly, using a 40 year time series from large salmon population, Czorlich et al. (2022) linked the evolutionary response in the *vgll3* genotype towards early maturation to changes in Capelin abundance in the Barents Sea, a major prey for Atlantic salmon in the region. On this background, one can posit that genetic variation in ontogeny dependent foraging behavior can be maintained in the populations via life-history trade-offs. For example, salmon carrying alleles associated with a foraging behavior that provides higher net-energy gain at early stages at sea will be more likely to acquire enough resources to initiate maturation, and mature at an earlier age (Chaput & Benoit, 2012; Thorpe, Mangel, Metcalfe, & Huntingford, 1998). However, demonstrating a genetic basis to foraging behavior, and how this might covary with sea-age at maturity, remains highly challenging in salmon due to a lack of adequate samples in the wild. As such, whether foraging behavior varies as a function of genotype, and the evolutionary consequences that this variation could have on the sea-age at maturity phenotype, remains largely unknown. One previous study has demonstrated a relationship between the L allele of *six6* and increased stomach content (that is composed of fish) among maturing Atlantic salmon sampled on their return migration along the Norwegian coast (Aykanat et al., 2020). However, a shared genetic basis between sea-age and foraging among sub-adult, immature fish (i.e. fish that are still in the oceanic feeding phase, before the onset of maturation) would be an indirect evidence for dietary ecology acting as a potential process that functionally links genomic diversity at the *vgll3* and *six6* loci with sea-age at maturity in salmon.

An extensive dataset of the diet of wild Atlantic salmon sub-adults (i.e., the marine stage prior to maturation) sampled in the oceanic feeding ground (Jacobsen & Hansen, 2001) provided us with the material to test if ontogenetic variation in foraging behavior is explained by sea-age at maturity loci (*vgll3* – *six6*) in Atlantic salmon. The Atlantic salmon in the study almost exclusively feed on crustaceans and fish, the former of which was more numerous (~95% of diet items were crustaceans) but comprised only 30% of the content by weight. We propose that a genetic basis in feeding behavior results in variation in the net-energy gain, which subsequently alters individuals' probability of reaching to maturation threshold. The salmon diet in our data has a right-skewed distribution with a substantial zero inflation, which we presumed to be shaped by two independent biological processes. The first process explains the "structural-zeros" in the data (i.e. zero inflation), which is used as a proxy to measure the active foraging frequency for particular diet types. The second process is the "count" component, and is used as a proxy to measure the foraging outcome providing that salmon actively pursue for a prey (see Materials and Methods for details). Thus, as a first step, using the a zero-inflation model to account for these two processes, we tested if foraging behavior changes along the ontogeny, and secondly, if genomic regions associated with sea-age at maturity in salmon, in part, explain the variation in foraging behavior, across age groups. Within the same framework, we also estimated if the variation in diet is also determined by age-dependent sex effects, since Atlantic salmon also exhibited sex dependent maturation pattern (Barson et al., 2015; Fleming & Einum, 2010).

Methods

Sampling procedure

Sampled fish used in this study are originally described in Jacobsen and Hansen (2001). Briefly, Atlantic salmon were sampled from known marine feeding grounds around the Faroe Islands, inhabited by all sea-age groups but predominately by MSW fish (Jacobsen & Hansen, 2001; O'Sullivan et al., 2022). Fish were sampled between November and March (excluding January due to rough sea conditions) during the 1992-'93 and 1993-'94 fishing periods. Salmon sampled from November-December were considered to have been caught in the autumn and those sampled from February-March in the winter, which exhibited marked differences in prey diversity, sea surface temperature and stomach content (Jacobsen & Hansen, 2001). The locations of the longlines used to sample fish were also recorded (n = 55, see Fig. S1 in O'Sullivan et al., 2022). Individual salmon had their fork lengths measured, were gutted, and gutted fish were weighed (in kilograms). Gut contents were also removed, identified, and enumerated. Fish scales were taken from each individual salmon for determination of sea-age via scale reading, and for later, DNA extraction for genotyping. The fish sampled in the study are immature, sub-adults with no phenotypic indication of maturation. However, it is reasonable to assume that virtually all 3SW fish will mature in the following autumn, since 4SW and above sea-ages are rare in salmon populations.

Dietary quantification and somatic measurements

The stomach content data used in this study is a subset of the data that was quantified by Jacobsen and Hansen (2001). We did not include data from the 1994-'95 fishing period in Jacobsen and Hansen (2001), since material for genotyping was not available. The most common

173 diet items among crustaceans were amphipods (e.g., *Themisto* spp.), shrimps (e.g., *Hymenodora*
174 *glacialis*) and euphausiids (e.g., *Meganyctiphanes norvegica*), and among fishes were pearlsides
175 (e.g., *Maurolicus muelleri*), lanternfishes (e.g., *Benthosema glaciale* and Myctophidae),
176 barracudinas (e.g., *Notolepis rissoi* and Paralepidae), blue whiting (*Micromesistius poutassou*), and
177 capelin (*Mallotus villosus*) (Supplementary table 1). Crustaceans were substantially more
178 numerous than fishes (~95% of diet items were crustaceans) but represented only 30% of the
179 content by weight (Supplementary table 1). For example, the average size of crustacean species
180 ranged from 0.027 g for *Themisto compressa* to 0.766 for *Sergestes arcticus*, and > 99% were
181 species that were smaller than 0.20 g. The average size of fish subcategories ranged from 0.26 g
182 for fry (mostly consisting of capelin) to 72.0 g for herring, *Clupea harengus* (Supplementary table
183 1). For the purposes of this study, and to reduce the complexity of data structure and statistical
184 analyses, the stomach contents were primarily categorized as crustaceans and fishes.

