1   Diet drives performance trade-offs along the ontogeny in the Atlantic salmon

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13   Abstract

Understanding the ecological basis of life-history trade-offs is fundamental for predictive ecology. Contrary to
the theory, the documentation of trade-offs between life-history traits 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 organisms. By quantifying the diet composition of wild Atlantic salmon
sampled from marine feeding grounds in the Northeast Atlantic Ocean, we showed that diet composition
(crustaceans *versus* fish) has an age-dependent effect on condition factor, a major determinant of maturation
in Atlantic salmon. Younger salmon have 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 suggest the presence of
age-dependent performance-diet trade-offs in wild Atlantic salmon, which may help explain the
spatiotemporal maturation dynamics and predict the age structure of wild populations.

Introduction

Variation in resource acquisition and allocation are central determinants of life-history divergence and evolution. For many years, an important focus of evolutionary biology has been to establish the underlying mechanisms of life-history trade-offs between fitness traits such as growth, maturation, and reproduction on the one hand and survival on the other (Stearns 1989). Although this may hold true for certain conditions with energy limitations or other physiological constrains, the expectation of negative phenotypic (or genetic) correlations between survival and other fitness traits has been difficult to demonstrate in natural populations (Haave-Audet *et al.* 2022; Chang *et al.* 2024). Essentially, such trade-off models do not account for variation in resource acquisition, the inclusion of which to the models not only explains a positive phenotypic (or genetic) correlation between fitness components (Van Noordwijk & Dejong 1986; Houle 1991) but also provides a realistic framework for assessing the life-history trade-offs. 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).

In the marine environment, Atlantic salmon (*Salmo salar*) achieve high growth rates and accumulate fat reserves to support energetically expensive maturation and reproductive activities (Jonsson & Jonsson 2011). As such, variation in resource acquisition between individuals may have a central role in shaping sea age at maturity variation, a major life-history trait in Atlantic salmon. The maintenance of variation in age at maturity 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). The proportion of early- and late-maturing salmon within a population may also be regulated by environmental factors (Jonsson & Jonsson 2004; Jonsson *et al.* 2012). Sea age at maturity in Atlantic salmon is a threshold trait (Thorpe *et al.* 1998) with a strong genetic component (Barson *et al.* 2015; Sinclair-Waters *et al.* 2020), environmental factors also play a central role in shaping the diversity of the trait. For example, a higher condition factor (weight-by-length relationship) is considered a liability trait and a major determinant of maturation (Herbinger 1987; Thorpe *et al.* 1998; Duston & Saunders 1999; Jonsson & Jonsson 2011; Debes *et al.* 2021), which further points out resource acquisition as an important ecological process shaping 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 ages 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 (Mittelbach & Persson 1998;

Ferry-Graham *et al.* 2002; Sanchez-Hernandez *et al.* 2019). Atlantic salmon are primarily considered

opportunistic feeders (Rikardsen & Dempson 2010). 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).

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.

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, studies that quantify inter-individual

variation in ontogenetic diet dynamics are relatively scarce (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 the 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 mature, 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 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 on how

resource acquisition mediates the trade-offs (Haave-Audet *et al.* 2022; Chang *et al.* 2024). 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).

Based on the predictions above, 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

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 hypothesize that salmon at younger ages have a higher condition factor if

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 are

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. However, virtually all 3SW fish mature in the following summer, as

maturation after that sea age is very rare in salmon populations.

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

$Y = \mu +$ Season $+$ fishing period $+$ Reporting Group $+$ Sea Age$_{categorical}$ x (Sex $+$ Length$_{residual}$) $+$Sea Age$_{continuous}$ x

(Diet$_{crus}$ $+$ Diet$_{fish}$) $+ \varepsilon_{location} + \varepsilon_{error}$

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 it was modelled 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). Length$_{residual}$ was scaled to have a

mean of zero and a standard deviation of one to improve convergence. Spatial variation in sampling effort was

accounted for by including sampling location as a random effect (N=55). The condition was quantified as

Fulton's condition factor K, ($K=10^5\,w\,/\,l^3$), in which w is gutted weight in kilograms divided by 0.9, to account for

gut weight, and l is fork length in cm (Supplementary Figure 1). The condition factor is based on the weight

obtained from gutted fish; therefore, it reflects the condition factor associated with muscle weight, with no

direct effect of visceral or gonadal tissues on variation. In immature Atlantic salmon parr, it has been shown

that there is a strong and significant positive correlation between condition factor and total lipid content

(Herbinger & Friars 1991).

