EVIDENCE FOR FISHERIES INDUCED EVOLUTION AT THE GENOME LEVEL IN A HEAVILY EXPLOITED FISH STOCK, THE EASTERN BALTIC COD (*GADUS MORHUA*)

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Dissertation

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ABSTRACT

Temporal genomics provides a unique opportunity to investigate selection signals that cannot be detected from single time points at the population level. Here, I used a 25-year time-series sequence data from a heavily overexploited fish stock, the Eastern Baltic cod (EBC), which shows a pronounced decline in their body length. I hypothesised that selection by size-selective trawling during periods of severe overfishing decreased growth rates, which in turn would be reflected in the genome. To test this, I was able to reconstruct full genome resequencing data from archived dried otolith (ear-bone) material of 152 individuals from 1996-2019. First, as a hypothesis-free approach to investigate any selection signal over time, detection of selection, both genome-wide and targeted, resulted in directional frequency change of inversion in linkage group 12. This suggests that directional selection acted on a specific region of the genome, while genome-wide pattern showed little change in the absence of migration and the cohesiveness of the EBC gene pool. Secondly, as hypothesised, a von Bertalanffy growth model using phenotype data (e.g., age, body length and chemical annuli of otoliths) of the sequenced individuals showed markedly impaired growth for the study period. A genotype-phenotype association study (GWAS) identified outlier loci near genes linked to growth and maturity. These outlier loci revealed signs of directional selection, showing markedly high temporal covariance and overlapping significantly with F_{st} based outliers than expected at random. This study is, to the best of my knowledge, the first in a fully marine species to provide leads that suggest genomic changes to underlie phenotypic evolution in response to overfishing in the field. It showcases the strength of combining temporal genomics of wild population with its phenotype data for the first time and eventually guides us through connecting dots of fisheries induced evolution. The evolutionary consequences of intense size-selective fishing pressure presented in this study implies the persistent impact of fisheries over multiple generations, limiting the recovery potential of the population. This research underscores the imperative for the informed fisheries management to mitigate long-term repercussions and conserve the adaptive potential of marine populations.

ZUSAMMENFASSUNG

Die zeitliche Genomik bietet eine einzigartige Möglichkeit, Selektionssignale zu untersuchen, die sich nicht anhand einzelner Zeitpunkte auf Populationsebene erkennen lassen. In meiner Dissertation habe ich eine 25-jährige Zeitserie von Sequenzdaten eines stark überfischten Fischbestands, des östlichen Ostseedorschs (EBC), untersucht, der einen ausgeprägten Rückgang seiner Körperlänge aufweist. Ich stellte die Hypothese auf, dass die Selektion durch größenselektive Schleppnetzfischerei in Zeiten starker Überfischung die Wachstumsraten verringert, was sich wiederum im Genom widerspiegelt. Um dies zu prüfen, konnte ich aus archiviertem getrocknetem Otolithenmaterial (Ohrknochen) aus den Jahren 1996-2019 vollständige Genom-Resequenzierungsdaten rekonstruieren. Als erster, hypothesenfreier Ansatz zur Untersuchung eines Selektionssignals im Laufe der Zeit ergab die genomweite Analyse der Selektion eine gerichtete Häufigkeitsänderung der Inversion in der Kopplungsgruppe 12. Dies deutet darauf hin, dass die gerichtete Selektion auf eine bestimmte Region des Genoms einwirkte, während sich genomweite Polymorphismen kaum veränderten, was auf das Fehlen von Migration und den Zusammenhalt des EBC-Genpools hindeutet. Zweitens bestätigte ein von-Bertalanffy-Wachstumsmodell unter Verwendung von Phänotypdaten (z. B. Alter, Körperlänge und chemische Ringstrukturen der Otolithen) von 152 sequenzierten Individuen ein deutlich beeinträchtigtes Wachstum für den Untersuchungszeitraum. Eine Genotyp-Phänotyp-Assoziationsstudie (GWAS) identifizierte Ausreißer-Loci in der Nähe von Genen, die mit Wachstum und Reife in Verbindung stehen. Diese Ausreißer-Loci zeigten Anzeichen für eine gerichtete Selektion, indem sie eine deutlich höhere zeitliche Kovarianz aufwiesen und sich signifikant mit F_{st}-basierten Ausreißern überschnitten als zufällig erwartet. Soweit ich weiß, ist diese Studie die erste bei einer rein marinen Art, die Hinweise auf genomische Veränderungen liefert, die der phänotypischen Evolution als Reaktion auf die Überfischung im Feld zugrunde liegen. Die Studie zeigt, wie wichtig es ist, die zeitliche Genomik von Freilandpopulationen mit den Daten ihrer Phänotypen zu kombinieren, und führt uns schließlich zu den Anknüpfungspunkten für die fischereiinduzierte Evolution. Die in dieser Studie aufgezeigten evolutionären Folgen des intensiven, größenselektiven Fischereidrucks deuten auf die anhaltenden Auswirkungen der Fischerei über mehrere Generationen hinweg hin und schränken das Erholungspotenzial der Populationen ein. Diese Forschung unterstreicht die Notwendigkeit eines wissenschaftsbasierten Fischereimanagements, um die langfristigen Auswirkungen abzumildern und das Anpassungspotenzial von marinen Populationen zu erhalten.

