Diet predicts performance trade-offs along Atlantic salmon ontology

Tutku Aykanat[1*], Jan Arge Jacobsen[2], Kjetil Hindar[3]

1. Organismal and Evolutionary Biology Research Program, Faculty of Biological and Environmental Sciences, PO Box 56, FI-00014 University of Helsinki, Finland. tutku.aykanat@helsinki.fi
2. Faroe Marine Research Institute, Nóatún 1, FO-100 Tórshavn, Faroe Islands. Council
3. Norwegian Institute for Nature Research (NINA), NO-7485 Trondheim, Norway. kjetil.hindar@gmail.com

[*] Corresponding author: tutku.aykanat@helsinki.fi

Running page head: Age dependent diet-performance trade-offs

Abstract

Understanding the mechanistic basis of life history divergence is fundamental for predictive ecology. Variation in resource use impacts life history divergence and provides a framework for studying life history trade-offs. Contrary to the theory, empirical evidence does not support that resource allocation alone mediates life history divergence in the wild, which subsequently suggests a pivotal role for resource acquisition, but this has not been empirically demonstrated in free-living populations. Here, we sampled wild Atlantic salmon (*Salmo salar*) from different age groups during their marine feeding stage and hypothesized that prey taxa (consumption of crustaceans *versus* fish) has an age-dependent effect on the condition factor. We found that salmon in their first year at sea had a higher condition factor when foraging on larger numbers of crustaceans and a lower condition factor when foraging on larger numbers of fish, and *vice versa* in older sea age groups. Provided that condition factor is a predictor of age-at-maturity, our results show that resource acquisition may be an important process shaping life history variation in Atlantic salmon via modulating age-dependent performance trade-offs. Our results also emphasize the importance of bottom-up trophic cascades for maturation age and help to better predict the maturation dynamics of wild populations in the marine environment.

Keywords: life history variation, resource acquisition, age at maturity, ontogenetic diet shift, trade-offs, Atlantic salmon.

1. INTRODUCTION

An important focus of evolutionary biology has been to identify and study the underlying mechanisms of life history trade-offs in wild populations (Reznick et al. 2000, Stearns 2000, Leroi 2001, Roff 2002, Braendle et al. 2011). By characterizing the physiological basis of the trade-offs between maturation timing and survival, the response to selection can be predicted more accurately (Roff 2002, Stearns 2011). Competitive resource allocation —the allocation of available energy to support various biological processes such as growth and reproduction—, has been suggested as the major contributor to the trade-offs dynamics in many life history models, such as in a trade-off between investing to current and future reproductive success (reviewed by Flatt et al. 2011). However, the expectation of negative phenotypic (or genetic) correlations between survival and other fitness traits lack confirmation in natural populations (Haave-Audet et al. 2022, Chang et al. 2024). Essentially, traditional trade-off models do not account for variation in resource acquisition, —the processes associated with obtaining energy from the environment to support biological processes—. Resource acquisition, however, could not only explain the observed positive phenotypic (or genetic) correlation between fitness components (Van Noordwijk & de Jong 1986, Houle 1991, 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 in non-human animals 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 a good model to study life history evolution and how life history variation is maintained (Schaffer 2003). Atlantic salmon is an anadromous species in which juveniles migrate to resourceful marine environment to enhance growth and subsequently increase reproductive success. The number of years that Atlantic salmon stay at sea prior to first reproduction (henceforth,

sea-age at maturity) and fecundity are coupled because fish size and, consequently, fecundity increases with age. By extension reproductive success and mortality are inherently negatively correlated due to deceasing overall survival probability of salmon by staying longer at sea before reproduction. 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 age structure, which also has substantial practical value for predicting the dynamics of the demographic structure of the populations. Whether resource acquisition is involved in life history trade-offs has yet to be empirically shown in wild systems.

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 variation (Jonsson & Jonsson 2004, Jonsson et al. 2012). 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 via its effect on lipid content, which is suggested as the underlying liability trait of maturation (Rowe et al. 1991, Thorpe et al. 1998). The changes in lipid content of individuals may be mirrored by changes in condition factor, hence condition factor can predict maturation (Herbinger 1987, Herbinger & Friars 199, Duston & Saunders 1999, Peterson & Harmon 2005, Jonsson et al. 2012, Jonsson et al. 2013, Debes et al. 2021). 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, resulting in 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 changes in food availability (Czorlich et al. 2022). At sea, the diet of sub-adult Atlantic salmon (the marine stage prior to maturation) mainly consists 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 (Mittelbach & Persson 1998, Ferry-Graham et al. 2002, Sanchez-Hernandez et al. 2019). Feeding also has an ontogenetic component: crustaceans-based diet in early marine phases switches to a more piscivorous diet as individuals grow larger. However, there is a considerable overlap in the distribution of prey groups between different sea ages (Jacobsen & Hansen 2001). Therefore, age-dependent dynamics of diet intake and how it affects condition factor, a strong predictor of maturation timing (Herbinger & Friars 1991, Jonsson et al. 2012), is unclear in wild Atlantic salmon.

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 (Villéger et al. 2017, Sanchez-Hernandez et al. 2019). However, few studies have quantified 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) changes as a function of ontogeny. As such, acquiring optimal resource type increases the net energy gain, which may facilitate lipid accumulation and condition factor (Jonsson et al. 2013), and subsequently probability of maturing

(Herbinger & Friars 1991, Rowe et al. 1991, Thorpe et al. 1998). Therefore, resource acquisition may be suggested as a functional ecological process explaining the dynamics of age at maturity, by demonstrating an age dependent relation between performance (condition factor) and diet composition (Haave-Audet et al. 2022, Chang et al. 2024).

