Diet drives performance trade-offs along Atlantic salmon ontology

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Abstract

Understanding the mechanistic basis of life-history trade-offs is fundamental for predictive ecology. Variation in resource use is a major determinant of life-history divergence and evolution, and provides a framework for studying life history trade-offs. Contrary to the theory, the documentation of trade-offs between life-history traits that are due to competitive resource allocation is mostly lacking in the wild, which is suggested to be masked by individual differences in resource acquisition. However, this effect has not been empirically demonstrated in free-living populations. In this study, we quantified the diet composition of wild Atlantic salmon (*Salmo salar*) from different age groups, sampled from marine feeding grounds in the Northeast Atlantic Ocean. We hypothesized that diet composition (i.e., consumption of crustaceans *versus* fish) has an age-dependent effect on the condition factor, which is a major determinant of age at maturity in Atlantic salmon. We demonstrated an age-dependent reversal of diet effect on condition factor, whereby salmon at younger ages had a higher condition factor when foraging on crustaceans, and a lower condition factor when foraging on fish, and *vice versa* in older age groups. Our results identify resource acquisition as an important process shaping life-history variation in Atlantic salmon via age-dependent performance trade-offs. Our result emphasize the importance of bottom-up trophic effects on maturation dynamics and help to better predict the maturation dynamics of wild populations in the marine environment.

Keywords: life-history trade-offs, resource acquisition, Atlantic salmon, age at maturity, ontogenetic diet shift, food-web dynamics

Introduction

An important focus of evolutionary biology has been to establish the prevalence of life-history trade-offs in the wild, and the underlying mechanisms of life-history trade-offs, i.e., between fitness traits such as growth, maturation, and reproduction on the one hand and survival on the other (Stearns 2000; Braendle *et al.* 2011; Reznick *et al.* 2000; Leroi 2001; Roff 2002). By characterizing the physiological basis of trade-offs, the agents of natural selection can be better elucidated, and the response to selection can be predicted more accurately (Stearns 2011; Roff 2002). While competitive resource allocation has been suggested as the major contributor to the trade-offs in many life history models (reviewed by Flatt *et al.* 2011), the expectation of negative phenotypic (or genetic) correlations between survival and other fitness traits has been difficult to demonstrate in natural populations (Chang et al. 2024; Haave-Audet et al. 2022). Essentially, traditional trade-off models do not account for variation in resource acquisition, the inclusion of which could not only explain the observed positive phenotypic (or genetic) correlation between fitness components (Houle 1991; Van Noordwijk & Dejong 1986; Snell-Rood *et al.* 2015), but also provide a realistic framework to assess the mechanistic basis and the role of life-history trade-offs in natural systems. For example, a recent meta-analysis found that differences in resource acquisition were more important than differences in resource allocation in mediating the relationship between behavior and fitness (Haave-Audet *et al.* 2022).

Atlantic salmon (*Salmo salar*) is s good model to study life-history evolution and how life-history variation is maintained within the species (Schaffer 2003). In Atlantic salmon, two major fitness traits, i.e., sea age at first maturity (the number of years that salmon stay at sea prior to first reproduction) and higher fecundity are always coupled (due to substantial increase in size by age), and by extension fecundity and mortality are inherently negatively correlated (e.g., due to increased mortality rates of older salmon by staying longer at seas before reproduction). Further, sea age at maturity is a threshold

trait (Thorpe *et al.* 1998) with a strong genetic component (Barson *et al.* 2015; Sinclair-Waters *et al.* 2020), and environmental factors also play a central role in shaping the trait diversity (Jonsson & Jonsson 2004; Jonsson *et al.* 2012). The maintenance of trait variation represents a classic case of fitness trade-off between reproductive success and survival: longer times at sea increase fitness via a size-dependent increase in reproductive success but at the expense of a higher risk of mortality prior to reproduction (Fleming & Einum 2010; Mobley *et al.* 2021). Subsequently, the species also represents a wild model to study the potential contribution of resource acquisition or allocation in mediating the optimal variation in age structure, which also has substantial practical value e.g., to better predict the dynamics of the demographic structure of the populations. However, whether resource acquisition is involved in life-history trade-offs has yet to be empirically shown in wild systems.

In the marine environment, Atlantic salmon achieve high growth rates and accumulate fat reserves to support energetically expensive maturation and reproduction (Jonsson & Jonsson 2011). As such, variation in resource acquisition between individuals may play a central role in shaping sea age at maturity variation. For example, a higher condition factor (weight-by-length relationship) is considered a liability trait and a major determinant of maturation (Debes *et al.* 2021; Duston & Saunders 1999; Jonsson & Jonsson 2011; Herbinger 1987; Thorpe *et al.* 1998), which further indicates that resource acquisition is an important ecological process that shapes trait variation. For example, Herbinger (1987) found by studying individually marked salmon, that maturation in the autumn was associated with a high growth rate during the previous winter, and that this growth was attained by weight rather than length increase (i.e., a higher condition factor). Concordantly, it has been suggested that food web changes in the ocean may have a substantial impact on the maturation age of salmon populations (Friedland *et al.* 2005; Vollset *et al.* 2022), and salmon populations may show evolutionary responses to such changes (Czorlich *et al.* 2022).