185 Apart from than crustaceans and fishes, the diet also contained remains from fish and
186 crustaceans, and organic remains, which were mostly not possible to further identify or
187 enumerate, (Supplementary table 1). In addition, a few stomachs contained bird remains (n=1)
188 and squid (n=11). Fish and crustacean remains were included in the count-data analysis if
189 numerated (n=12 and n=16, respectively). Squids were grouped together with other fishes due to
190 their size similarity (excluding them from the analysis did not change any results). One fish with
191 bird remains was excluded from the analysis.

192 ***Genotyping and data filtering***

193 DNA was extracted from the sampled fish scales (O'Sullivan et al., 2022). Individuals were
194 genotyped using a GTSeq approach (Campbell, Harmon, & Narum, 2015) with a panel of 167

195 SNPs as outlined in (Aykanat et al., 2020). This panel allowed individuals to be assigned to their
196 reporting group of origin (O'Sullivan et al., 2022), as well as to score the genotypes at focal SNPs
197 within our target loci. The focal SNPs were *vgll3*$_{TOP}$ and *six6*$_{TOP.LD}$ (hereafter, *vgll3* and *six6*).
198 *Vgll3*$_{TOP}$ exhibits the strongest association with sea-age within the haploblock (Barson et al.,
199 2015), while *six6*$_{TOP.LD}$ exhibits the second strongest association overall with sea-age prior to
200 population structure correction (Barson et al., 2015) . If an individual was missing a genotype for
201 *vgll3*$_{TOP}$, the missing genotype was inferred from the genotypes of adjacent SNP markers in the
202 same haploblock, which display strong linkage disequilibrium due to close physical proximity to
203 *vgll3*$_{TOP}$ (The loci with the strongest linkage with *vgll3*$_{TOP}$ was prioritized when imputing the
204 missing genotype, with an order of *vgll3*$_{missense1}$, *vgll3*$_{missens2}$, *akap11*, see, Aykanat, Lindqvist,
205 Pritchard, & Primmer, 2016). Sex was determined genetically by targeting the sex determination
206 locus (*sdy*, Yano et al., 2013), as outlined in Aykanat et al. (2016). There was 82.3 % concordance
207 between phenotypic and genetic sex, of which, we prioritize genetic sexing over phenotypic
208 sexing since sub-adults at sea do not yet develop secondary sexual characteristics, hence
209 phenotypic sex may be prone to misidentification. For a small subset (n = 39), the genetic sex of
210 an individual could not be determined, and phenotypic sex was used instead. Individuals lacking
211 genotypic information for either the *vgll3*, *six6* loci, or sex, were excluded from downstream
212 analyses (n = 77). A small number of fish with sea-age greater than 3SW were also excluded from
213 the data (n=15). Reporting group was included as a three-level categorical variable, in which an
214 individual is assigned to a reporting group with the highest assignment probability, where levels
215 corresponded to large-scale geographical regions based on the genetic stock identification in
216 O'Sullivan et al. (2022). These reporting groups were Ireland and the UK (n = 473), Southern
217 Norway (n = 832), and the Northern group (n = 271), the latter which consisting of fish from

Northern Norway, including Teno River, Eastern Finnmark/Northern coast of Kola, and the Barents/White Sea reporting groups. In total, 1536 individual salmon consisting of 168 1SW, 950 2SW and, 418 3SW individuals were used in the downstream analyses.

Statistical analyses

We modelled the total number of crustaceans and the total number of fishes in the stomachs of individual salmon as a pair of separate two-component zero-inflation models, for which 46.1 and 79.9 % of stomachs had no crustaceans and fishes, respectively (Supplementary Figure 1, Supplementary Table 2). Zero-inflation models simultaneously estimated two independent processes that shapes the distribution of the response variable (diet in the stomach). The first process was modelled with the zero inflation component (using binomial error distribution), and quantified for the "structural-zeros" (i.e., inflated zero counts) in the data that were due to individuals not actively foraging for the specific prey type. We used this statistic as a proxy to measure the active foraging frequency. The second process is modelled with the count component (using a negative binomial error distribution that includes the "random zeroes" in the data) that were due to sampling variation when salmon actively forage for prey. We used this statistic as a proxy to measure the outcome of the active feeding, i.e. foraging outcome.

The model structure (for both components) is as follows:

$$Y = \mu + \text{Season} + \text{fishing period} + \text{Reporting Group} + \text{Sea-Age} \times (\text{Sex} + \textit{vgll3} + \textit{six6} + L_{age.std}) + \varepsilon_{location} + \varepsilon_{\text{error}}$$

whereby, for both for crustacean and fish models, season (autumn, winter), fishing period (1992-'93, 1993-'94), and reporting group were included as categorical fixed effects. The *vgll3* and *six6* genotypes, as well as sex and age-standardized length ($L_{age.std}$) were modelled interacting with

240 sea-age, since we quantify a sea-age-dependent diet response associated with these variables. For
241 the crustacean diet model, sea-age was parameterized as a continuous variable, which was more
242 parsimonious than models that parameterize sea-age as a categorical variable (see results). For
243 the fish diet model, sea-age was also parameterized as a continuous variable, but comparing
244 continuous vs categorical parameterization was not possible due to convergence problems with
245 the latter (see results). For both crustaceans and diet models, the *vgll3* and *six6* genotypes were
246 modelled additively (EE, EL, and LL genotypes were coded numerically by 1, 2, and 3) which
247 were more parsimonious than non-additive models (i.e., when genotype values were
248 categorically modelled. See results.). All covariates interacting with sea-age (*vgll3*, *six6, sex, and*
249 $L_{age.std}$) were scaled by their respective means and standard deviations to improve convergence,
250 and interpretability of the coefficient tables. Spatial variation in sampling effort (sampling
251 location, N=55) was included in the model as a random effect.