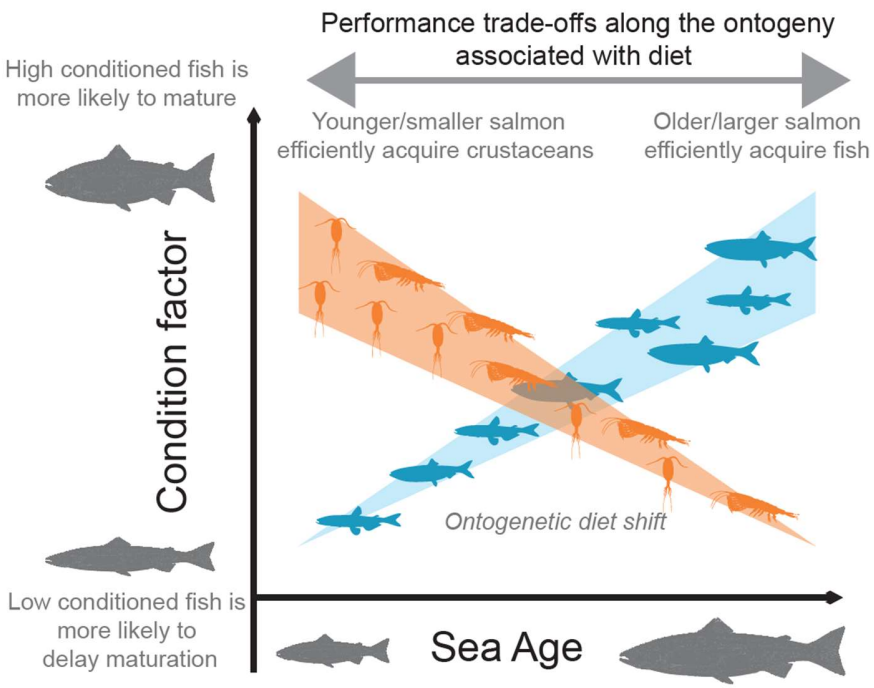

Fig. 1. Conceptual model that links performance (condition factor) to diet type (crustacean versus fish) of sub-adult Atlantic salmon during the marine feeding stage.

Based on the above predictions, we hypothesized there is an ontogeny-dependent performance trade-off for consuming different diet items (Fig. 1). Specifically, we hypothesize that eating smaller food items early in the marine stage is an optimal feeding strategy for smaller-sized salmon, and increases their probability of maturation in the following year by facilitating lipid depositions, which may be predicted

by the condition factor (Herbinger & Friars 1991, Todd et al. 2008). Lipids are essential, for example, during vitellogenesis (egg production), which comprises a substantial amount of energy expenditure of females during the reproduction period (Jonsson & Jonsson 2003), as well as for other energetically expensive migration and reproductive activities (Jonsson & Jonsson 2011). Concordantly, lipid content has been suggested as the underlying, liability trait that triggers the developmental switch to initiate the maturation the following year (Thorpe et al. 1998). Likewise, we hypothesize that switching to larger food items is more beneficial to older, larger-sized salmon, leading to higher net energy gain, also to support future reproduction activities. Such age dependent trade-off between performance (condition factor) and diet composition would provide an ecological explanation of how a life history trait (age at maturity) is mediated by resource acquisition variation (marine diet composition). As such, we quantified the diet of wild Atlantic salmon sub-adults 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 factor in relation to diet.

2. MATERIALS & METHODS

2.1. Study system

Atlantic salmon 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 in the prior study due to missing genotype information in two focal life history loci. Briefly, the dataset comprises 1604 individuals collected from the Northeast Atlantic Ocean in their ocean feeding ground North of the Faroe Islands, 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 at 55 locations during fishing

periods in autumn (November and December) and winter (February and March) in 1992-93 and 1993-94 (Fig. S1). The fish were genetically assigned to large-scale reporting groups (Ireland and the UK, Southern Norway, and Northern Norway; the latter encompassing fish assigned to Barents Sea drainages (O'Sullivan et al. 2022), which descibes broad phylogenetic groups associated with large geographical regions. Compared to the original study (Jacobsen & Hansen 2001), which comprised of N=1765 wild individuals from the 1992-93, and 1993-94 fishing periods, we excluded 161 individuals, of which N=34 did not have any material to genotype (i.e. no scales), N=9 did not have sex information, N=15 had sea age larger than 3SW, and 103 were not assigned to the reporting groups indicated above (out of 103, N=88 was assigned to North American phylogenetic groups). Individual salmon had their fork lengths measured in centimeters, and gutted, and gutted fish were weighed in kilograms to two decimal places. The gut contents were identified to taxon level and enumerated. Fish scales were used to determine sea age (via scale reading), and for DNA extraction and genotyping. The fish sampled in this study were sub-adults with no phenotypic indications of maturation. An independent, earlier study from the Faroese feeding grounds indicates that 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), hence may not be reliable.

2.2. Data analysis

We employed a two-step multi-model inference approach using linear mixed models, using condition factor as the response variable. Condition factor is a strong predictor of lipid content in Atlantic salmon (Herbinger & Friars 1991, Todd et al. 2008) which is suggested as the liability trait of the maturation timing (Thorpe et al. 1998). In this framework, we first identify the most parsimonious null model

structure by comparing the fit of the models parameterized with different combination of non-focal variables, and their interactions. The global null model structure is as follow:

Global null model = CF ~ μ + fishing period + Season x Sea Age x Sex x $Length_{age.std}$ + $\varepsilon_{reporting\ group}$ + $\varepsilon_{location}$ + ε_{error}

Whereby, μ is the intercept and ε_{error} is the residual errors. The condition factor (CF) is Fulton's condition factor K, ($K=10^5\ w / l^3$), in which w is the gutted weight in kilograms divided by 0.9, to account for gut weight, and l is fork length in cm (Fig. S2). Fulton's condition factor is a common condition index that has been a sufficient standard in physiological studies in fishes (Stevenson & Woods 2006). The condition factor is based on the weight obtained from gutted fish; therefore, it reflects the condition factor associated with body weight excluding the gut weight and visceral fat and gonadal tissue weights. This is pertinent since subcutaneous adipose tissue and musculature lipids have been suggested as the main energy reserves during the spawning period (Jonsson et al. 1997).

The model included season, fishing period, sea age, sex, and age-standardized length ($Length_{age.std}$) as fixed effects. Spatial variation in sampling effort was accounted for by including sampling location as a random effect ($\varepsilon_{location}$, N=55). Likewise, variation due to geographical origin of individuals was accounted for by including reporting groups ($\varepsilon_{reporting\ group}$, N=3) as random terms. $Length_{age.std}$ was scaled to have a mean of zero and a standard deviation of one to improve convergence. All four-way combinations of season, sex, sea age, and age-standardized length and their reduced models were fitted and compared. Models were fitted by parameterizing sea-age both as a continuous or factorial variable (Table 1). All models were then compared using corrected Akaike Information Criteria (AICc), which corrects for bias for small sample sizes. The model with lowest AICc value is considered as the most parsimonious null model and used in the following analyses.

Next, on top of the most parsimonious null model, we fitted models that also include combinations of focal variables ($Diet_{crus}$ and $Diet_{fish}$) and their interaction with sea age, the fit of which was then compared using AICc. These models reflected hypotheses explaining the diet type effect on condition (Table 2). The global model structure is as follow:

Global model: CF ~ terms as in the most parsimonious null model + Sea Age x ($Diet_{crus}$ + $Diet_{fish}$)

Whereby, $Diet_{crus}$ and $Diet_{fish}$ are log-normalized number of diet items in the stomach. Both crustacean and fish diets had highly left-skewed distributions with many zero entries (i.e., empty stomach, Fig. S3). To avoid undefined zero values after log transformation, we added 1 to the number of diet variables. As above, sea-age was modelled both as a continuous or categorical variables.