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

Diet number was primarily parameterized either as log-normalized weight or log-normalized number of items

in the stomach. Both crustacean and fish diets have highly left-skewed distributions with many zero entries

(i.e., empty stomach, Supplementary Figure 2). To avoid undefined zero values after log transformation, we

added 1 to the number of diet variables, and we added the minimum observed weight in the dataset to the

weight of diet variables.

The number and total weight of the diet items in the stomach were highly correlated (Supplementary Figure 3);

thus, any effect due to the number of diet items could equally be attributed to diet weight. To assess whether

the number or total mass of the diet explains 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.

Next, we evaluated whether any taxonomic groups within crustaceans drive the relationship between

crustaceans and diet by partitioning crustaceans into lower-order taxonomic groups, providing that the

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 (Supplementary Table 1) and are substantially
different in size, with the latter being larger than the former (Supplementary Table 1). We did not implement
the same approach in fishes which had restrictively small number of prey items per species (Supplementary
Table 1).

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 is coded with 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), again, 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, Supplementary Figure 4). 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, Supplementary Figure 4). 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). The number
and total weight of the diet items in the stomach were highly correlated (Supplementary Figure 3); thus, any
effect due to the number of diet items could equally be attributed to diet weight. However, 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 (Supplementary Figure 5), suggesting that numbers were the primary factor
associated with the ontogenetic effect.

Figure 3: Marginal effect of crustacean (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.

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.

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 classes (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, Supplementary Table 2). 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, Supplementary Table 2).

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, Supplementary Table 1). 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), while 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 parallel analysis for the fish diet because the numbers became prohibitively small when the fish diet

data were partitioned into smallar taxonomic groups.

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. As such, 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 (Supplementary Figure 6),

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 the condition factor

was qualitatively similar in all the three models (data not shown).

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.

Discussion

We demonstrated that resource acquisition drives ontogenetic performance trade-off and is likely an
important factor shaping life-history divergence, that is, via its effect on age at maturity. 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 smaller than krill or other crustaceans taxa observed
in the diet (Supplementary Table 1). 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 sizes exist. Taken together, our
study demonstrates an age-dependent optimal foraging strategy for Atlantic salmon, which might have a
significant impact on maturation rates.

Our results have implications for understanding the dynamics of salmon age structure at sea. In light of our
results, 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 maturation timing. They further demonstrated a temporal correlation between an
increase in the proportion of older sea age groups and a number of abiotic and biotic factors, such as a
decrease in planktonic biomass, an increase in sea surface temperature (SST), decrease in Arctic water flux, and
decrease in fish (mackerel) length. Our study linked individual-based diet patterns to condition factors 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 the 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 substantially high (Pedersen & Hislop 2005; Nowicki *et al.* 2023).
This suggests that the energy cost in the acquisition processes prior to prey capture likely underlies
performance variation among different age groups in the wild setting. The result that this relationship is mostly
driven by the smaller (and more numerous) Hyperiid amphipods (Figure 5) further support this notion.
Therefore, we suggest that foraging for crustaceans, which are relatively small in size, 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 smaller salmon to capture larger fish species (Keeley & Grant 1997; Scharf *et al.*
2000), or they may not sustain cruising speeds foraging for fish prey as efficient as larger salmon (Webb *et al.*
1984; Sanchez-Hernandez *et al.* 2019).