In marine feeding grounds, the majority of sub-adult Atlantic salmon diets consist of crustaceans and fish, with large spatiotemporal variation (Jacobsen & Hansen 2001; Rikardsen & Dempson 2010). These two major taxonomic groups have fundamentally different properties as potential prey, such as size, behavior, and availability, which ultimately require different foraging strategies to utilize them (Ferry-Graham *et al.* 2002; Mittelbach & Persson 1998; Sanchez-Hernandez *et al.* 2019). Feeding also has an ontogenetic component: individuals switch to a more piscivorous diet as they grow larger, from a crustaceans-based diet in early marine phases. However, there is a considerable overlap in the distribution of prey groups between age classes (Jacobsen & Hansen 2001).

The ontogenetic diet shift is an adaptive trait in which an optimal feeding strategy is attained to supply the increasing energetic demands of a larger body, and is mostly linked to changes in habitat and life-stage transitions (Sanchez-Hernandez *et al.* 2019; Villéger *et al.* 2017). However, few studies have quantifed inter-individual variation in ontogenetic diet dynamics (Mittelbach & Persson 1998; Sanchez-Hernandez *et al.* 2019), with no assessment of potential performance trade-offs in free-living populations. An ontogenetic diet shift in the marine environment implies that the net adaptive value of energetic gain obtained from a particular feeding regime (e.g., diet type) is a function of ontogeny. For example, an individual's condition factor, and subsequently, its probability of maturing, is predicted to be determined by what they eat at a particular age. Surprisingly, however, there are no documented cases in the wild that quantify the diet-performance trade-offs along the ontogeny. Demonstrating such a trade-off between performance and diet composition would provide a functional ecological basis for how life-histories (i.e., age at maturity) are variable within and among populations, and across spatiotemporal dimensions, and may provide insights into how resource acquisition mediates trade-offs (Chang *et al.* 2024; Haave-Audet *et al.* 2022). As such, one can postulate that eating smaller food items early on (that is, a more optimal diet for smaller-sized salmon) is linked to earlier maturation (by

facilitating a higher condition factor to pass the maturation threshold), while switching to larger food items might be more beneficial later on (by facilitating a rapid body size increase).

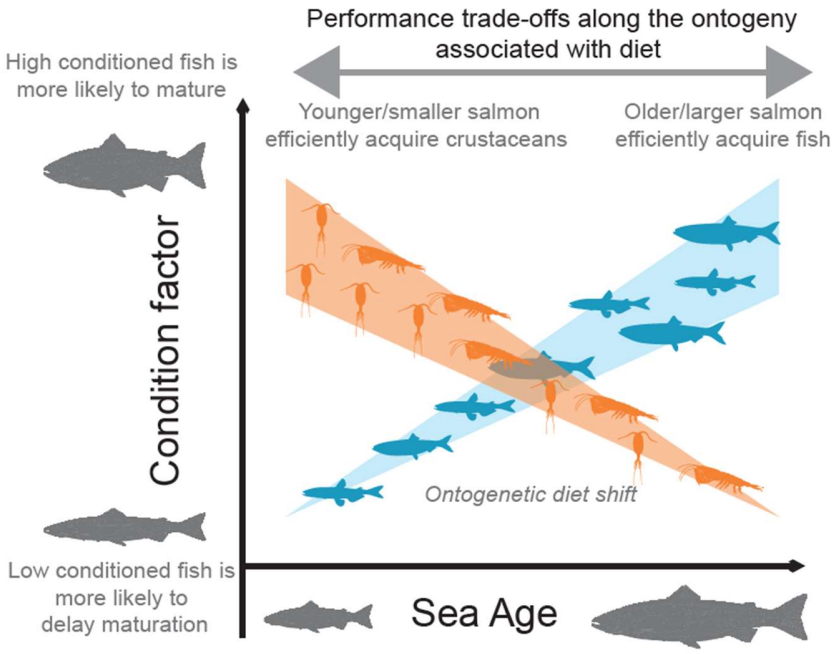

Figure 1: Conceptual model that links performance (condition factor) to diet type (crustacean *versus* fish) of sub-adult Atlantic salmon during the marine feeding stage.