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1. INTRODUCTION

1.1. Humans as the Strongest Evolutionary Force

Human beings play a significant ecological role as they manipulate and disrupt various species and communities. This impact extends beyond a population's distribution and its relevant ecological landscape of one time point and influences future generations by exerting strong selective pressures. (Vitousek et al. 1997; Palumbi 2001; Hendry, Gotanda, and Svensson 2017). Indirect perturbations, such as pollution-induced eutrophication and hypoxia, landscape modifications, effects of climate change, and introduction of invasive species act via shifting surrounding environments, either abiotic or biotic, thus shifting the optimal fitness of a species or a population. Direct perturbations such as indiscreet use of antibiotics and pesticides triggers an evolutionary arms race between microbial and host species, leading to unwanted consequences such as antibiotic resistance and uncontrollable disease endemics. With substantial technological improvements, human-induced evolution has accelerated more than ever in the past decades, resulting in a change and partial loss of diversity at genetic, phenotypic and functional levels in both species and communities. This, in turn, contributes to enormous economic costs (e.g. 33 billion to 50 billion in the US every year) (Palumbi 2001), impinging on human societies. Therefore, understanding the processes and their evolutionary principles driving human-induced evolution is crucial to decelerate its pace and be able to intervene with appropriate protocols and necessary to balance perturbations and social needs.

Harvesting posits a special case in human-induced evolution as this often has very strong selectivity directly onto size, traits, and behaviours of other species (Ricker 1981; Handford, Bell, and Reimchen 1977). Among various forms of human perturbations, harvest pressure provokes stronger disturbance in an ecosystem than others, when humans act as a predator (Allendorf and Hard 2009; Sanderson et al. 2022). Fisheries induced evolution, in particular, arises from deliberate and strong size selectivity. When fishing regulations established a minimum mesh size threshold, it is meant to only allow those larger individuals to be caught that have already reproduced once, a demographic argument. Yet, the unintended evolutionary consequence is that smaller, early maturing individuals that slip through the nets, survive and reproduce. Persistent overfishing, combined with size-selective practices over multiple generations within a fish population, results in an evident truncation of size distribution. This scenario presents a very interesting and seemingly simple test case for human-induced evolution.

1.2. Fisheries Induced Evolution

The theoretical background of fisheries induced evolution (FIE) is based on fundamental principles of quantitative genetics in combination with the field of life history evolution (Law 2000). Fishing results in non-random mortality on a fish stock. The selectivity can be imposed on size by the mesh size or more subtle attributes such as behaviour by gear types, which influences catchability. In addition, overall increased mortality to all sizes from overharvesting imposes selectivity on maturation schedule (Heino, Díaz Pauli, and Dieckmann 2015). Any heritable traits which guarantee higher fitness to escape the mortality and at the same time vary in a population will evolve in response to the selective pressure. Usually, these traits are quantitative (Wright 1984; Falconer 1960) and include life history traits such as growth and maturation as well as any behaviours that render individuals vulnerable to fishing (Law 2000; Claireaux, Jørgensen, and Enberg 2018; Andersen, Marty, and Arlinghaus 2018). Both overfishing and size-selective fishing favouring larger, thus older, individuals, cause fish to grow faster as a juvenile, grow at the same pace but mature earlier, or grow slower as an adult to escape the specific mortality (Heino, Díaz Pauli, and Dieckmann 2015).