252 In order to evaluate if any taxonomic groups within crustaceans drive the relation between
253 genotypes and diet, we further broke down the response variable into lower order taxonomic
254 groups when numbers within specific taxa were sufficiently large. For that, we reanalyzed the
255 data using Hyperiid amphipods (*Themisto* spp.) and Euphausiids as the response variable, which
256 comprised the majority of the crustacean diet in the stomach (Supplementary Table 1). The
257 representative sizes in the diet between these two groups were also different, with the latter
258 being substantially larger than the former (Supplementary Table 1). We did not implement the
259 same approach in fishes which had restrictively small number of prey items per species.

260 All models were run using the *glmmTMB* package (version 1.1.5, Brooks et al., 2017) in R version
261 4.1.0 (R Core Team, 2019), using a negative binomial error structure with a logit link function for
262 the count component, and with a binomial error structure with a logit link function for the zero-

263 inflation (zi) component, using default optimizer settings. Marginal means for genotype effects
264 and their confidence intervals were calculated using the *emmeans* package (version, 1.8.2, Lenth,
265 2023). Model diagnostics were carried out using *DHARMa* package in R (version 0.4.5, Hartig
266 2022), whereby randomized quantile residuals were simulated for both models in order to
267 determine if any explanatory covariate displayed heteroscedasticity (Hartig 2022). Using the
268 aforementioned two-component models, we primarily asked whether sub-adult foraging
269 behavior varies as a function of life history genotype and age. We also tested if sex had an age-
270 dependent effect on adult foraging behavior.

271 Results

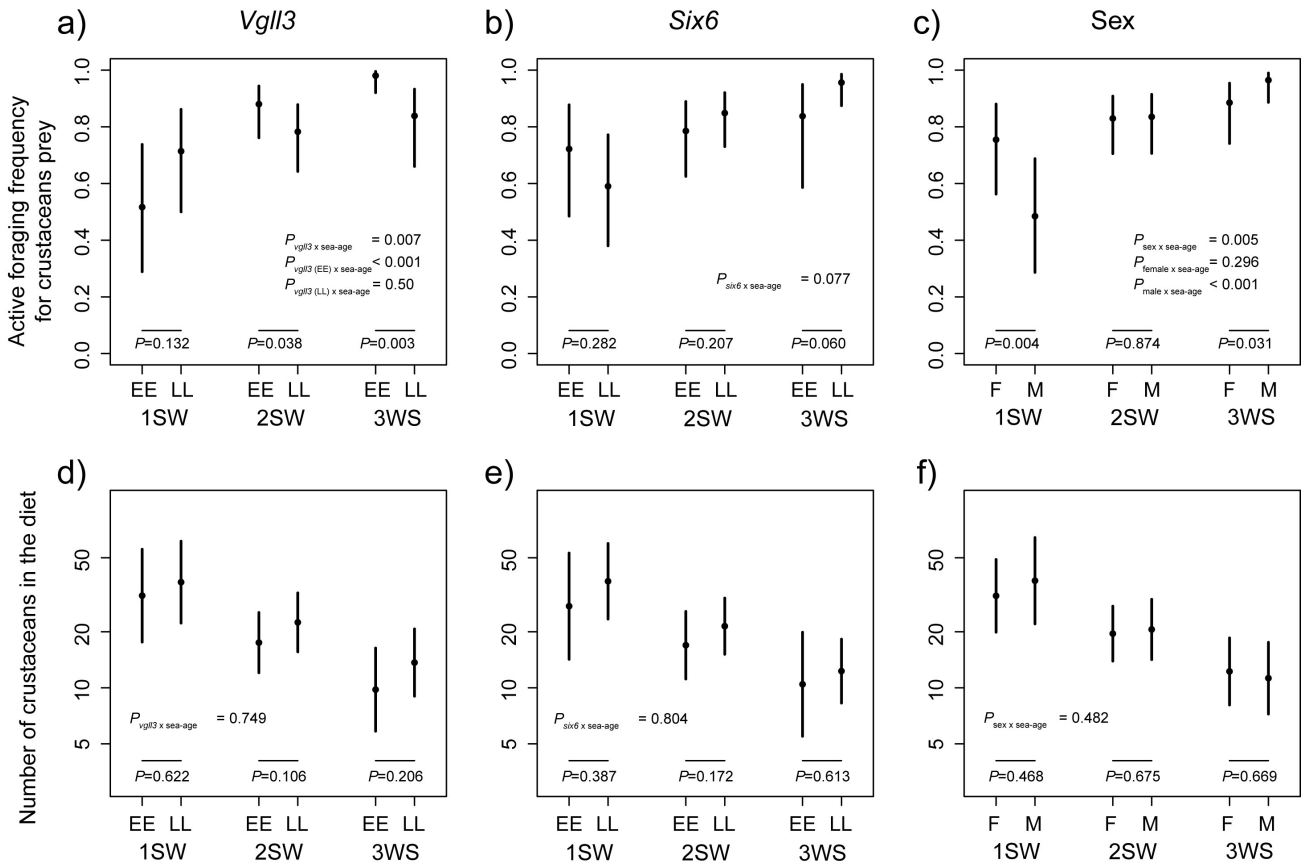
272 *Crustaceans model*

273 *Sea-age:* Based on the zero-inflation models, older sea-age groups more likely forage for
274 crustaceans (zi component: z = -3.196, P = 0.001), but younger sea-age groups had substantially
275 higher number of crustaceans in the stomach, indicating a higher foraging outcome (count
276 component: z= -4.478, P < 0.001, Supplementary Table 3, Figure 1).