Based on the above predictions, we hypothesized that there is an ontogeny-dependent performance trade-off for consuming different diet items (Figure 1). Such a trade-off between performance and diet composition would provide an ecological/mechanical explanation of how a life-history trait (age at maturity) is mediated by variation in resource acquisition (i.e., marine diet composition). We quantified the diet of wild Atlantic salmon subadults (i.e., the marine stage prior to maturation) sampled in the oceanic feeding ground, quantified their stomach contents (consisting of crustaceans and fishes, Jacobsen and Hansen 2001), and compared the age-dependent changes in condition factors in relation

to diet. We show that salmon at younger ages have a higher condition factor when foraging on crustaceans, and a lower condition factor when foraging on fish, and that this pattern is reversed in older age groups.

Materials and Methods

Sampled fish used in this study were originally described by (Jacobsen & Hansen 2001), and the final data were identical to (Aykanat *et al.* 2024) except that we retained N=68 individuals that were filtered out due to missing genotype information. Briefly, the dataset comprises 1604 individuals, of which 178, 995, and 431 are from 1SW, 2SW, and 3SW sea-age groups, respectively (SW, "sea-winter" is the number of winters a fish has been in the marine environment and is equivalent to the sea age). Samples were collected in autumn (November and December) and winter (February and March) seasons in 1992-93, 1993-94 fishing periods from 55 locations (see Figure 2). The fish were genetically assigned to large-scale regional groups (Ireland and the UK, Southern Norway, and Northern Norway; the latter encompassing fish assigned to Barents Sea drainages (O'Sullivan *et al.* 2022)). Individual salmon had their fork lengths measured and gutted, and gutted fish were weighed (in kilograms). The gut contents were identified and enumerated. Fish scales were used to determine sea age (via scale reading), and DNA extraction for genotyping. The fish sampled in this study were sub-adults with no phenotypic indications of maturation. The fish sampled in the study were immature, sub-adults with no phenotypic indication of maturation. Earlier studies indicate as high as 80% of individuals are likely to mature in the following autumn, but these estimates are based on limited number of tag recapture studies, or based on assessing the maturation probability via hormonal expression using hatchery reared salmon as the baseline (Youngson & McLay 1984; Jacobsen *et al.* 2001).

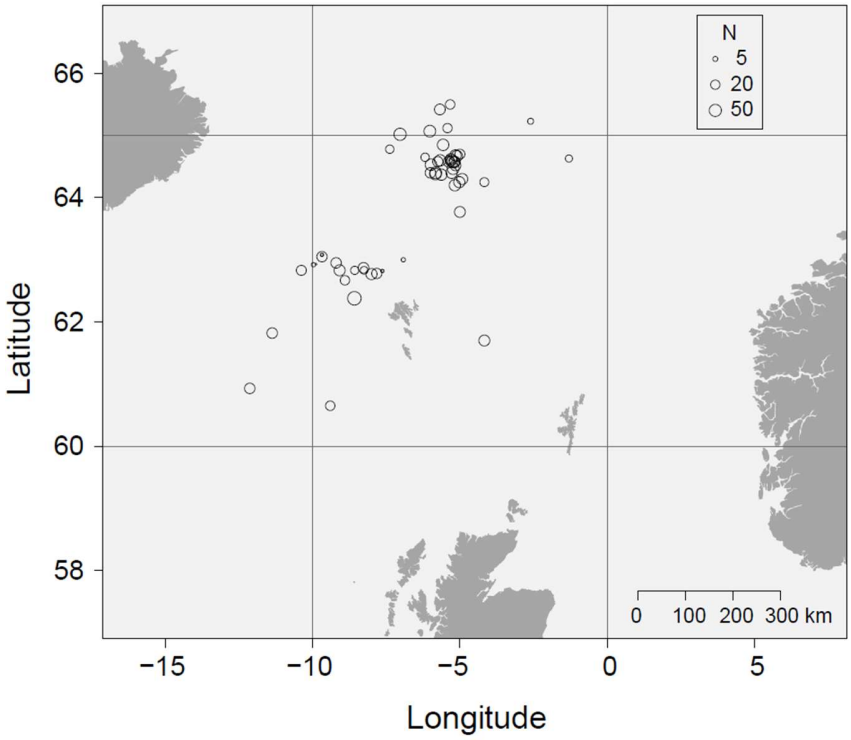

Figure 2: Sampling locations (N=55) and sample sizes (N=1604) used in this study.

We employed a linear mixed model with a general structure as follows:

$$Y = \mu + \text{Season} + \text{fishing period} + \text{Reporting Group} + \text{Sea Age}_{\text{categorical}} \times (\text{Sex} + \text{Length}_{\text{residual}}) + \text{Sea Age}_{\text{continuous}} \times (\text{Diet}_{\text{crus}} + \text{Diet}_{\text{fish}}) + \varepsilon_{\text{location}} + \varepsilon_{\text{error}}$$

Season, fishing period, and reporting group were included as categorical fixed effects. Crustacean and fish diets, as well as sex and age-standardized length, were modelled as fixed effects, interacting with sea age. We modelled sea age as a numerical variable when interacting with diet, and as a categorical variable when interacting with sex and residual length. This model was more parsimonious than models with sea age parameterized numeric or categorical for all interactions (see Results section).