Although the theoretical background is sound and empirical observations with phenotypic changes, mainly size at maturity, in heavily fished stocks have been well noted (Stokes, McGlade, and Law 2013; Trippel 1995; Law 2000), it took some resistance until FIE was widely accepted in the fisheries science (Hilborn 2006; Miller 1957). This is primarily because of other sources of decreasing size at maturity, such as food availability and various adverse environmental conditions which attribute to phenotypic plasticity of the life history traits (Marshall and McAdam 2007; Ra, Ja, and Nj 1996; Lorenzen and Enberg 2002). As a major development to account for environmental variability, probabilistic maturation reaction norms in a function of age and size were introduced to disentangle the phenotypic plasticity and the evolutionary component (Heino, Dieckmann, and GODø 2002). However, the strength of the method in the disentanglement has been debated since with a realisation that environmental factors could also affect the reaction norms (Marshall and McAdam 2007; Law 2007). In addition, validations in experimental settings emphasised the need for inclusion of non-genetic factors when interpreting the reaction norm. (Uusi-Heikkilä et al. 2010; Morita, Tsuboi, and Nagasawa 2009; Diaz Pauli and Heino 2013)

Early studies of FIE focused on phenotypic changes in overfished stocks, such as maturation at an earlier age and smaller size (Rijnsdorp 1993; Olsen et al. 2004; Swain, Sinclair, and Mark Hanson 2007; Vainikka et al. 2009; Sharpe and Hendry 2009) and lowered growth rate (Nusslé, Bréchon, and Wedekind 2011; Nusslé, Bornand, and Wedekind 2009). More recently, behavioural differences, e.g. home range and swimming depth (Claireaux, Jørgensen, and Enberg 2018; Monk et al. 2021; Thorbjørnsen et al. 2021; Olsen et al. 2012; Guerra et al. 2020), as well as physiological impacts (Hollins et al. 2018) were documented in

the wild populations. These behavioural shifts were dependent on gear types and selectivity, which offset the encounter rate of fish.

With the ongoing revolution in DNA sequencing technology and the concomitant drop in costs, direct evolutionary changes were examined using molecular markers in overexploited populations. As a starting point, a meta-analysis using microsatellite (MSAT) loci demonstrated declined genetic diversity in overexploited fish species compared to closely related species (Pinsky and Palumbi 2014), even though the review study designs did not permit to assess temporal changes. Temporal comparisons of genetic markers, ranging from one gene locus (Jakobsdóttir et al. 2011) to multiple (Chebib et al. 2016) to thousands of MSAT or single nucleotide polymorphism (SNP) loci (Therkildsen et al. 2013; Bowles et al. 2020; Allen et al. 2018), have identified changes in either allele frequency or genetic diversity in 10-50 year time scales. However, the significant contribution and causation of fisheries in these observations is still contentious, in addition to the previously stated debate of probabilistic maturation reaction norm. For example, Pukk et al. (Pukk et al. 2013) concluded that migration from a neighbouring population could also explain the observed size, growth, and maturity changes as well as genetic changes in a Baltic perch population. Moreover, two recent independent studies have shown contrasting signals using the same population genomic dataset comprising of Atlantic cod (*Gadus morhua*) populations (Reid, Star, and Pinsky 2023; Pinsky et al. 2021).

A parallel strand of evidence supporting the possibility of FIE came from experiments in model fish species that can be easily cultivated. A landmark study of FIE by Conover and Munch (Conover and Munch 2002) used experimental evolution to mimic size-selective harvesting of Atlantic silversides. During only 4 generations of selection, marked changes in body size were observed, where up-harvested lines were on average 25% longer than the down-harvested lines. The experimental lines were full genome sequenced 15 years later to confirm the genomic changes accompanying the phenotype changes which also matched with small and large phenotypes of wild populations of silverside (Therkildsen et al. 2019). Since then, there have been a handful of experimental studies using different model fish species, zebra fish (Uusi-Heikkilä et al. 2015; Amaral and Johnston 2012; Crespel et al. 2021), guppies (van Wijk et al. 2013), and medaka fish (Renneville et al. 2020). These experiments have confirmed and strengthened the theoretical predictions on changes in life history traits, e.g., body size, growth rate, maturation, and investment in reproduction, while showing minor variations in specific responses depending on their experimental settings. Along with the life history traits, behavioural shifts in their boldness and shoaling and mating behaviour, which in turn might affect reproductive success, were observed under higher size-selective mortality (Uusi-Heikkilä et al. 2015; Sbragaglia et al. 2022; 2019; Biro and Post 2008). Importantly,

evolutionary responses were observed either in genetic or transcriptional level in most of the experiments, though little parallelism was observed among them.