277 *Vgll3 and six6:* Genetic variation in the *vgll3* locus was strongly associated with an age-dependent
278 change in the crustacean foraging frequency (zi component: z = 2.690, $P_{\text{sea-age x } vgll3}$ = 0.007, Figure
279 1a, Supplementary Table 3). As such, *vgll3*^{LL} genotype was insignificantly associated with
280 increased foraging in younger sea-age groups (Odds ratio = 2.33, 95% CI = 0.78 – 7.04, P = 0.132,
281 Figure 1d), but in the older sea-age groups, the alternative, *vgll3*^{EE} genotype, was significantly
282 associated with increased foraging for crustaceans (for 2SW, odds ratio = 2.04, 95% CI = 1.04–
283 3.98, P = 0.038; for 3SW, odds ratio = 9.67, 95% CI = 2.15– 43.57, P = 0.003, Figure 1a). The
284 difference appeared to be driven by the *vgll3*^{E} allele, which exerts a significant age-dependent

response to crustacean's foraging frequency in the diet (z = -4.081, $P_{\text{sea-age}|vgll3EE} < 0.001$), while the *vgll3*^{L} allele had no age-dependent effect (z = - 1.112, $P_{\text{sea-age}|vgll3EE} = 0.507$, Figure 1a). However, *vgll3* genotypes did not alter the foraging outcome, as there was no difference in in the abundance of crustaceans in salmon diet in relation to *vgll3* genotype (Figure 1d).

Figure 1: Crustaceans acquisition patterns of sub-adult Atlantic salmon as a function of sea-age-dependent genotype (*vgll3* and *six6*) and sex. Upper and lower panels indicate marginal means for foraging frequency (zero-inflation component), and foraging outcome (count component), respectively. Error bars are 95% confidence intervals.



Crustacean diet as a function of *six6* locus was insignificant for both foraging frequency (zero-inflation components), and foraging outcome (zero-inflation components, Figure 1b,e, Supplementary Table 3).

296 *Sex:* Sex exhibited a strong age-dependent association with foraging frequency (zi component: z =
297 -2.822, P = 0.005, Figure 1c), but did not alter the foraging outcome (count component: z = -0.703,
298 P = 0.482, Figure 1f). Female salmon forages for crustacean more often than males in the 1SW
299 group (Odds ratio = 3.27, 95% CI = 1.46 – 7.31, P = 0.0042), whereas the pattern reversed in the
300 older sea-age groups and the 3SW males forage crustaceans more often than the 3SW females
301 (Odds ratio = 3.55, 95% CI = 1.13 – 11.21, P = 0.031, Figure 1c). The difference appeared to be
302 driven by greater age-dependent response by males (z = -4.297, $P_{\text{sea-age x females}}$ < 0.001), compared
303 to females (z = -1.489, $P_{\text{sea-age x males}}$ = 0.296, Figure 1c).

304 *Season, year, reporting group and length effects:* Season was an important determinant for
305 crustacean diet. Salmon more likely forage for crustaceans in the winter (zi component: z = -
306 2.439, P = 0.015), but had overall lower abundance of prey in the diet (count component: z = -
307 5.107, P < 0.001, Supplementary Table 3). Fishing period did not have a significant effect on
308 foraging frequency yet the number of crustaceans in the diet was significantly different between
309 the two sampling years (count component: z = 5.512, P < 0.001, Supplementary Table 3).
310 Reporting group generally did not affect variation in the crustacean diet, but fish assigned to the
311 Northern Norway reporting group had marginally fewer crustaceans in the diet than the fish
312 assigned to Ireland and the UK reporting group (z = -2.504, P = 0.037, Supplementary Table 3).
313 Age standardized length as a function of sea-age ($L_{\text{age.std}}$) was not a significant factor for the
314 crustaceans diet (Supplementary Table 3). Sequential exclusion of these variables from the model
315 (Season, fishing period, reporting groups, and $L_{\text{age.std}}$) did not meaningfully influence the
316 genotype or sex effects observed in the crustacean diet (data not shown).

317 *Alternative parameterization of variables:* When crustaceans diet was subdivided into lower
318 taxonomic orders, two major groups (Hyperiid amphipods and Euphausiids) appeared to exhibit

319 similar effects and effect sizes (and similar to the overall crustaceans model) in the *vgll3* locus,
320 albeit not always significant due to lower sample sizes, (Supplementary Table 4 and 5),
321 suggesting neither a particular order nor size drives the age-dependent genetic or sex relation.

322 In the implemented framework, we modelled the life-history loci and sea-age as a continuous
323 variable, assuming additivity for the latter, and linear relation of the response variable with the
324 former. This model structure was substantially more parsimonious than models that assume
325 non-additivity (where genotypes were modelled as categorical variables), and/or non-linear age-
326 dependent response (where sea-age was modelled as a categorical variable, Supplementary
327 Table 6). Similarly, a model that accounts for sex and *vgll3* interaction, which was previously
328 suggested as a mechanism for a sex dependent genetic effect on sea-age at maturity (Barson et al.,
329 2015), was not supported any better (data not shown).

330 *Convergence and diagnostics:* Convergence was achieved in all models enabling us to compare
331 different parameterizations of sea-age and genotype. Overall, the diagnostics for the crustaceans
332 model suggested a good model fit (Supplementary Figure 2a).