145 $Length_{residual}$ was scaled to have a mean of zero and a standard deviation of one to improve
146 convergence. Spatial variation in sampling effort was accounted for by including sampling location as a
147 random effect (N=55). The condition was quantified as Fulton's condition factor K, ($K=10^5\ w / l^3$), in
148 which w is the gutted weight in kilograms divided by 0.9, to account for gut weight, and l is fork length
149 in cm (Appendix S1: Figure S1). The condition factor is based on the weight obtained from gutted fish;
150 therefore, it reflects the condition factor associated with muscle weight, with no direct effect of visceral
151 fat or gonadal tissue on the variation. In immature Atlantic salmon parr, it has been shown that there is
152 a strong and significant positive correlation between condition factor and total lipid content (Herbinger
153 & Friars 1991).

154 Diet number was primarily parameterized either as log-normalized weight or log-normalized number of
155 items in the stomach. Both crustacean and fish diets had highly left-skewed distributions with many
156 zero entries (i.e., empty stomach, Appendix S1: Figure S2). To avoid undefined zero values after log
157 transformation, we added 1 to the number of diet variables and added the minimum observed weight in
158 the dataset to the weight of diet variables.

159 The number and total weight of the diet items in the stomach were highly correlated (Appendix S1:
160 Figure S3); thus, any effect due to the number of diet items could be attributed to diet weight. To assess
161 whether the number or total mass of the diet explains the change in the condition factor, we
162 implemented the same model as above but used total diet weight as a factor instead of the number of
163 prey items acquired.

164 Next, we evaluated whether any taxonomic groups within crustaceans drive the relationship between
165 crustaceans and diet by partitioning crustaceans into lower-order taxonomic groups, provided that the
166 numbers within a specific taxon were sufficiently large. As such, we reimplemented the model above

by replacing crustaceans with Hyperiid amphipods (*Themisto* spp.) and Euphausiids as factors. These two taxa comprise the majority of the crustacean diet in the stomach (Appendix S1: Table S1) and were substantially different in size, with the latter being larger than the former (Appendix S1: Table S1). We did not implement the same approach in fishes which had restrictively small number of prey items per species (Appendix S1: Table S1).

The relationship between the condition factor and number of prey items might be driven by different ecological processes associated with foraging, such as active foraging frequency or foraging efficiency (Aykanat *et al.* 2024). We assessed the contribution of these two possibilities by repeating the analysis after readjusting diet parameters to account for these factors. As such, we first quantified the presence or absence of prey as a proxy for active foraging frequency using the model described above but replaced diet item numbers with a Boolean parameter (presence or absence of diet was coded as 1 and 0, respectively) for crustaceans and fish in two separate models. Likewise, we employed models by excluding salmon with empty stomachs to quantify the effect of foraging efficiency (when actively forged for prey), separately for crustaceans and fish.

All models were run using the glmmTMB package (version 1.1.5, Brooks *et al.* 2017) in R version 4.1.0 (R Core Team 2019), using a Gaussian error structure. Marginal means for genotype effects and their confidence intervals were calculated using the emmeans package (version, 1.8.5, Lenth, 2023). Model diagnostics were performed using the DHARMa package in R (version 0.4.6, Hartig 2022).

Results

As predicted by the hypothesis, crustacean numbers in the diet had an age-dependent effect on the condition factor ($t = 3.276$, $p = 0.001$, Figure 3a, Appendix S1: Figure S4). The condition factor of 1SW was marginally higher when the diet contained more crustaceans ($t=1.938$, $p = 0.053$), but the

relation was reversed in 2SW (t = -1.821, p = 0.069) and became highly negatively associated in the 3SW age class (t = -3.621, p < 0.001). In contrast, the effect of fish diet on the condition factor marginally but significantly increased along the ontogeny (t = -1.977, *p* = 0.048, Figure 3b, Appendix S1: Figure S4). Eating more fish did not affect the condition factor in the 1SW age class (t = -0.556, *p* = 0.55) but had a gradually increasing and significant effect on older sea age groups (for 2SW: t = 2.214, *p* = 0.027, for 3SW: t = 3.260, *p* = 0.001, Figure 2b). When the total diet weight was parametrized in the model, instead of the number of prey items acquired, it did not explain ontogenetic effects in the diet (Appendix S1: Figure S5), suggesting that numbers were the primary factor associated with the ontogenetic effect.