1.3. Challenges for Detecting FIE in the Wild

As hinted from above, difficulties in providing direct evidence for FIE are due to two main factors. 1) In wild populations, demonstrating causality of fishing pressure in the phenotypic and genetic change is complicated. Unlike in experimental settings, there are several additional abiotic and biotic environmental factors that affect the population dynamics in nature. These include abiotic drivers such as temperature and oxygen levels, population dynamics such as migration and population density, and ecological factors such as prey-predator interactions and food availability. On this account, simulation and modelling studies as well as a comparative approach using populations with and without fishing pressure have been undertaken to test the impact of fisheries (Laugen et al. 2014; Andersen and Brander 2009; Pinsky and Palumbi 2014). 2) Whether any observed phenotypic shifts from exploitation are based on phenotypic plasticity or evolutionary adaptation has been at the centre of the ongoing debate. Although we have learned that any changes in a phenotype from fishing pressures are not merely plastic from above mentioned experiments, providing concrete evidence to connect the phenotype to genotype from field data is more challenging (Enberg et al. 2012) thus relevant studies are still very rare. Especially, phenotypes targeted by FIE are mostly quantitative traits, which adds another layer of complexity to detect the evolutionary basis of FIE (Watanabe et al. 2019).

The most concrete case of genetic or genomic evidence for FIE was demonstrated in an anadromous species, Atlantic Salmon (*Salmo salar*). The age at maturity (sea age) was associated with the gene *vgll3*, which explained 39% of the phenotypic variation in wild populations (Barson et al. 2015; Ayllon et al. 2015). With 40 years of annual time series data, a clear decrease in age at maturity was accompanied with directional change in allele frequency of *vgll3* gene (Erkinaro et al. 2019; Czorlich et al. 2018). When possible drivers of those changes were assessed, direct effect of fishing in the river and indirect effect of fishing through harvesting one of the prey species were found to be highly correlated (Czorlich et al. 2022). Conclusive evidence in these studies is certainly attributed to the simple genotypic basis of the phenotypic trait under selection, in this case the life-history trait “age at maturity”, featuring a large effect locus, while most other life-history traits are decidedly polygenic (Roff 1993). On top of that, the availability of high-resolution time series data of the genetic materials, the environmental factors, as well as fisheries metrics of the population and the ecosystem allowed for the detailed examinations of intricately related factors.

As much as promising, the field of FIE still lacks case studies from the wild that establish clear links between evolutionary changes respective to different life history traits as

well as to fishing pressure, as the dynamics are highly context dependent (Crespel et al. 2021; Thambithurai and Kuparinen 2023). Notably, among other anthropogenic threats to biodiversity, harvest ranks the lowest in the number of studies incorporating genetic evidence (Pelletier and Coltman 2018). In addressing this research gap, temporal sampling of overexploited populations brings a major benefit to examining the ongoing evolution in action. Most of the above exemplified studies of FIE, both wild and experimental, took advantage of comparing samples from two or more time points. For evolutionary processes within shorter evolutionary time scales, such as those associated with harvest, conventional population genetics approaches, detecting signatures of selection by comparing spatial populations, often fail to provide clear signals. Only by direct observation of changes in allele frequencies or population indices over several time points, selections in shorter time frames can be unveiled (Clark et al. 2023; Jensen and Leigh 2022). Fortunately, more and more genetic materials stored in time series archives such as museum samples and data collection have been becoming available (e.g. Baltic Sea Integrative Long-Term Data Series at GEOMAR by RV Alkor used in this study) (Habel et al. 2014). Simultaneously, methodological developments utilising genomic data have advanced rapidly, facilitated by technological advancement of sequencing. With this confluence of resources and advancements, temporal genomics (or genetics) studies are gaining significance in researching evolving populations under anthropogenic pressures (Habel et al. 2014; Nielsen and Hansen 2008; Jensen and Leigh 2022).