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. Null model selection and AICc calculations was performed using MuMin package (version 1.48.4, Barton et al 2024). Marginal means for genotype effects and their confidence intervals were calculated using the emmeans package, and significance was assessed by t-test (version 1.8.5, Lenth, 2023). Model diagnostics were performed using the DHARMa package in R (version 0.4.6, Hartig 2022).

2.3. Post-hoc analyses

We implemented a number of post-hoc analysis in which we revise original parameterization of terms to further break down the structure of the diet effect on condition.

2.3.1. The effect of different taxonomic groups within crustaceans.

We evaluated whether any taxonomic groups within crustaceans drive the relationship associated with the crustaceans diet, by partitioning crustaceans diet into lower taxonomic groups, provided that the

numbers within a specific taxon were sufficiently large. As such, we implemented the most parsimonious model structure, but by replacing $Diet_{crus}$ term with either $Diet_{Hyperiid.amphipods}$ or $Diet_{Euphausiids}$, which are the log-normalized number of hyperiid amphipods (*Themisto* spp.) and euphausiids in the diet, respectively. These two taxa comprise the majority of the crustaceans in the stomach (Table S1), and were substantially different in size, with the latter being larger than the former (Table S1). We did not implement the same approach in fishes due to small number of prey items per species (Table S1).

2.3.2.Partitioning the underlying resource acquisition processes

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 restructuring diet variables to account for these factors. As such, the presence or absence of prey was used as a proxy for active foraging frequency, using the model structure described above, but replacing the diet variable with a Boolean parameter, for crustaceans and fish in two separate binomial models. Using the data with which diet was present, log-transformed number of diet items was modelled as a proxy for foraging efficiency (when actively foraging for prey), for crustaceans and fish in two separate models.

2.3.3. Comparing the importance of weight vs number of diet in the stomach

The number and total weight of the diet items in the stomach were highly correlated (Fig. S4); thus, any effect due to the number of diet items could be attributed to diet weight. To assess whether the number or total mass of the diet better explain the change in the condition factor, we implemented the same model as above but used total diet weight as a factor instead of the number of prey items acquired.

3. RESULTS

3.1. Null model structure and parametrization of sea age

The most parsimonious null model included fishing period, season, $length_{age.std}$, sex, and sea age as parameters, and second order interactions between $length_{age.std}$, sex, and sea age, (Table S2). Notably, a model that parameterizes sea age categorically was substantially better than a model with continuous parametrization (ΔAICc = 67.18, Table S3). However, we modelled sea age continuously when interacting with diet variables. Such a model was more parsimonious than a model that parameterizes sea age continuously (ΔAICc = 87.78) or categorically (ΔAICc = 4.01) across all the interactions. In all three models, main results regarding age-dependent diet association on condition factor was qualitatively similar (data not shown).

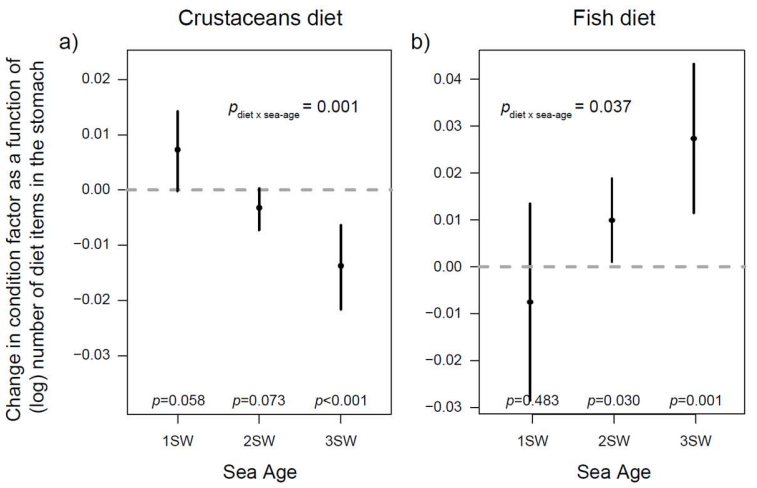

Fig. 2. Marginal effect of the number of crustaceans (a) and fish (b) prey items (log scale) on condition factor in Atlantic salmon sub-adults in the marine environment. Dashed line indicates a zero slope, no relation between the number of diet items and condition factor. Error bars indicate 95% confidence intervals.

3.2. Age dependent diet effect on condition factor

Our analysis supported the hypothesis that suggests an age dependent diet effect on condition factor (Table 1). In this model, the number of diet items in the stomach had a significant age dependent association with condition factor, but the direction of the age effect was in contrasting for crustaceans and fish diets. In other words, the age dependent slope of the relation was negative for crustaceans diet (for crustaceans diet by sea age interaction: t-test, $t_{1585} = -3.208$, $p = 0.001$, Fig. 1a), but it was positive for fish diet (for fish diet by sea age interaction $t_{1585} = 2.088$, $p = 0.037$, Fig. 1b). Within 1SW age group, the number of crustaceans in the diet was positively associated with condition factor ($t_{1585} = 1.901$, $p = 0.058$), but the relation was increasingly negative as the age of salmon progresses (for 2SW: $t_{1585} = -1.794$, $p = 0.073$, for 3SW: $t_{1585} = -3.572$, $p < 0.001$. Fig. 2a). The number of fish in the diet did not affect the condition factor in the 1SW age group ($t_{1585} = -0.702$, $p = 0.48$), but the relation was increasingly positive as the age of Atlantic salmon progresses (for 2SW: $t_{1585} = 2.177$, $p = 0.030$, for 3SW: $t_{1585} = 3.367$, $p < 0.001$, Fig. 2b, Fig. S5). The scenario where crustaceans and fish diets were modelled age dependently with continuous parameterization of sea age significantly outperformed any other alternative hypotheses (Table 1).

3.3. Age dependent sex and length effects on condition factor

Sex and length also exhibited age-dependent patterns, which had an apparent non-linear dependency with sea age (Fig. 3). Notably, there was a substantial reversal of sex-dependent changes in the condition factor between the 1SW and 2SW age groups (Fig. 3a). Males had significantly higher condition factors in the 1SW age group ($t_{1585} = 2.693$, $p = 0.007$) and significantly lower condition factors in the 2SW age group ($t_{1585} = -5.254$, $p < 0.001$), and there was no difference between sexes in the 3SW age group ($t_{1585} = 0.026$, $p = 0.98$, Fig. 3a). Length was positively associated with the

condition factor positively in the 2SW age group (t_{1585} = 5.040, p <0.001) but the association was not significant in other age groups (Fig. 2b). As expected, winter was associated with a lower condition factor (t_{1585} = -8.123, p < 0.001), and there was a marginal fishing-period effect ($_{1585}$ = -1.989, p < 0.047, see also Table S2).