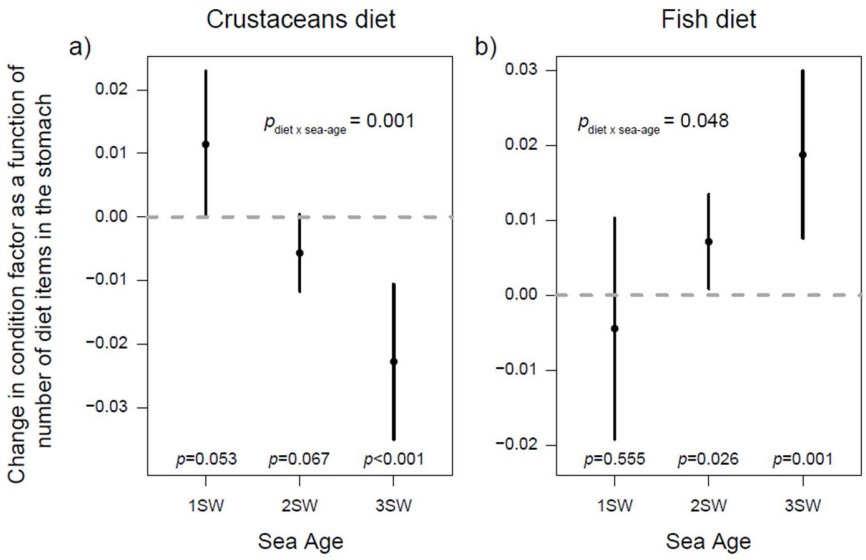

Figure 3: Marginal effect of crustaceans (a) and fish (b) prey numbers on condition factor in Atlantic salmon sub-adults in the marine environment. Positive slope a positive association between the number of diet and condition factor.

Sex and length also exhibited age-dependent patterns, which had an apparent non-linear pattern across sea ages (Figure 4). Notably, there was a substantial reversal of sex-dependent changes in the condition factors between the 1SW and 2SW age groups (Figure 4a). Males had significantly higher condition factors in the 1SW age class (t = 2.707, p = 0.007) and significantly lower condition factors in the 2SW age class (t = -5.345, p < 0.001), while there was no difference between sexes in the 3SW age class (t = -0.077, p = 0.94, Figure 4a). Length affected the condition factor positively in the 2SW age class (t = 5.446, p <0.001) but did not affect the condition in other age groups (Figure 3b). As expected, winter was associated with a lower condition factor (t = -8.19, p < 0.001, Appendix S1: Table S2). There was a marginal fishing-period effect (t = -2.039, p < 0.042). Ireland and the UK regional groups had significantly smaller condition factors than Northern Norway (t = -6.87, p < 0.001) and Southern Norway reporting groups (t = -8.10, p < 0.001), but no difference was detected between Northern Norway and Southern Norway reporting groups (t = 1.03, p = 0.31, Appendix S1: Table S2).

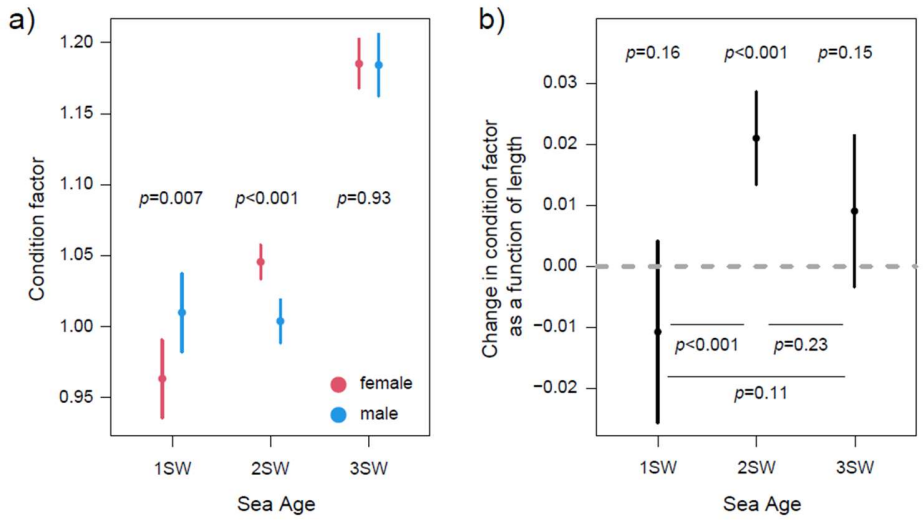

Figure 4: Marginal effects of sex (a) and length (b) on condition factor in Atlantic salmon sub-adults in the marine environment. Positive slope in (b) indicates a positive association between (age standardized) length of salmon and condition factor.