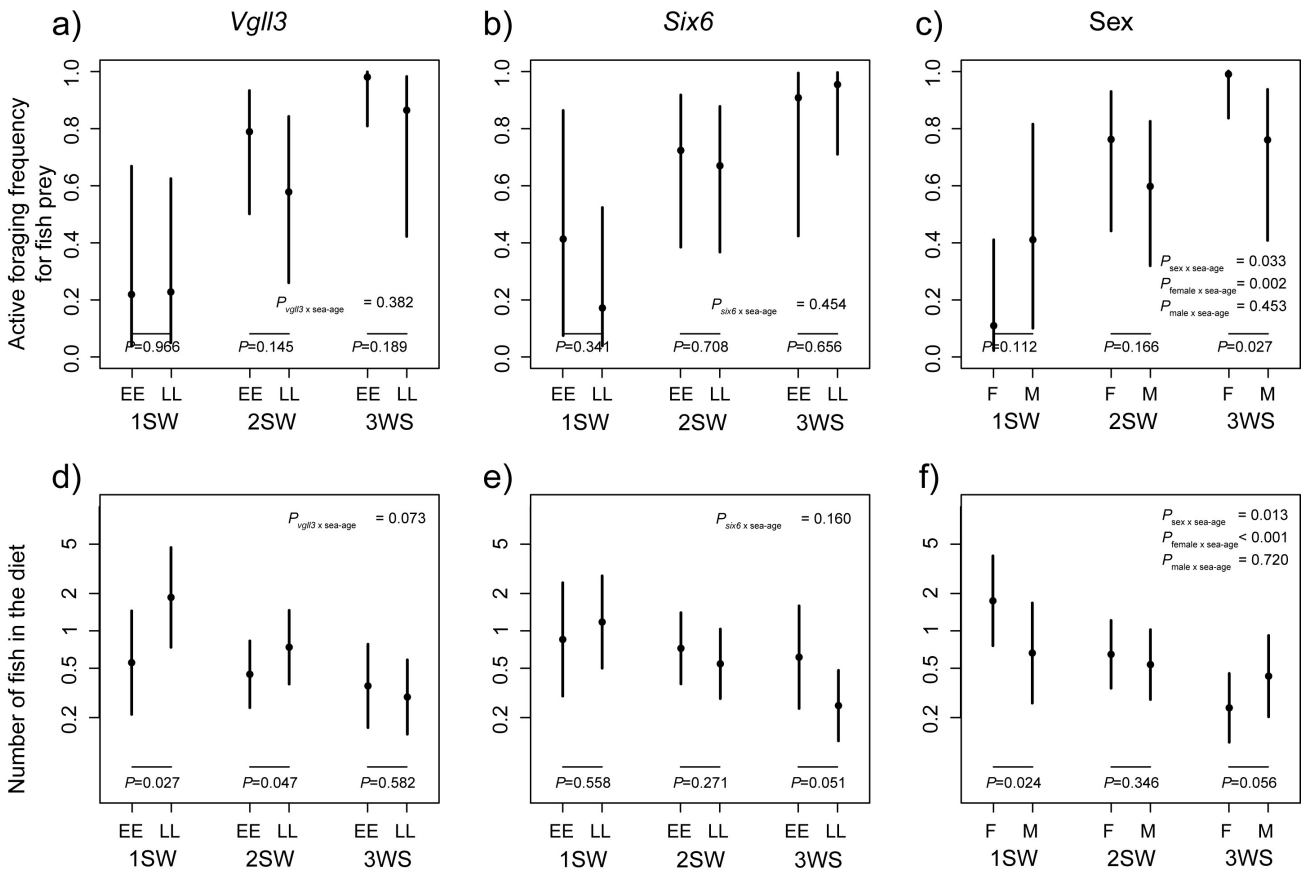
333 ***Fish model***

334 *Sea-age:* Similar to the crustaceans model, older sea-age groups more likely forage for fish (zi
335 component: z = -3.704, $P < 0.001$), and younger sea-age groups exhibited higher foraging
336 outcome (count component: z= -4.204, $P < 0.001$, Supplementary Table 7, Figure 2).

337 *Vgll3 and six6:* Frequency of foraging for fish was generally insignificant for *vgll3* and *six6* loci.
338 The foraging outcome, however, was significantly higher for $vgll3^{L}$ allele (count component: z =
339 2.088, $P = 0.037$, Supplementary Table 7), whereby the effect was diminished in older age-groups
340 due to a marginal age-dependent effect (count component: z = -1.796, $P_{\text{sea-age x } vgll3} = 0.073$,

Supplementary Table 7). Salmon with *vgll3*^{LL} genotype had more fish in the stomach than salmon with *vgll3*^{EE} genotype in 1SW and 2SW sea-age groups (for 1SW, odds ratio = 3.36, 95% CI = 1.15 – 9.81, P = 0.027; for 2SW, odds ratio = 1.65, 95% CI = 1.01 – 2.71, P = 0.047), but the difference was negligible in the 3SW age group (odds ratio = 0.81, 95% CI = 0.39 – 1.70, P = 0.582, Figure 2d). *Six6* was not a significant factor for foraging outcome for fish diet.

Figure 2: Fish acquisition patterns of immature Atlantic salmon as a function of sea-age-dependent genotype (*vgll3* and *six6*) and sex. Upper and lower panels indicate marginal means for foraging frequency (zero-inflation component), and foraging outcome (count component), respectively. Error bars are 95% confidence intervals.