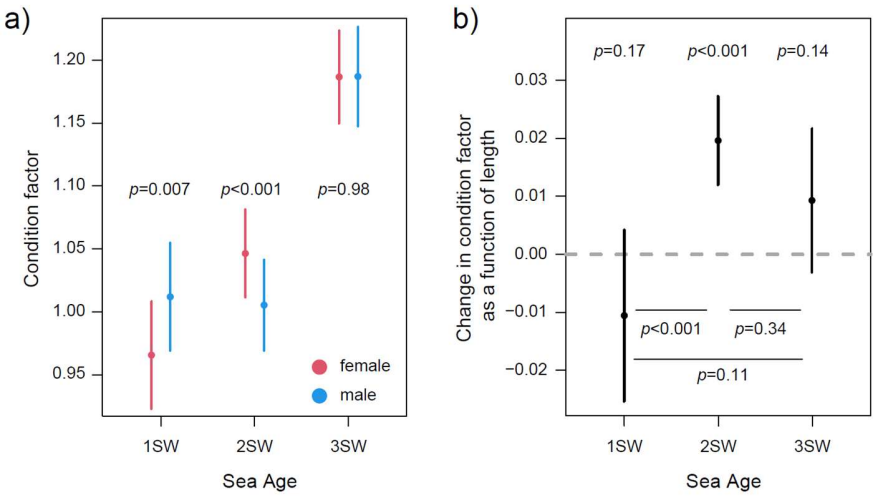

Fig. 3. Marginal effects of sex (a) and length (b) on condition factor in Atlantic salmon sub-adults in the marine environment. Dashed line in b indicates a zero slope, no relation between (age standardized) length of salmon and condition factor. Error bars indicate 95% confidence intervals.

3.4. Taxon specificity of crustacean diet effect

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, Table S1). When the number of diet specific to these taxa was separately parameterized in the model, instead of crustaceans as a whole, hyperiid amphipods, but not krill numbers, explained the ontogenetic diet effect on the condition factor (Fig. 4, Table S4), suggesting that the overall pattern was driven by hyperiid

amphipods acquisition. As such, a model that contained hyperiid amphipods explained the data substantially better than the original model that had parameterized crustaceans as a whole (ΔAICc = 2.53, Table S4). Concordantly, the age-dependent slope of the association between the number of hyperiid amphipods in the diet and condition factor was strongly significant (for hyperiid amphipods diet by sea age interaction: t_{1583} = -3.621, p < 0.001). The condition factor of 1SW was significantly higher when the diet contained more hyperiid amphipods (t_{1583} = 2.146, p = 0.032), but the relation was directly opposite direction in 2SW (t_{1583} = -2.112, p = 0.035) and 3SW age groups (t_{1583} = -3.941, p < 0.001, Fig. 4a). A parallel analysis for the fish diet was not performed because the number of diet items was prohibitively small when the fish diet data were partitioned into smaller taxonomic groups.

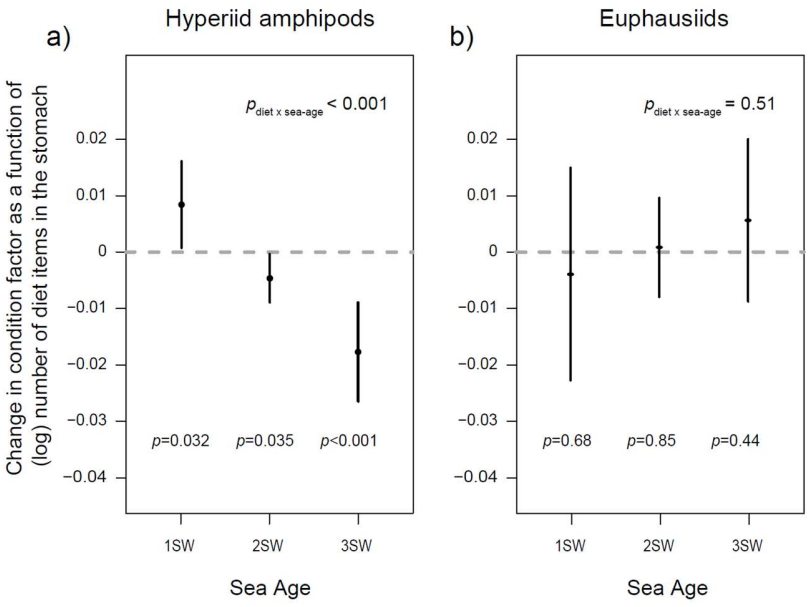

Fig. 4. Marginal effects of the number Hyperiid amphipods (a) and Euphausiids (b) prey items (log scale) on condition factor in Atlantic salmon sub-adults in the marine environment. Dashed line indicates a zero slope, no relation between the number of diet items and condition factor. Error bars indicate 95% confidence intervals.

295 *3.5. Contribution of diet weight vs. number of diet items on condition factor*

296 The relationship between the condition factor and number of prey items might be driven by different
297 ecological processes associated with foraging, such as foraging frequency or foraging efficiency
298 (Aykanat et al. 2024). We assessed the contribution of these two processes after restructuring the
299 response variable into two parts, first to quantify foraging frequency (approximated with a Boolean diet
300 presence and absence), and second to quantify foraging efficiency (i.e. approximated with log-
301 transformed number of diet items, when diet was present in the stomach), and by repeating the analysis
302 above. The effects of diet on the condition factor were qualitatively similar to each other and to the
303 original models for both crustaceans and dish diets (Fig. S7), ruling out the sole contribution of any of
304 the two processes.

305 When the total diet weight was parameterized in the model, instead of the number of prey items
306 acquired, it did not explain ontogenetic effects in the diet (Fig. S6), suggesting that number of diet
307 items but not weight were the primary factor associated with the ontogenetic effect.