However, the ontogenetic effect of diet on condition was not solely explained by foraging strategy, as
demonstrated by similar effects when diet was parameterized as presence/absence (i.e., as an indication of
frequency of active foraging) or total prey numbers in the diet (when diet items were non-zero, and indication
of foraging outcome). This suggests that ontogenetic effects are independent of foraging strategy.
Interestingly, (Aykanat *et al.* 2024) suggested that the *vgll3* locus, a major locus influencing age at maturity,
was associated with age-dependent differences in crustaceans foraging frequency, but not foraging outcome.
As such, fish with *vgll3* early maturing genotype appear to gain similar amounts of food with less foraging
activity, suggesting that an increase in acquisition efficiency may be one of the factors that allows salmon with
the *vgll3* early genotype to mature earlier, that is, by allocating surplus resources towards reproductive
investment. However, they did not find any evidence of an age-dependent association between condition

factor and *vgll3* genetic variation. These results suggest that the effect of diet on the condition factor in the

present study likely has an independent pathway than that of the *vgll3* locus. However, the condition factor

that we used here (and in (Aykanat *et al.* 2024)) is based on the gutted fish weight, which does not include

visceral fat when calculating the condition factor. Therefore, it is unclear whether diet and/or the *vgll3* locus

influence weight gain by increasing visceral fat and/or gut weight.

Similar to diet, our results show that sex has an ontogenetic effect on condition factor, with 1SW salmon males

tending to have a higher condition factor, whereas this pattern was reversed in 2SW (Figure 3b). This result is

consistent with the general maturation pattern of the species associated with sex-specific fitness differences,

whereby size is a stronger predictor of higher reproductive success in females (Fleming *et al.* 1996; Barson *et*

al. 2015). As such, males mature more often as 1SW than females, which tends to delay maturation to achieve

a larger body size. While the maturation threshold might have a sex-specific component (Reid 2022), our

results indicate that ontogenetic differences in condition factor might be a proximal mechanism explaining sex-

specific maturation differences, perhaps via differences in resources allocation for specific energy requirements

for future spawning (Jonsson & Jonsson 2003; Persson & De Roos 2006). The energy expenditure during

spawning is also higher among younger males than females, but increases more by size in females than in

males (Jonsson & Jonsson 2003). Likewise, repeat spawning (i.e., saving energy for a second spawning) is more

common in females than in males and more common in populations with a high average age at maturation

(Persson *et al.* 2023), indicating consistent sex- and age-specific energy requirements during spawning and

suggesting complex sex-specific maturation norms in Atlantic salmon.

Linking stomach content to general resource acquisition patterns has often been criticized because it reflects

only a snapshot of the diet (i.e., until it is assimilated), and other methods, such as quantifying stable isotopes,

have been suggested to be more robust when assessing long-term feeding habits (e.g. (Power *et al.* 2023)).

However, our results are remarkably consistent across ontogeny and provide a well-supported and predictable

relationship with the condition factor, a body index that should not be affected by only very recent feed intake.

Hence, our results confirmed that stomach content analysis accurately reflects general feeding patterns.

The sampling sites for this study are one of the major marine feeding grounds for the majority of European

salmon populations, especially for older sea age groups such as 2SW and 3SW salmon (Jacobsen & Hansen

2001; O'Sullivan *et al.* 2022). This region is a diverse habitat for both fish and crustacean prey (Jacobsen &

Hansen 2001), the dynamics of which may be important for salmon maturation (Vollset *et al.* 2022). On the

other hand, 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 dynamics of trophic cascades in the two regions (Czorlich *et*
al. 2022; Vollset *et al.* 2022). Therefore, it is important to quantify trophic dynamics in different marine regions
to better understand their effects on performance and subsequent maturation.

Despite immense field effort, the data collected in the wild has 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 covaries) 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. While climate-induced effects on Atlantic
salmon performance have been suggested previously (Jonsson & Jonsson 2004; Todd *et al.* 2008; Friedland *et*
al. 2009; Vollset *et al.* 2022), our results indicate that bottom-up trophic cascades are an important underlying
factor associated with such large-scale climate events. Our study provides a mechanistic basis to better predict
Atlantic salmon maturation dynamics and performance trajectories across large spatiotemporal scales. Our
study also highlights the importance of exploiting and refurbishing old but gold datasets to address novel
ecological questions.

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Data accessibility

329 The compiled datasets and R-codes used to reproduce the results are available at the Dryad repository
330 https://doi.org/XXX.

Author contributions

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

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