The crustacean diet in the stomach consisted of a few major taxonomic groups, the majority of which were Hyperiid amphipods (~93% and 69% by number and weight, respectively, and mostly *Themisto* species) and Euphausiids (krill), ~ 6% and 15% by number and weight, respectively (Appendix S1: Table S1). When the number of these taxa was included in the model, instead of crustaceans as a whole, Hyperiid amphipods, but not krill numbers, explained the ontogenetic diet effects on the condition factor (Figure 5), suggesting that the overall pattern was driven by Hyperiid amphipods acquisition. This model explained the ontogenetic effect substantially better (t = 3.620, $p < 0.001$), whereby the condition factor of 1SW was significantly higher when the diet consisted of more Hyperiid amphipods (t = 2.129, p = 0.033), whereas the relation was significant in the opposite direction in 2SW (t = -2.157, $p < 0.031$), and 3SW age classes (t = -3.982, $p < 0.001$). We did not perform a parallel analysis for the fish diet because the numbers became prohibitively small when the fish diet data were partitioned into smaller taxonomic groups.

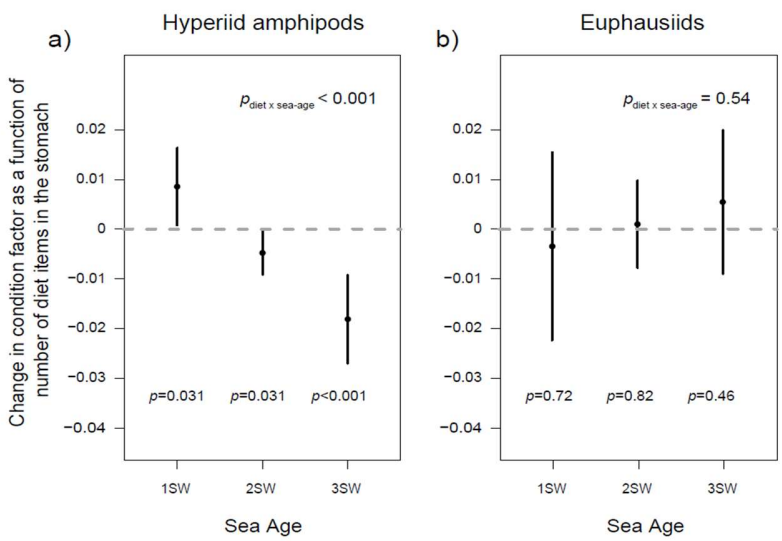

Figure 5: Marginal effects of Hyperiid amphipods (a) and Euphausiids (b) prey numbers on condition factor in Atlantic salmon sub-adults in the marine environment. Positive slope a positive association between the number of diet and condition factor.

The relationship between the condition factor and number of prey items might be driven by different ecological processes associated with foraging, such as foraging frequency or foraging efficiency (Aykanat *et al.* 2024). We assessed the contribution of these two possibilities by repeating the analysis and readjusting the diet parameters to account for these factors. Therefore, we first quantified the presence or absence of prey as a proxy for foraging frequency, in which the presence of diet was attributed to active foraging, and then quantified the (log-transformed) number of diet items, given that diet was present in the data, as a proxy for foraging efficiency. For both the models, we used the structure described above. The effects of diet on the condition factor were qualitatively similar to each other and to the original models (Appendix S1: Figure S6), ruling out the sole contribution of any of the two processes.

In our study, we modelled sea age continuously when interacting with diet variables and categorically when interacting with sex and length, which was more parsimonious (AIC = -2412.1) than modelling all four variables continuously (AIC = -2325.0) or categorically (AIC = -2408.2). However, the effect of diet on condition factor was qualitatively similar in all three models (data not shown).

Discussion

We demonstrated that resource acquisition drives ontogenetic performance trade-offs and is likely an important factor shaping life-history divergence via the causal effect of condition factor on maturation. Competitive resource allocation has been the major mechanism suggested to mediate life-history trade-offs within species but lacks evidence in natural systems despite being a focal process in the field (Flatt & Heyland 2011; Haave-Audet *et al.* 2022; Chang *et al.* 2024). The theoretical premise of resource acquisition in shaping life-history trade-offs dynamics has been acknowledged directly (Flatt & Heyland 2011), or indirectly across different approaches, i.e. as a potential outcome through the effect

of signaling networks (Stearns 2011) or via the effect of changing environmental plasticity to couple-decouple the correlations between life history traits. However, the empirical studies involve common garden designs under controlled conditions (Messina & Fry 2003; Ernande *et al.* 2004; Lailvaux *et al.* 2005). Our results, obtained in the wild, demonstrate a link between diet-preference and the liability trait of age-at-maturity provides a mechanistic link on how life-history dynamics shapes by resource acquisition in the wild.