308 4. DISCUSSION

309 We demonstrated that resource acquisition predicts ontogenetic performance trade-offs via its effect on
310 condition factor. Competitive resource allocation has been the major mechanism suggested to mediate
311 life history trade-offs within species but lacks evidence in natural systems (Flatt & Heyland 2011,
312 Haave-Audet et al. 2022, Chang et al. 2024). The theoretical premise of resource acquisition in shaping
313 life history trade-offs dynamics has been acknowledged directly (Flatt & Heyland 2011), or indirectly
314 across different approaches, as a potential outcome through the effect of signaling networks (Stearns
315 2011) or via the effect of changing environmental plasticity to couple-decouple the correlations
316 between life history traits. However, the empirical studies involve only 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 the numbers of different prey species in the diet and condition factor, a strong predictor of the liability trait of age-at-maturity. Therefore, we suggest that Atlantic salmon life history dynamics may be shaped by resource acquisition dynamics in the wild via the availability and composition of different prey species.

Among crustacean taxa, hyperiid amphipods (mostly *Themisto* spp.), but not euphausiids (krill), were associated with an age-dependent decrease in condition factor. Hyperiid amphipods are much more abundant prey type 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 (Table S1). Optimal foraging theory predicts that organisms select prey that maximize net energy gain (Pyke et al. 1977). It is plausible that acquiring hyperiid amphipods becomes increasingly energetically expensive as salmon get older and larger, perhaps due to size dependent changes in morphology and swimming ability (Sanchez-Hernandez et al. 2019). In contrast, the influence of fish diet on the condition factor increases with sea age. Consuming fish increases the condition factor only in older sea age groups, suggesting that some energetic constraints associated with smaller fish size exist, which may be associated with gape size (Keeley & Grant 1997, Scharf et al. 2000), or size dependent attributes that makes younger fish to foraging for fish less efficient (Webb et al. 1984, Sanchez-Hernandez et al. 2019, see also below). Taken together, foraging predominantly on hyperiid amphipods at younger ages and shifting to foraging fish prey at older ages may signify an age-dependent optimal foraging strategy for Atlantic salmon, at least in the environmental settings that the sampling have taken place.

Combined with the fact that winter condition factor at sea is a strong predictor of maturation timing in the following season (Herbinger 1987, Herbinger & Friars 1991), our results may have significant implication for understanding the maturation dynamics of Atlantic salmon. For example, we predict

that a younger age structure at maturity will be associated with relatively higher crustacean abundances (mainly hyperiid amphipods). Likewise, relatively higher fish prey abundances might negatively affect condition factor at younger age groups, leading to delayed maturation and older age structure at maturity. Vollset et al. (2022) suggested that broad-scale changes in oceanic conditions led to an ecological regime shift that subsequently affected the age at maturity. In their 28-year time series data, the decrease in planktonic biomass was highly correlated to an increase in the proportion of older sea age groups (Vollset et al. 2022), which corroborates our prediction. In their study, there was a strong covariation across several abiotic and biotic factors during the regime shift, making it challenging to break down the drivers of this change further. Our study linked individual-based diet patterns to condition factor across a heterogeneous spatial distribution of Atlantic salmon and its prey, and within a narrow temporal window, thus providing an assessment that is independent from the effect of temporally covarying factors, such as temperature. As such, we can suggest, among other factors outlined in Vollset et al. (2022), that decreased crustacean abundances are likely the driver of observed older age structure.

While the ontogenetic diet shift towards a more piscivorous diet has been demonstrated in this system earlier (Jacobsen & Hansen 2001), its effect on condition factor was not known until this study. Based on our results, one can suggest that the net benefit of a crustaceans oriented diet is diminishing with age, while a fish-based diet becomes more rewarding. Since the ontogenetic relationship is driven by prey numbers, but not mass (Fig. S6), we can postulate that the age-dependent diet benefits are caused not by post-acquisition processes, such as differences in prey energy content or potential differences in nutrient stoichiometry between diet types, but by differences in energy use prior to or during prey acquisition. The result that this relationship is mostly driven by the smaller (and more numerous) hyperiid amphipods (Fig. 4) further supports this notion. Therefore, our results are consistent with a

363 scenario that foraging for smaller crustaceans becomes increasingly energetically unsustainable for
364 larger salmon. Similarly, we suggest that foraging for fish is only energetically advantageous for larger
365 salmon, which may be due to size-dependent changes in morphology or behavior (Smith & Skúlason
366 1996). For example, gape size may restrict smaller salmon from capturing larger fish (Keeley & Grant
367 1997, Scharf et al. 2000), or they may not sustain cruising speeds that are required for foraging for fish
368 prey as efficiently as larger salmon (Webb et al. 1984, Sanchez-Hernandez et al. 2019).

369 The ontogenetic effect of diet on condition was not solely explained by age-dependent changes in
370 foraging strategy, as demonstrated by similar effects between when diet was parameterized as
371 presence/absence (as an indication of frequency of active foraging), or total prey numbers in the diet
372 (when diet items were non-zero, and indication of foraging outcome). This suggests that ontogenetic
373 effects are independent of the foraging strategy. Interestingly, Aykanat et al. (2024) suggested that the
374 *vgll3* locus, a major locus influencing age at maturity, was associated with age-dependent differences in
375 crustaceans foraging frequency, but not foraging outcome. Fish with *vgll3* early maturing genotype
376 appeared to gain similar amounts of food with less foraging activity, suggesting that an increase in
377 acquisition efficiency may be one of the factors that allow salmon with the *vgll3* early genotype to
378 mature earlier, that is, by allocating surplus resources towards reproductive investment (Aykanat et al.
379 2024). However, they did not find any evidence of an age-dependent association between condition
380 factor and *vgll3* genetic variation. These results suggest that the association between diet and condition
381 factor in the present study likely has an independent physiological pathway than how *vgll3* locus
382 effects diet.

383 Similar to diet, our results show that sex has an ontogenetic effect on condition factor, in which 1SW
384 salmon males have a higher condition factor, whereas this pattern reversed for 2SW age group (Fig.
385 2b). In Atlantic salmon, males mature more often as 1SW, and females more often delay maturation to

386 achieve a larger body size since size is a stronger determinant of reproduction success in females via its
387 effect on fecundity (Fleming & Einum 2010). Similarly, energy expenditure during spawning is higher
388 among younger males than females but increases more by size in females than in males (Jonsson &
389 Jonsson 2003, Persson & De Roos 2006). The reversal in sex-specific differences in condition factor
390 between 1SW and 2SW age groups (Fig. 4) is consistent with the indicated maturation trends above,
391 providing that condition factor predicts maturation via its effect on the lipid conetnt. This result is also
392 consistent with the proposed sex-specific variation in the liability distribution of of age at maturity,
393 which explains the emergence of sex-specific dominance reversal (Reid 2022), an adaptation to offset
394 sex differences in optimal age at maturity in Atlantic salmon (Jonsson & Jonsson 2003, Fleming &
395 Einum 2010, Barson et al. 2015).