In these respects, Eastern Baltic cod is an ideal study case, attributed to 1) clear phenotypic response to high fishing pressure, 2) availability of time-series records of phenotypes and genetic materials and 3) that the system is semi-enclosed with negligible gene flow with a neighbouring population in the Baltic Sea (Box1), which reduces the possible error sources in interpreting any genetic changes.

1.4. Eastern Baltic Cod

Eastern Baltic cod (EBC) is an Atlantic cod (*Gadus morhua*) population residing in the central Baltic Sea, with the last remaining spawning ground being the Bornholm basin (ICES 2022). They are biologically and genetically differentiated to their neighbouring ecotype, Western Baltic cod (WBC) and all other Atlantic cod ecotypes (e.g., North Sea cod) (Box1 for EBC and WBC). They are known to have diverged from WBC 7-8 thousand years ago when the Baltic sea was created, which is considered evolutionarily young (Martínez-García et al. 2021; Matschiner et al. 2022; Schmölcke et al. 2006). As the Baltic Sea has a specific environment of brackish water with a salinity gradient, high pCO_2, and prevalent hypoxia (Reusch et al. 2018; Zillén et al. 2008), they have diverged to adapt to these environments and occupy the periphery of the species continuum (Berg et al. 2015). From molecular

evidence, the divergence and adaptations of EBC took place in the past concurrent with development of Baltic sea (Martínez-García et al. 2021; Matschiner et al. 2022) and it is at present isolated from WBC in the absence of genetic inflow (Hemmer-Hansen et al. 2019; Helmerson et al. 2023). Ecologically, EBC plays a major role as a key predator species in the food web especially in Baltic-specific low biodiversity. Historically, the EBC has been the largest target species for commercial fisheries with an annual catch of up to 400,000 tons in the mid-1980s and contains values in recreational fisheries (ICES 2022), based on continual monitoring data of the population since the 1920s (Eero et al. 2023; ICES 2019).

Since the mid-1990s, multiple aspects of the EBC population have been deteriorating, though fluctuated, and now reached the unprecedented lowest point in their state since the 1950s (Birgersson 2022; Eero et al. 2023). The spawning stock biomass (fish sized over 35cm) has declined sharply in recent years, together with recruitment and loss of two major spawning grounds (Cardinale and Svedäng 2011; Köster et al. 2017a). The size at first maturity, growth, and condition of the fish marked the lowest value with L50 (length at 50% of population reaches maturity) being under 20 cm in recent years (Mion et al. 2021; Eero et al. 2015; Svedäng and Hornborg 2017; ICES 2021). A complete collapse of the stock has resulted in a ban on targeted fishing on EBC since 2019 (ban renewed recently for 2023) but the condition of the population has not been able to recover to a healthy status so far.

A number of factors may have contributed to the deterioration of EBC size distribution and condition. Overfishing is well documented through ICES data series (ICES 2019). They reveal that over many years, the total allowable catch was set too high such that the fishing mortality was 2-3 times the limit set by the maximum sustainable yield (MSY) (ICES 2019; Eero et al. 2011; Zeller et al. 2011; Birgersson 2022). Consequently, the total landings of EBC have declined below the total allowable catch, seemingly due to the diminished stock abundance. Likewise, long-term trends of fishing mortality and L95 (95% quantile of length distribution (Shin et al. 2005)) showed an inverse correlation from the 1970s to 2000s.