<u>*Sex:*</u> Sex exhibited a marginal effect for foraging frequency and outcome for fish diet. Frequency of foraging for fish increases in females as salmon gets older (zi component: z = 2.127$P_{\text{sea-age x } sex}$ =

352 0.033, Figure 2c, Supplementary Table 7), and females forage for fish more often than males in
353 the 3SW age group (odds ratio = 26.506, 95% CI = 1.45 – 483.96, P = 0.027, Figure 2c). In
354 contrast, the number for fish in the diet was higher in females in 1SW age groups (odds ratio =
355 2.64, 95% CI = 1.14 – 6.14, P = 0.024, Figure 2f, Supplementary Table 5), and the pattern was
356 reversed in 3SW, and males had marginally higher fish diet in the 3SW age group (odds ratio =
357 1.80, 95% CI = 0.99 – 3.29, P = 0.055, Figure 2f) suggesting an age specific sex pattern in foraging
358 outcome (count component: z = 2.484, $P_{\text{sea-age x } sex}$ = 0.013) . For both foraging frequency and
359 outcome the age-dependent effects were driven by age-dependent response of females, rather
360 than males (Figure 2c, f).

361 *Season, year, reporting group and length effects:* Season was an important determinant of fish diet.
362 Salmon forage for fish more often in the winter (zi component: z = -2.014, P = 0.044), and acquire
363 more fish (count component: z = 4.413, P < 0.001, Supplementary Table 7). Fishing period,
364 reporting group, or age standardized length did not have a significant effect on fish diet
365 (Supplementary Table 7).

366 The estimated effects of season or reporting group did not meaningfully influence the genotype
367 or sex effects observed, since the sequential exclusion of these parameters did not meaningfully
368 change the effect size and/or significance (data not shown). However, the model did not converge
369 when fishing period was excluded from the model, so their effect on the focal variables are not
370 assessed. On the other hand, the marginal *vgll3* effect to foraging outcome appeared to be
371 improved and became significant upon excluding $L_{\text{age.std}}$ from the model, suggesting possible
372 covariation between the two (Supplementary Figure 3). As such, salmon with *vgll3*^{LL} genotype
373 had more fish in the stomach than salmon with *vgll3*^{EE} genotype in 1SW and 2SW sea-age groups
374 (for 1SW, odds ratio = 4.64, 95% CI = 1.52 – 14.16, P = 0.007; for 2SW, odds ratio = 2.02, 95% CI

375 = 1.22 – 3.35, P = 0.006), but the difference was negligible in the 3SW age group (odds ratio =
376 0.88, 95% CI = 0.41 – 1.90, P = 0.746, Supplementary Figure 3).

377 *Convergence and diagnostics:* As evidenced from diagnostics plot from obtained from the
378 DHARMa package, the fish model had suboptimal fitting (Supplementary Figure 2b). Yet, this
379 shortcoming may have little impact to main conclusions. For example, when additional
380 dispersion parameters were added to account for variance heterogeneity for fishing season,
381 reporting group, season and sex, the homogeneity of variance (or within group deviation from
382 uniformity) was achieved for all parameters except for fishing season, and Kolmogorov–Smirnov
383 deviation test was not significant anymore (Supplementary Figure 2c). The addition of these
384 dispersion parameters did not alter the conclusions associated with genetic or sex effects
385 (Supplementary Table 8). The convergence was not achieved when testing for alternative
386 parameterization of model covariates, such as when sea-age and genotype effects was modelled
387 as a categorical variables, or when testing the effect of non-focal variables to main conclusions
388 (by sequentially excluding them from the model). Therefore, the model results from continuous
389 parametrization of sea-age should be cautiously approached.

390 Discussion

391 We demonstrated an age-dependent genetic pattern in marine diet variation in wild, sub-adult
392 Atlantic salmon. By simultaneously capturing the effects of two biological processes that shape
393 the diet variation, namely active foraging frequency (via the zero-inflated component) and
394 foraging outcome (via the count component), we provided insights to the foraging dynamics of
395 Atlantic salmon at sea.

Intriguingly, the two processes had remarkably different sea-age-dependent patterns: younger individuals contain more crustaceans in the stomach than older age groups suggesting a higher foraging outcome, despite lower foraging frequencies. This pattern cannot be explained by higher assimilation rate of older salmon (i.e. which have larger guts) since higher assimilation rates should also correlate with higher frequencies of empty stomach. Results from these two biological process combined, suggest older sub-adult salmon adopts a continuous feeding strategy, albeit a less efficient one, perhaps to fulfill the energetic demands of a larger body size (Jonsson & Jonsson, 2011; Nina Jonsson & Jonsson, 2003). On the other hand, these results are in contrast with the previous findings by (Aykanat et al., 2020), whereby an opposite pattern was shown in mature Atlantic salmon that were sampled in coastal waters, on their migration to freshwaters for reproduction. Their study suggested that older age groups adopted a feast and famine strategy as a foraging adaptation to maintain high energy balance. It is unclear what underlies these opposing patterns in our study. However, it might be possible that a combination of physiological and behavioral differences associated with differences in life histories (immature sub-adults vs mature adults), habitat (oceanic feeding grounds vs coastal vs oceanic feeding), or diet composition could be the underlying reason for the contrast. For example, the diet was primarily composed of four fish species in Aykanat et al. (2020), a substantial portion of which was larger than three grams while only a small number of fish species in the diet had on average weighed more than three grams, suggesting a striking difference in diet breadth. All above factors may contribute to change in feeding strategies as a function of age.