396 Linking stomach content to general resource acquisition patterns has sometimes been criticized because
397 it is only a snapshot of the diet, a measure of a very recent feeding activity, as opposed to methods such
398 as stable isotopes that can assess long-term trends (e.g., Power et al. 2023). While integration of
399 multiple approaches (that includes analysis of stomach content, and stable isotope and fatty acid
400 profiling) may help to better understand complex trophic relationships (Nielsen et al. 2017), a careful
401 formulation of hypotheses and statistical methods could avoid limitations associated with sole use of
402 stomach content data (Nielsen et al. 2017, Amundsen & Sánchez-Hernández 2019). As such, our
403 results remarkably explain an ontogenetic diet shift in the species (Klemetsen et al. 2003), and provide
404 a well-supported and predictable relationship with condition factor, a body index that should not be
405 affected by only very recent feed intake. Hence, our results confirmed that stomach content analysis
406 reflects general feeding patterns.

407 The sampling site for this study was one of the major marine feeding grounds for European salmon
408 populations, especially for older, 2SW and 3SW sea age groups (Jacobsen & Hansen 2001, O'Sullivan

et al. 2022). However, many salmon populations from geographically distant localities, such as North America and the Baltic Sea, utilize other marine feeding areas, and salmon of the youngest sea age groups (1SW) may inhabit marine feeding areas that are closer to their native rivers (Rikardsen & Dempson 2010, Gilbey et al. 2021, Rikardsen et al. 2021). Subsequently, prey compositions may be substantially different in those habitats which potentially different factors effecting feeding and maturation dynamics. Therefore, the age-dependent diet performance relation that we observed here, and its potential effect on maturation may not readily be generalized across species range.

Data collected in the wild has high dimensionality. Our model contains several parameters that could otherwise be controlled under common garden conditions. While important, testing all possible interactions between covariates (which may covary with focal covariates) is not feasible owing to the number of possible combinations, and unobserved variables are also likely important for diet variation. Nonetheless, our model appears robust to the exclusion of observed variables from the model (see Results). Furthermore, despite a strong statistical support, and multiple lines of indirect evidence supporting the main conclusion, such as observing an ontogenetic diet shift that is common in salmonids (Klemetsen et al. 2003) and functional morphological variation associated with size and diet type, the age-dependent diet effect on condition factor is based on correlation of observational data. Ideally, controlled experiments are required to confirm the causality, but this may be unfeasible for this case, given impracticalities, at the very least, associated with rearing salmon long periods and using forage species as food sources.

5. CONCLUSIONS

In this study, we provide a clear case of an ontogenetic performance trade-off associated with diet in a 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 previously (Jonsson & Jonsson 2004, Todd et al. 2008, Friedland et al. 2009, Vollset et al. 2022). However, covariation between critical biotic and abiotic physiological factors (such as temperature and forage composition and abundances) in longitudinal data is insufficient to identify primary factors driving these patterns (Friedland et al. 2009). Our results contribute to the knowledge by providing a spatial analysis in which the effect of forage species (diet) on performance (condition factor) could be factored out from covarying factors that intrinsically exist in longitudinal data structures. Our results indicate bottom-up trophic dynamics as likely underlying factor that links large-scale ecological regime shifts to changes in maturation patterns (Vollset et al. 2022). Our study also highlights the importance of exploiting and repurposing old but gold datasets to address novel ecological questions.

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453 LITERATURE CITED

454 Amundsen PA, Sanchez-Hernandez J (2019) Feeding studies take guts - critical review and
455 recommendations of methods for stomach contents analysis in fish. Journal of Fish Biology
456 95(6) 1364-1373

457 Aykanat T, Jacobsen JA, Hindar K (2024) Ontogenetic variation in the marine foraging of Atlantic
458 salmon functionally links genomic diversity with a major life history polymorphism. Molecular
459 Ecology e17465

460 Barson NJ, Aykanat T, Hindar K, Baranski M and others (2015). Sex-dependent dominance at a single
461 locus maintains variation in age at maturity in salmon. Nature 528 405-408

462 Bartoń K (2024) MuMIn: Multi-Model Inference. R package version 1.48.4, https://CRAN.R-
463 project.org/package=MuMIn.

464 Braendle C, Heyland A, Flatt T (2011) Integrating mechanistic and evolutionary analysis of life history
465 variation. In: Mechanisms of Life History Evolution: The Genetics and Physiology of Life
466 History Traits and Trade-Offs (eds. Flatt T, Heyland A). Oxford University Press

467 Brooks ME, Kristensen K, van Benthem KJ, Magnusson A and others (2017) glmmTMB Balances
468 Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling.
469 R Journal, 9, 378-400

470 Chang CC, Moiron M, Sanchez-Tojar A, Niemela PT, Laskowski KL (2024) What is the meta-analytic
471 evidence for life-history trade-offs at the genetic level? Ecology Letters 27 e14354

472 Czorlich Y, Aykanat T, Erkinaro J, Orell P, Primmer CR (2022) Rapid evolution in salmon life history
473 induced by direct and indirect effects of fishing. Science 376 420-423

474 Debes PV, Piavchenko N, Ruokolainen A, Ovaskainen O and others (2021) Polygenic and major-locus
475 contributions to sexual maturation timing in Atlantic salmon. Molecular Ecology 30 4505-4519

Duston J, Saunders RL (1999) Effect of winter food deprivation on growth and sexual maturity of Atlantic salmon (*Salmo salar*) in seawater. Canadian Journal of Fisheries and Aquatic Sciences 56 201-207

Ernande B, Boudry P, Clobert J, Haure J (2004) Plasticity in resource allocation based life history traits in the Pacific oyster, *Crassostrea gigas*. I. Spatial variation in food abundance. Journal of Evolutionary Biology 17 342-356

Ferry-Graham LA, Bolnick DI, Wainwright PC (2002) Using functional morphology to examine the ecology and evolution of specialization. Integrative and Comparative Biology 42 265-277

Flatt T, Heyland A (2011) Mechanisms of life history evolution : the genetics and physiology of life history traits and trade-offs. Oxford University Press, Oxford; New York

Flatt T, Heyland A, Stearns SC (2011) What mechanistic insights can or cannot contribute to life history evolution: An exchange between Stearns, Heyland, and Flatt. In: Mechanisms of Life History Evolution: The Genetics and Physiology of Life History Traits and Trade-Offs (eds. Flatt T, Heyland A). Oxford University Press

Fleming IA, Einum S (2010) Reproductive Ecology: A Tale of Two Sexes. In: Atlantic Salmon Ecology (eds. Aas Ø, Einum S, Klemetsen A, Skurdal J). Wiley-Blackwell pp 33-65

Friedland KD, Chaput G, MacLean JC (2005) The emerging role of climate in post-smolt growth of Atlantic salmon. ICES Journal of Marine Science 62 1338-1349

Friedland KD, MacLean JC, Hansen LP, Peyronnet AJ and others (2009) The recruitment of Atlantic salmon in Europe. ICES Journal of Marine Science 66 289-304

Gilbey J, Utne KR, Wennevik V, Beck AC and others (2021) The early marine distribution of Atlantic salmon in the North-east Atlantic: A genetically informed stock-specific synthesis. Fish and Fisheries 22 1274-1306.

