

# Environmental change unlinks a gene from its trait

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In Atlantic salmon (*Salmo salar*), sea age is a major life history trait governed by a sex-specific trade-off between reproductive success and survival. In this issue of *Molecular Ecology*, Besnier et al. (*Molecular Ecology*, 2023) found evidence to suggest that the disassociation between sea age and major effect loci, including the previously identified candidate genes *vgll3* and *six6*, may be related to the recently observed trend towards slower growth and later maturation. These results are of importance because they challenge the prevailing view that evolution moves in a slow shuffle, and they provide a pertinent example of how an optimal phenotype can change due to growth-driven plasticity and lead to contemporary molecular and phenotypic evolution.

## KEYWORDS

adaptation, climate change, contemporary evolution, fish, life history evolution, polygenic, trait architecture

Understanding the processes that generate differences in complex life history traits among individuals, populations, and species has been a central challenge to evolutionary biology since Darwin. However, overcoming this challenge has been complicated by the generally complex polygenic architecture that underlies most growth-related life history traits (Wellenreuther & Hansson, 2016). Consequently, progress to unravel the evolution of life history traits in the wild has been slow. 'Sea age' in Atlantic salmon, defined as the number of years spent in the ocean before reaching maturity and returning to the natal river to reproduce, marks a notable exemption to this rule. Unlike the majority of life history traits related to growth, sea age is not polygenic, but is better characterised by an oligogenic genetic architecture, containing a few large-effect loci and numerous smaller-effect loci. This makes sea-age an interesting trait to study. Indeed, theoretical research indicates that the genetic structure of these traits are best described as a dynamic system, where the number and effects of genes can change over time, responding to shifts in environmental conditions and allelic frequencies at other loci (Hansen, 2006). Sea age is also an exception because some of its major-effect loci have been exceptionally

well-studied and described, most notably the vestigial-like protein 3 (*vgll3*) gene on chromosome 25, and the sine oculis-related *homeobox* (*six6*) gene on chromosome 9 (Barson et al., 2015; Sinclair-Waters et al., 2020). Differences in sea age among individuals can vary by 1–5 years, and *vgll3* and *six6* have been recurrently linked to this variation in both wild and domesticated aquaculture populations, collectively explaining up to ~30%–50% of trait variation. This high variability in sea age is thought to have evolved to maximize evolutionary fitness in the greatly variable river and ocean environments that salmon experience. Consequently, variability in this important life history trait is thought to underpin enhanced population stability in the face of environmental stochasticity via the portfolio effect, a phenomenon where biological intraspecific diversity reduces population size fluctuations. In addition to these large-effect loci, many additional smaller-effect loci have been detected over the years, making this a truly oligogenic trait, and these smaller effect loci are thought to be important for fine-tuning the trait across heterogeneous environments.

Building on this rich foundation of knowledge, Besnier et al. (2023) set out to investigate the evolutionary potential

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of sea age using an exceptional dataset of 1500 salmon from the River Etne in western Norway. Importantly, these samples were collected across two time periods spanning 30 years and then genotyped at 50,000 SNPs, allowing the authors to glean insights into possible genetic changes over that time. Across the Northeast Atlantic, many salmon habitats have faced degradation of marine conditions over the last decades, and multiple studies have not only reported an associated decrease in survival, but also a decline in sea age (e.g. Long et al., 2023). Furthermore, recent work on salmon in the large Teno River in Finland has shown that the ongoing and intense fishing activity has resulted in human-induced selection toward earlier maturing salmon, a trend not observed in salmon from other parts of the North Atlantic (Czorlich et al., 2022). While it is not known if fisheries induced selection is also occurring in the Etne River, the results from the Teno River do suggest that fishing pressure can provide additional selective forces that pushes salmon to mature at a smaller size. Examining the salmon samples from the River Etne, the authors were able to identify three major-effect loci that govern variation in sea age, including the well-known large-effect loci *vgll3* and *six6*, and these three loci collectively explained 36%–50% of sea age variation in first sampling period between 1983 and 1984.