Diet type, both crustaceans and fish, has an age-dependent effect on the condition factor of wild sub-adult Atlantic salmon, a trait that has a major influence on maturation timing (e.g., Duston & Saunders 1999). Among crustacean taxa, Hyperiid amphipods (mostly *Themisto* spp.), but not euphausiids (krill), drive the age-dependent decrease in the condition factor. Hyperiid amphipods are much more abundant prey types in the marine feeding grounds of the Northeast Atlantic (Jacobsen & Hansen 2001) but are smaller than krill or other crustaceans taxa observed in the diet (Appendix S1: Table S1). It is plausible that acquiring Hyperiid amphipods becomes increasingly energetically expensive as salmon get older and larger. In contrast, the influence of fish diet on the condition factor increases with sea age. Consuming fish affected the condition factor positively only in older sea age groups, suggesting that some energetic constraints associated with smaller fish size exist. Taken together, our study demonstrates an age-dependent optimal foraging strategy for Atlantic salmon, which may have a significant impact on maturation rates.

Our results have implications for understanding the dynamics of salmon age structure at sea. We can predict that a younger age distribution in salmon populations will be positively associated with crustacean prey abundance (mainly Hyperiid amphipods), and negatively associated with fish prey abundance. Vollset *et al.* (2022) suggested that broad-scale changes in oceanic conditions led to an ecological regime shift, which subsequently affected the age at maturity. They further demonstrated a

temporal correlation between an increase in the proportion of older sea age groups and abiotic and biotic factors, such as a decrease in planktonic biomass, an increase in sea surface temperature (SST), a decrease in Arctic water flux, and a decrease in fish (mackerel) length. Our study linked individual-based diet patterns to condition factor within a narrow temporal window and across a heterogeneous spatial distribution of Atlantic salmon and its prey. This allows us to suggest a causality between prey abundance and maturation via the profound effect of the former on the condition factor, among other factors outlined in (Vollset *et al.* 2022).

While the ontogenetic diet shift towards a more piscivorous diet has been demonstrated in this system earlier (Jacobsen & Hansen 2001), its effect on performance was not investigated until this study. Based on our results, one can suggest that the net benefit of a crustaceans-oriented diet is diminishing, while a fish-based diet becomes more rewarding as the marine age progresses. Since the ontogenetic relationship is driven by prey numbers, but not mass, we can postulate that the age-dependent diet benefits are not caused by post-acquisition processes, such as differences in energy content or potential differences in nutrient stoichiometry between diet types. In fact, the energy densities of the preferred prey species, both crustaceans and fishes, of Atlantic salmon in the Faroes is quite high (Pedersen & Hislop 2005; Nowicki *et al.* 2023). This suggests that the energy cost in the acquisition processes prior to prey capture likely underlies the performance variation among different age groups in the wild. The result that this relationship is mostly driven by the smaller (and more numerous) Hyperiid amphipods (Figure 5) further supports this notion. Therefore, we suggest that foraging for crustaceans, which are relatively small, becomes increasingly energetically unsustainable for larger salmon. Similarly, we suggest that foraging for fish is only energetically sustainable for larger salmon, which may be due to size-dependent changes in morphology or behavior, eventually leading to changes in foraging efficiency for a particular prey type (Smith & Skúlason 1996). For example, gape size may restrict

303 smaller salmon from capturing larger fish (Keeley & Grant 1997; Scharf *et al.* 2000), or they may not
304 sustain cruising speeds foraging for fish prey as efficient as larger salmon (Sanchez-Hernandez *et al.*
305 2019; Webb *et al.* 1984).

306 However, the ontogenetic effect of diet on condition was not solely explained by foraging strategy, as
307 demonstrated by similar effects when diet was parameterized as presence/absence (i.e., as an indication
308 of frequency of active foraging) or total prey numbers in the diet (when diet items were non-zero, and
309 indication of foraging outcome). This suggests that ontogenetic effects are independent of the foraging
310 strategy. Interestingly, (Aykanat *et al.* 2024) suggested that the *vgll3* locus, a major locus influencing
311 age at maturity, was associated with age-dependent differences in crustaceans foraging frequency, but
312 not foraging outcome. Fish with *vgll3* early maturing genotype appeared to gain similar amounts of
313 food with less foraging activity, suggesting that an increase in acquisition efficiency may be one of the
314 factors that allows salmon with the *vgll3* early genotype to mature earlier, that is, by allocating surplus
315 resources towards reproductive investment Aykanat *et al.* 2024. However, they did not find any
316 evidence of an age-dependent association between condition factor and *vgll3* genetic variation. These
317 results suggest that the effect of diet on the condition factor in the present study likely has an
318 independent pathway than that of the *vgll3* locus. However, the condition factor that we used here (and,
319 in Aykanat *et al.* 2024) is based on the gutted fish weight, which does not include visceral fat when
320 calculating the condition factor. Therefore, it is unclear whether diet and/or the *vgll3* locus influence
321 weight gain by increasing visceral fat and/or gut weight.