Haave-Audet E, Besson AA, Nakagawa S, Matho, KJ (2022) Differences in resource acquisition, not allocation, mediate the relationship between behaviour and fitness: a systematic review and meta-analysis. Biological Reviews of the Cambridge Philosophical Society 97 708-731

Hartig F (2022) DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.4.6

Herbinger CM (1987) A study of Atlantic salmon (*Salmo salar*) maturation using individually identified fish. Dalhousie University Halifax, Canada

Herbinger CM, Friars GW (1991) Correlation between condition factor and total lipid content in Atlantic salmon, *Salmo salar* L., parr. Aquaculture Research 22 527-529

Houle D (1991) Genetic covariance of fitness correlates - what genetic correlations are made of and why it matters. Evolution 45 630-648

Jacobsen JA, Hansen LP (2001) Feeding habits of wild and escaped farmed Atlantic salmon, *Salmo salar* L., in the Northeast Atlantic. ICES Journal of Marine Science 58 916-93

Jacobsen JA, Lund RA, Hansen LP, O'Maoileidigh N (2001) Seasonal differences in the origin of Atlantic salmon (*Salmo salar* L.*)* in the Norwegian Sea based on estimates from age structures and tag recaptures. Fisheries Research 52:169-177

Jonsson B, Jonsson N, Finstad AG (2013) Effects of temperature and food quality on age and size at maturity in ectotherms: an experimental test with Atlantic salmon. Journal of Animal Ecology 82(1) 201-210

Jonsson N, Jonsson B, Hansen LP (1997) Changes in proximate composition and estimates of energetic costs during upstream migration and spawning in Atlantic salmon *Salmo salar*. Journal of Animal Ecology 66(3) 425-436

Jonsson B, Finstad AG, Jonsson N, Bradford M (2012) Winter temperature and food quality affect age at maturity: an experimental test with Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 69 1817-1826

Jonsson B, Jonsson N (2011) Ecology of Atlantic salmon and brown trout: habitat as a template for life histories. Springer, Dordrecht

Jonsson N, Jonsson B (2003) Energy allocation among developmental stages, age groups, and types of Atlantic salmon (*Salmo salar*) spawners. Canadian Journal of Fisheries and Aquatic Sciences 60 506-516

Jonsson N, Jonsson B (2004) Size and age of maturity of Atlantic salmon correlate with the North Atlantic Oscillation Index (NAOI). Journal of Fish Biology 64 241-247

Keeley ER, Grant JWA (1997) Allometry of diet selectivity in juvenile Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 54 1894-1902

Klemetsen A, Amundsen P-A, Dempson JB, Jonsson B, Jonsson N, O'Connell MF, Mortensen E (2003) Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. Ecology of Freshwater Fish 12 1–59

Lailvaux SP, Hathway J, Pomfret J, Knell RJ (2005) Horn size predicts physical performance in the beetle *Euoniticellus intermedius* (Coleoptera: Scarabaeidae). Functional Ecology 19:632-639

Lenth R (2023) emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.8.5

Leroi AM (2001) Molecular signals versus the Loi de Balancement. Trends in Ecology and Evolution 16 24-29

Messina FJ, Fry JD (2003) Environment-dependent reversal of a life history trade-off in the seed beetle *Callosobruchus maculatus*. Journal of Evolutionary Biology 16 501-509

Mittelbach GG, Persson L (1998) The ontogeny of piscivory and its ecological consequences. Canadian Journal of Fisheries and Aquatic Sciences 55 1454-1465

Mobley KB, Aykanat T, Czorlich Y, House A and others (2021) Maturation in Atlantic salmon (*Salmo salar*, Salmonidae): a synthesis of ecological, genetic, and molecular processes. Reviews in Fish Biology and Fisheries 31 523-571

Nielsen, JM Clare EL, Hayden B, Brett MT, Kratina P, Gilbert MTP (2018) Diet tracing in ecology: Method comparison and selection. Methods in Ecology and Evolution 9(2) 278-291

Nowicki RC, Borgå K, Gabrielsen GW, Varpe Ø (2023) Energy content of krill and amphipods in the Barents Sea from summer to winter: variation across species and size. Polar Biology 46 139-150

O'Sullivan RJ, Ozerov M, Bolstad GH, Gilbey J and others (2022) Genetic stock identification reveals greater use of an oceanic feeding ground around the Faroe Islands by multi-sea winter Atlantic salmon, with variation in use across reporting groups. ICES Journal of Marine Science 79 2442-2452

Pedersen J, Hislop JRG (2005) Seasonal variations in the energy density of fishes in the North Sea. Journal of Fish Biology 59 380-389

Peterson RH, Harmon PR (2005) Changes in condition factor and gonadosomatic index in maturing and non-maturing Atlantic salmon (*Salmo salar* L.) in Bay of Fundy sea cages, and the effectiveness of photoperiod manipulation in reducing early maturation. Aquaculture Research 36(9): 882-889

Persson L, De Roos AM (2006) Food-dependent individual growth and population dynamics in fishes. Journal of Fish Biology, 69, 1-20.

Power M, Thorstad EB, Forseth T, Fiske P (2023) Temporal shifts in the marine feeding of individual Atlantic salmon inferred from scale isotope ratios. Ecology and Evolution 13 e10656

Pyke GH, Pulliam HR, Charnov EL (1977) Optimal foraging: a selective review of theory and tests. The Quarterly Review of Biology 52:137-154

R Core Team (2019) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Reid JM (2022) Intrinsic emergence and modulation of sex-specific dominance reversals in threshold traits. Evolution 76 1924-1941

Reznick D, Nunney L, Tessier A (2000) Big houses, big cars, superfleas and the costs of reproduction. Trends in Ecology and Evolution 15 421-425

Ricker WE (1975) Computation and inter pretation of biological statistics of fish populations. Bulletin of the Fisheries Research Board of Canada 191:1-382

Rikardsen AH, Dempson JB (2010) Dietary Life-Support: The Food and Feeding of Atlantic Salmon at Sea. In: Atlantic Salmon Ecology (eds. Aas Ø, Einum S, Klemetsen A, Skurdal J). Wiley-Blackwell pp 115-143

Rikardsen AH, Righton D, Strom JF, Thorstad EB and others (2021) Redefining the oceanic distribution of Atlantic salmon. Scientific Reports 11 12266

Roff DA (2002) Life history evolution. Sinauer Associates, Sunderland, Mass.