Our results indicate that older sea-age groups feed more frequently, despite that they lack the foraging outcome of younger age groups. This is especially intriguing in relation to the crustaceans diet, since it is contrary to the expected patterns of ontogenetic diet shifts in salmon

419 (Rikardsen & Dempson, 2010). The larger body of older sea-age groups are energetically more
420 demanding (Jonsson & Jonsson, 2011; Jonsson & Jonsson, 2003), and it might be that older
421 salmon are in need of constant searching for food to support the energetic demands of larger
422 body, relative to younger age groups, especially when prey size is small, a strategy of which may
423 come in the expense of efficiency of foraging. It could be also speculated that the salmon partly
424 use filter feeding using their gill-rakers as sieve during high density crustacean prey
425 distributions. Small salmon (parr and smolts) uses filter feeding to catch small prey (e.g. Keeley &
426 Grant, 1997). If ocean feeding post-smolts and small salmon also uses this technique,
427 acknowledging that gill-raker spacing is proportional to fish length (Wankowski 1979), 1SW
428 salmon might benefit from their smaller gill-raker spacing when targeting the relatively small
429 crustacean prey compared to larger MSW salmon.

430 We also demonstrate a shared genetic basis between a major life-history polymorphism (sea-
431 age) and feeding strategy in Atlantic salmon with a substantial sea-age-dependence. Specifically,
432 the age-dependent patterns associated with the *vgll3* locus, predominantly in crustacean foraging
433 rates, provides evidence that feeding strategy is a functional ecological process by which
434 differences between sea-age phenotypes might be realized. This is a rare example of genetically-
435 controlled differences in resource acquisition of a highly migratory fish species in the wild and
436 demonstrates that salmon could be subject to selection if oceanic food webs change (Czorlich et
437 al., 2022; Strøm, Ugedal, Rikardsen, & Thorstad, 2023; Vollset et al., 2022). Crustaceans are a
438 primary source of dietary material for Atlantic salmon in the Northeastern Atlantic (Jacobsen &
439 Hansen, 2001; Rikardsen & Dempson, 2010). A reduction in the water flux from the colder Arctic
440 region into the northern Atlantic around 2005 was associated with a decrease in biotic and
441 abiotic factors including plankton abundance, as well as specific growth rate of salmon, the latter

442 which eventually resulted in delay in maturation timing (Vollset et al., 2022). While our results
443 do not support that *vgll3* is linked to a change in feeding efficacy (as quantified by the count
444 component of the model), foraging for crustaceans (as quantified by the zi component) appeared
445 to be regulated by the *vgll3* locus. These results suggest that an ecological shift in the northeast
446 Atlantic might exert an evolutionary change in the *vgll3* genomic region.

447 The crustacean acquisition patterns in relation to *vgll3* might provide some clues on how the
448 variation in sea-age at maturity may be mediated via a genetic polymorphism in resource
449 acquisition. To illustrate, 1SW salmon with the *vgll3*^{*EE} genotype appear to obtain as many
450 crustaceans as 1SW salmon with the the *vgll3**^{LL} genotype (Figure 1d) despite foraging for
451 crustaceans less frequently (Figure 1a). In other words, 1SW individuals with *vgll3*^{EE} genotype
452 gain a similar amount of food (estimated from count model) with less active foraging. Such
453 increase in acquisition efficiency may be one of the factors that allows salmon with the *vgll3*^{EE}
454 genotype to mature earlier as 1SW fish, i.e. by allocating surplus resources (saved through
455 efficient foraging) towards fat deposition and reproductive investment. Furthermore, we also
456 observed a parallelism in age-dependent crustaceans foraging activity between *vgll3* genotypes
457 and sex, and in relation to their effect to maturation timing. For example, females, which matures
458 later than males (Barson et al., 2015; Fleming & Einum, 2010), forage for crustaceans more often
459 than males (and with similar acquisition efficiencies), a pattern that is similar between *vgll3*^{LL}
460 and *vgll3*^{EE} genotypes. Similar to salmon with *vgll3*^{LL} locus, perhaps, females' foraging behavior is
461 not sufficient to acquire energy to trigger early maturation. It might be that an optimal foraging
462 strategy for earlier maturation is to decrease active foraging time and to increase the foraging
463 efficiency. On the other hand, it is not clear if age-dependent changes in diet patterns associated
464 with early maturation in *vgll3*^{EE} genotype and males indicate an age-dependent trade-off

465 associated with early maturation. In fact, the age-dependent changes in foraging time were
466 mainly driven by age-dependent changes in the *vgll3*^{EE} genotype and males, which are associated
467 with early maturing. Based on the foraging patterns, early maturation genotype and males are
468 becoming less efficient in acquiring crustaceans in older sea-ages (i.e., 3SW). Thus, we propose
469 that early maturation genotype and males have evolved to have higher foraging efficiencies for
470 crustaceans in early ages, potentially linked to earlier maturation, but this may come with an
471 efficiency trade-off in later years at sea. In turn, a seemingly maladapted foraging strategy in
472 younger ages might be selected for in salmon populations by eventual delay in the maturation
473 timing, resulting to mature at a larger size.

474 The crustacean acquisition model provides a functional ecological process that explains genetic
475 (via the *vgll3* locus) and between sexes basis of maturation timing. However, it is not clear if this
476 effect may be manifested via condition factor, a primary phenotypic trait associated with
477 maturation timing (Thorpe et al., 1998), and one that is linked to *vgll3* during precocious male
478 maturation (Debes et al., 2021). To explore if *vgll3* or sex was linked to age-dependent
479 differences in condition factor, and consistently so with the expected maturation patterns, we
480 implemented a linear mixed model with a Gaussian error structure using condition factor as
481 response variable, and using a similar covariate structure as above (except that sea-age was
482 modeled categorically which was more parsimonious than a numeric model). There was no
483 evidence of age-dependent association between condition factor and *vgll3* structure
484 (Supplementary Table 9). Males, on the other hand exhibited a higher condition factor in 1SW age
485 group (z = 1.982, P = 0.0476), and a lower condition factor in 2SW (z = -4.776, $P < 0.001$)
486 compared to females, but not in 3SW sea-age groups (t = -0.282, P = 0.7779). This is indeed
487 consistent with expected maturation patterns in Atlantic salmon, where 1SW is more

488 predominately males, compared with 2SW more females (Fleming & Einum, 2010), suggesting
489 that the sex specific diet differences might drive maturation via condition factor effects. However,
490 the condition factor used here was calculated using the gutted weight, hence did not include any
491 variation in condition that might be related to guts and other visceral tissue, both of which are
492 likely important ecological traits in the processes of maturation (Mobley et al., 2021).