322 Similar to diet, our results show that sex has an ontogenetic effect on condition factor, with 1SW
323 salmon males tending to have a higher condition factor, whereas this pattern was reversed in 2SW
324 salmon (Figure 3b). This result is consistent with the general maturation pattern of the species
325 associated with sex-specific fitness differences, whereby size is a stronger predictor of higher

326 reproductive success in females (Barson *et al.* 2015; Fleming *et al.* 1996). As such, males mature more
327 often as 1SW than females, which tends to delay maturation to achieve a larger body size. While the
328 maturation threshold might have a sex-specific component (Reid 2022), our results indicate that
329 ontogenetic differences in condition factor might be a proximal mechanism explaining sex-specific
330 maturation differences, perhaps via differences in resource allocation for specific energy requirements
331 for future spawning (Jonsson & Jonsson 2003; Persson & De Roos 2006). Energy expenditure during
332 spawning is also higher among younger males than females but increases more by size in females than
333 in males (Jonsson & Jonsson 2003). Likewise, repeat spawning (i.e., saving energy for a second
334 spawning) is more common in females than in males and is more common in populations with a high
335 average age at maturation (Persson *et al.* 2023), indicating consistent sex- and age-specific energy
336 requirements during spawning and suggesting complex sex-specific maturation norms in Atlantic
337 salmon.

338 Linking stomach content to general resource acquisition patterns has often been criticized because it
339 reflects only a snapshot of the diet (i.e., until it is assimilated), whereas other methods, such as
340 quantifying stable isotopes, have been suggested to be more robust when assessing long-term feeding
341 habits (e.g., Power *et al.* 2023). However, our results are remarkably consistent across ontogeny and
342 provide a well-supported and predictable relationship with the condition factor, a body index that
343 should not be affected only by very recent feed intake. Hence, our results confirmed that stomach
344 content analysis reflects general feeding patterns.

345 The sampling sites for this study are one of the major marine feeding grounds for most European
346 salmon populations, especially for older sea age groups such as 2SW and 3SW salmon (Jacobsen &
347 Hansen 2001; O'Sullivan *et al.* 2022). This region is a diverse habitat for both fish and crustacean prey
348 (Jacobsen & Hansen 2001), the dynamics of which may be important for salmon maturation (Vollset *et*

al. 2022). However, many salmon populations from geographically distant localities, such as North America and the Baltic Sea, have other marine feeding areas, and salmon of younger age groups inhabit marine feeding areas close to the shores of their native rivers (Gilbey *et al.* 2021; Rikardsen *et al.* 2021). Such large differences in habitat distribution may have a profound impact on prey dynamics, especially in the early stages of the marine environment (Rikardsen & Dempson 2010), and in relation to changes in preference and subsequent effects on maturation. In fact, two studies that investigated the population dynamics of salmon populations inhabiting the North Atlantic and the Barents Sea marine feeding ground post-smolts have found opposite long-term maturation patterns, likely as a result of differing trophic dynamics between the two regions (Czorlich *et al.* 2022; Vollset *et al.* 2022). Therefore, it is important to quantify trophic dynamics in different marine regions in order to better understand their effects on performance and subsequent maturation.

Despite immense field effort, the data collected in the wild have high dimensionality. Hence, the model contains several parameters that would otherwise be controlled under common garden conditions. While relevant, testing all possible interactions between covariates (which may covary with focal covariates) is not feasible owing to the number of possible combinations. Nonetheless, our model appears robust to the exclusion of variables from the model.

In this study, we provide a clear case of an ontogenetic trade-off in performance-associated individual variation in diet type in freely roaming species across large geographical areas. The empirical evidence here supports the notion that trade-offs mediating life history divergence could be explained by variation in resource acquisition in the wild, and could explain the lack of genetic or phenotypic correlations observed between life-history traits. Our study provides a mechanistic basis to better predict Atlantic salmon maturation dynamics and performance trajectories across large spatiotemporal scales. Climate-induced effects on Atlantic salmon performance and demography have been suggested

372 previously (Friedland *et al.* 2009; Jonsson & Jonsson 2004; Todd *et al.* 2008; Vollset *et al.* 2022), and
373 our results add to this knowledge by identifying bottom-up trophic dynamics as important underlying
374 factor associated with the effect of such large-scale climate events to maturation. Our study also
375 highlights the importance of exploiting and refurbishing old but gold datasets to address novel
376 ecological questions.

377 Author contributions

378 TA conceptualized the paper. KH organized sample retrieval from scale archives at NINA. JAJ
379 coordinated the Faroese fieldwork and collected diet data. TA conducted the statistical analyses. TA
380 and KH drafted the MS and all coauthors contributed to subsequent drafts.

381 Conflict of Interest

382 The authors declare no competing interests.

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