Rowe DK, Thorpe JE, Shanks AM (1991) Role of fat stores in the maturation of male Atlantic salmon (*Salmo salar*) parr. Canadian Journal of Fisheries and Aquatic Sciences 48(3) 405-413

Sanchez-Hernandez J, Nunn AD, Adams CE, Amundsen PA (2019) Causes and consequences of ontogenetic dietary shifts: a global synthesis using fish models. Biological Reviews of the Cambridge Philosophical Society 94 539-554

Schaffer W (2003) Life histories, evolution, and salmonids. In: Evolution illuminated: Salmon and Their Relatives (eds. Hendry AP, Stearns SC). Oxford University Press pp 20-51

Scharf FS, Juanes F, Rountree RA (2000) Predator size-prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. Marine Ecology Progress Series 208 229-248

Sinclair-Waters M, Odegard J, Korsvoll SA, Moen T and others (2020) Beyond large-effect loci: large-scale GWAS reveals a mixed large-effect and polygenic architecture for age at maturity of Atlantic salmon. Genetics Selection Evolution 52 9

Smith TB, Skúlason S (1996) Evolutionary Significance of Resource Polymorphisms in Fishes, Amphibians, and Birds. Annual Review of Ecology and Systematics 27 111-133

Snell-Rood E, Cothran R, Espeset A, Jeyasingh P, Hobbie S, Morehouse NI (2015) Life-history evolution in the anthropocene: effects of increasing nutrients on traits and trade-offs. Evolutionary Applications 8 635-649

Stearns SC (1989) Trade-Offs in Life-History Evolution. Functional Ecology, 3.

Stearns SC (2000) Life history evolution: successes, limitations, and prospects. Naturwissenschaften 87 476-486

Stearns SC (2011) Does impressive progress on understanding mechanisms advance life history theory? In: Mechanisms of Life History Evolution: The Genetics and Physiology of Life History Traits and Trade-Offs (eds. Flatt, T, Heyland, A). Oxford University Press.

Stevenson RD, Woods WA Jr (2006) Condition indices for conservation: new uses for evolving tools. Integrative and Comparative Biology 46(6) 1169-1190

Thorpe JE, Mangel M, Metcalfe NB, Huntingford FA (1998) Modelling the proximate basis of salmonid life-history variation, with application to Atlantic salmon, *Salmo salar* L. Evolutionary Ecology 12 581-599

613 Todd CD, Hughes SL, Marshall CT, MacLean JC, Lonergan ME, Biuw EM (2008) Detrimental effects
614 of recent ocean surface warming on growth condition of Atlantic salmon. Global Change
615 Biology 14 958-970
616 Van Noordwijk AJ, de Jong G (1986) Acquisition and allocation of resources - their influence on
617 variation in life-history tactics. American Naturalist 128 137-142
618 Villéger S, Brosse S, Mouchet M, Mouillot D, Vanni MJ (2017) Functional ecology of fish: current
619 approaches and future challenges. Aquatic Sciences 79 783-801
620 Vollset KW, Urdal K, Utne K, Thorstad EB and others (2022) Ecological regime shift in the Northeast
621 Atlantic Ocean revealed from the unprecedented reduction in marine growth of Atlantic salmon.
622 Science Advances 8 eabk2542
623 Youngson AF, McLay HA (1985) Changes in steroid hormone levels in blood serum as an early
624 predictor of approaching maturity in Atlantic salmon. ICES Journal of Marine Science 69(1-2)
625 145-157
626 Webb PW, Kostecki PT, Stevens ED (1984) The Effect of Size and Swimming Speed on Locomotor
627 Kinematics of Rainbow Trout. Journal of Experimental Biology 109 77-95

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Table 1: Parsimony of models with different parametrizations. Null model is the most parsimonious structure containing non-focal terms, and this structure included in hypothesis-specific models. LL indicates log likelihood of the model.

Model type	Hypothesis	Model structure	LL	df	AICc	dAICc
Null	No diet effect on condition factor. Other non-focal variables explains the diet variation.	Fishing period + season + $SeaAge_{factorial}$ x $Length_{age.std}$ + $Length_{age.std}$ x Sex + $SeaAge_{factorial}$ x Sex + $\varepsilon_{regional.group}$ + $\varepsilon_{location}$ + ε_{error}	1210.16	15	-2390.01	14.4
No sea age effect on diet	Both crustaceans and fish diet effects condition factor age independently.	Null model parameters + $Diet_{crus}$ + $Diet_{fish}$	1210.92	16	-2389.49	14.96
	Crustaceans diet effects condition factor age independently.	Null model parameters + $Diet_{crus}$	1213.76	16	-2395.17	9.28
	Fish diet effects condition factor age independently.	Null model parameters + $Diet_{fish}$	1215.17	17	-2395.95	8.50
Diet effect on condition factor changes non-linearly with sea age (categorical parametrization)	Crustaceans diet effects condition factor age dependently. Fish diet affects condition factor age independently.	Null model parameters + $SeaAge_{factorial}$ x $Diet_{crus}$ + $Diet_{fish}$	1219.30	19	-2400.12	4.33
	Fish diet affects condition factor age dependently. Crustaceans diet affects condition factor age independently.	Null model parameters + $SeaAge_{factorial}$ x $Diet_{fish}$ + $Diet_{crus}$	1216.34	19	-2394.2	10.25
	Both crustaceans and fish diet effects condition factor age dependently.	Null model parameters + $SeaAge_{factorial}$ x ($Diet_{crus}$ + $Diet_{fish}$)	1221.51	21	-2400.44	4.01
Diet effect on condition factor changes linearly with of sea age (continuous parametrization)	Crustaceans diet effects condition factor age dependently. Fish diet affects condition factor.	Null model parameters + $SeaAge_{continious}$ x $Diet_{crus}$ + $Diet_{fish}$	1219.29	18	-2402.14	2.31
	Fish diet effects condition factor age dependently. Crustaceans diet affects condition factor age independently.	Null model parameters + $SeaAge_{continious}$ x $Diet_{fish}$ + $Diet_{crus}$	1216.34	18	-2396.24	8.21
	Both crustaceans and fish diet effects condition factor age dependently.	Null model parameters + $SeaAge_{continious}$ x ($Diet_{crus}$ + $Diet_{fish}$)	1221.46	19	-2404.45	0