Traits that are regulated either partly or fully by large-effect loci, as it is the case for sea age, are predicted to be under balancing selection (Llaurens et al., 2017). Balancing selection can be caused by sexually antagonistic, spatially or temporally varying selection and this type of selection can maintain trait diversity by facilitating the persistence of multiple variants over time, as seen in cryptic colour morphs of walking sticks (*Timema cristinae*), or ecotypes of Atlantic cod (*Gadus morhua*). In salmon, balancing selection acts to resolve sexual antagonism, as males and females have different size-related fitness optima that govern sea age. On average, males reach maturity earlier and at a smaller size, while females mature later, and show a stronger correlation between body size and reproductive success compared with males. The dilemma is that the longer salmon stay at sea, the bigger they are prior to spawning which increases the number of offspring they will have. However, this also increases the risk that salmon will die *before* being able to reproduce at all. The elegant solution that has evolved to navigate this sexual conflict is sex-dependent dominance of different *vgll3* alleles: late-maturing *vgll3* alleles are favoured in females and early-maturing alleles are favoured in males (Barson et al., 2015). Investigating the River Etne samples collected during the first time period, the authors detected that both *vgll3* and *six6* displayed strong sex-specific epistasis, since the effect of *six6* on sea age was present only when males carried two copies of the late *vgll3* maturation allele. Unexpectedly, however, when examining the role of these major-effect loci in the second sampling period from 2013 to 2016, this association was partially unlinked. This partial disassociation between the trait and the combined influence of these loci occurred despite the allelic frequencies of *vgll3* remaining similar, and was paralleled by a decrease in genome-wide heritability for sea age.

Besnier et al. (2023) were able to exclude admixture of farmed salmon as the origin of the observed disconnection between gene(s) and sea age, and postulated that the unlinking was driven by growth-related plasticity. They proposed a scenario whereby the role of *vgll3* in salmon experiencing either unlimited food supply (e.g. aquaculture scenario) or limited food supply (caused by environmental degradation) is bypassed by environmental conditions. Once bypassed, sea age under this scenario is then determined by a combination of additional genetic and environmental factors. This two-threshold model is in line with the finding that despite the temporal unlinking, the difference in sea age between the sexes was upheld in populations even with the loss of effect from the candidate loci. Together these findings strongly support the idea that additional causative mechanisms modulate sea age, and that these can also contribute to resolving sexual conflict under certain circumstances.

This research untangles recent genetic changes in sea age in one population of wild Atlantic salmon—and demonstrates how anthropogenic impacts can alter the genetic architecture of major traits. The work also supports the view that sea age has a labile genetic architecture and that this facilitates the rapid evolutionary response to environmental challenges. This notion has also received support from another study on Atlantic salmon documenting that sexual conflict has eroded after a few generations in aquaculture lines, in response to the altered selective environment where males and females are strictly selected for the same age at maturation (Sinclair-Waters et al., 2020). Taken together, these studies suggest that in some cases the genetic architecture of major life history traits can be rapidly altered within a few generations, and can affect evolutionary fitness. This adds nuance to the prevailing Neo-Darwinian paradigm that more or less defines evolution as a change in allele frequencies, yet leaves little room for the evolution of allelic effects, or the integration of evolutionary responses due to modified gene expression and/or methylation patterns. This view, however, has recently changed owing to several conceptual advances. These include the notion that gene effects, and not just gene frequencies, are evolutionary variables, as well as the distinctions between variation and variability and between statistical and biological effects. Particularly important is the emerging understanding that the statistical notion of gene interaction is not always a true reflection of how the genes interact in the genotype–phenotype map, and that different types of interactions can have very different evolutionary consequences.

How organisms adapt to their environment is not only a central topic of evolutionary biology but also a pressing question in the light of recent global change. To survive, affected populations must respond to these changes by means of adaptive plasticity or adaptive trait evolution. While the extinction of populations affected by anthropogenic activity is unfortunately a common outcome, some populations manage to adapt and survive. Detailed studies of these successful evolvers are not only warranted but are urgently needed to identify the potential for evolutionary rescue and adaptation



**FIGURE 1** This photo collage shows the Institute of Marine Research (IMR) field station at the river Etnelva, Norway. This institute has access to long time series data of salmonid species and associated environmental factors, providing researchers with opportunities for addressing a range of broad and in-depth studies on salmonid genomics, ecology and natural and anthropogenic impact factors associated with their abundance, distribution and evolution. Photo credit: Øystein Paulsen, Eric Verspoor, Øystein Skaala.

(Figure 1). While this study provides evidence that salmon possess the evolutionary potential to adapt quickly to environmental challenges, it is less clear if this species can keep up with the pace of change in the longer term.

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#### CONFLICT OF INTEREST STATEMENT

The author declares no conflict of interest.

#### DATA AVAILABILITY STATEMENT

None declared.

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