493 Unlike crustaceans, the fish acquisition was generally similar between genotypes across sea-age
494 groups. However, foraging outcome was meaningfully different within *vgll3* genotypes and sexes
495 across sea-ages, whereby *vgll3*^{LL} genotype and females consumed higher number of fish in the
496 1SW age group with marginal and significant age-dependent changes for *vgll3* and sex,
497 respectively. This pattern further highlight resource acquisition as a potential ecological function
498 that links maturation timing to genetic polymorphisms in the *vgll3* locus, and sex. However,
499 caution is required when interpreting the results for the fish model, the fit of which had some
500 deviations from linear model assumption and since convergence for alternative parameterization
501 options was not achieved.

502 ***Caveats***

503 Studying the evolutionary ecology of Atlantic salmon in the marine phase provides
504 unprecedented possibilities to understand the ecological and evolutionary basis of life history
505 variation in the wild, but is inherently difficult. This is due to their extensive oceanic migration
506 with substantial spatio-temporal variation both within (Gilbey et al., 2021) and between age-
507 classes. Such stochasticity (due to the marine ecology of salmon as well as the way fish were
508 sampled) results in structurally complicated data. It was impossible for us to quantify and
509 compare all possible model structures to account for this complexity. Likewise, the complex

model structure resulted in convergence issues, especially with alternative parameterization of the fish model, which limits exploration of potential confounding effects. However, especially for the crustaceans model, we were able to assess the effect of alternative parameterizations at a great extent, which appears to not affect the main conclusions.

1SW salmon utilize the feeding grounds around the Faroe Islands relatively less often than older age groups, suggesting that the 1SW fish have spatially distinct feeding ranges in the ocean. Therefore, it is unclear if the patterns in this study are also observed on feeding grounds that are predominantly used by 1SW salmon. This encourages further work to verify potential acquisition patterns on such feeding grounds, and to better understand acquisition-dependent life history variation associated with the *vgll3* haploblock. Similarly, the low numbers in 1SW are associated with large 95% prediction intervals around 1SW. This limits the inferential strength of the relevant results, and predictive power of the analyses.

Given the complex data structure and associated challenges with the interpretations, we limited our analyses to asking broad questions concerning the eco-evolutionary dynamics of marine feeding strategy and sea-age phenotype. As such, we primarily grouped diet into two major categories (crustaceans and fish), and did not address more detailed or refined hypotheses, due to lacking the statistical power to do so robustly. However, two major crustacean taxa (Hyperiid amphipods and Euphausiids) had sufficient data to achieve model convergence, by which we concluded that the general patterns observed in crustaceans were similarly reflected in these taxa, also irrespective of their size distribution, suggesting prey size may not be important in shaping age-dependent genetic and sex diversity on diet acquisition.

Conclusions

532 An important consequence of anthropogenic change has been the large-scale disturbance of
533 ecosystems globally (Sydeman, Poloczanska, Reed, & Thompson, 2015; Vollset et al., 2022). In
534 particular, climate-mediated changes are predicted to continue altering marine food webs, with
535 ecological, genetic, and economic consequences (Daufresne, Lengfellner, & Sommer, 2009;
536 Pershing et al., 2015). Therefore, linking community-level processes to eco-evolutionary
537 processes at the individual-level (such as polymorphic expression) is a prerequisite for
538 understanding how taxa will respond to these large-scale changes. Such an understanding is
539 essential for effective conservation and ecologically sensitive fisheries management.

540 This study demonstrates that individual-level variation in prey acquisition both within and
541 between sea-age phenotypes, which also displays a shared genetic basis (to varying degrees)
542 with the *vgll3* locus. Furthermore, we show an apparent decrease in crustacean feeding efficiency
543 for MSW salmon with the *vgll3*^{EE} genotype relative to 1SW salmon with the same genotype, but
544 not for the *vgll3*^{LL} genotype. Taken together, these results are indicative of variation in feeding
545 strategy acting as a functional ecological process that links *vgll3* genotype and sea-age in Atlantic
546 salmon. Our results could help to provide a mechanism to explain the observed changes in the
547 frequencies of 1SW and MSW phenotypes in some Atlantic salmon populations (Czorlich,
548 Aykanat, Erkinaro, Orell, & Primmer, 2018; Utne et al., 2021; Vollset et al., 2022). Changes in
549 marine food webs have long been expected to negatively impact the energetic status of salmon
550 (Friedland, Chaput, & MacLean, 2005; B. Jonsson, Jonsson, & Albretsen, 2016; N. Jonsson &
551 Jonsson, 2004; Strøm et al., 2023). The shared genetic basis between prey acquisition and sea-age
552 that we demonstrate indicates that Atlantic salmon sea-age is susceptible to evolution from
553 human-induced changes to marine ecosystems.

Data accessibility

The compiled datasets and R-codes to reproduce the results are available from the dryad repository https://doi.org/XXX

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Author contributions

TA and KH conceptualized the paper. KH organized sample retrieval from scale archives at NINA. JAJ coordinated the Faroese fieldwork and collected the diet data. TA conducted the statistical analyses, genotyped the samples, and drafted the MS. All co-authors contributed to subsequent drafts.

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