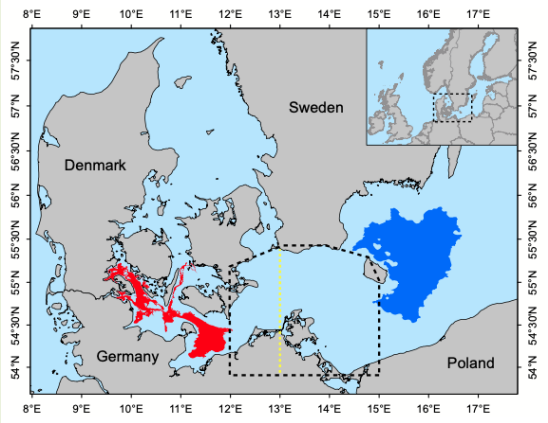
In the meantime, continuous size-selective fishing has imposed a higher mortality on older individuals, leading to observed size truncation, growth retardation, and worsened condition (Svedäng and Hornborg 2017; 2014; Eero et al. 2023; Möllmann et al. 2009). Here, different mechanisms, albeit interconnected, can be involved. Removal of larger sized cod could reduce cannibalism and generally intensify intraspecific competition among small sized cod (Möllmann et al. 2014). Additionally, bottom trawling can disturb the cod nursery habitat where hatched cod larvae would grow (Birgersson 2022; Bryhn et al. 2022). Decrease in size, then, could amplify the feedback loop to stunt individual growth through the food web interactions, changes in the biomass (Audzijonyte et al. 2013), as well as altering the social context (Buston 2003). Most importantly, the fishing pressure induces transgenerational

effects that persist in the longer term, which may partially explain the ongoing and unabated deterioration of EBC even after the implementation of the moratorium.

Apart from overexploitation, EBC suffers from adverse environmental conditions. Widespread hypoxia in the Baltic sea, induced by eutrophication (Zillén et al. 2008; Reusch et al. 2018) significantly impacts cod reproduction. EBC requires deeper water to spawn due to the low salinity environment of the Baltic Sea (Nissling and Westin 1997). However, the prevalent hypoxic conditions in the bottom water create a critical depth for neutral egg buoyancy, essential for successful spawning and larval survival (Vallin and Nissling 2000). Increases in hypoxia areal extent, duration and severity over last decades caused severe loss of spawning grounds and reduced the rate of survival of cod eggs and juveniles (Carstensen et al. 2014; Conley et al. 2009; Köster, Schnack, and Möllmann 2003; Westin and Nissling 1991; Casini et al. 2016). Ecological factors such as lower prey availability, higher predation by grey seal, and infestation of its parasite further exacerbate the low condition, individual growth, and high natural mortality (Casini et al. 2016; Horbowy, Podolska, and Nadolna-Ałtyn 2016; Mehrdana et al. 2014; Neuenfeldt et al. 2020; Mion et al. 2018). While the impacts and causal relationship of some of the listed factors may be subject to debate, it is highly likely that fishing and non-fishing factors interplay, rendering EBC more vulnerable to various threats and intensifying the deteriorating condition of the stock (Eero et al. 2023).

BOX1 Eastern and Western Baltic cod

The Eastern and Western Baltic cod (EBC and WBC, respectively) stocks are distinct populations inhabiting different parts of the Baltic Sea. These populations exhibit marked phenotypic and genetic differences, attributed to ecological and environmental factors. EBC grows slower and mature at smaller size, although historically they are generally larger in size, compared to WBC (McQueen et al. 2019; Bagge 1994; Berner and Vaske 1985). Reproductive traits further contribute to the differences, with EBC adapted to the low salinity environment of the Baltic Sea. Different salinity requirements for sperm activation (Nissling and Westin 1997) and neutral egg buoyancy (Nissling and Westin 1997; Petereit et al. 2014; Nissling, Kryvi, and Vallin 1994), create a reproductive isolation between the two stocks, while adults co-occur physically in the transition area of Arkona Basin with little hybridization (Hemmer-Hansen et al. 2019) (Box Figure1).



Box Figure 1. Map of region inhabited by eastern (blue) and western (red) Baltic cod stocks. The box with dashed black line marks the transition area, Arkona Basin, where they co-exist and the yellow dashed line marks the stock separation used by ICES assessment and management. Figure taken from Hemmer-Hansen et al 2019

While WBC spawns throughout deeper parts of the Arkona Basin, Mecklenburg Bight and Kiel Bight at the Baltic Sea's entrances, EBC primarily spawn in Bornholm Basin, having lost two other spawning grounds in the central Baltic region (Köster et al. 2017b). Environmental conditions and incompatible spawning times create a reproductive barrier. The hostile environment of Arkona Basin for EBC, such as inadequate salinity, oxygen concentration and temperature, supports very low survival of eggs or sperms and vice versa for WBC in Bornholm Basin (Nissling and Westin 1997; Köster et al. 2017b; Petereit et al. 2014; Hinrichsen, Hüssy, and Huwer 2012). The optimal spawning timings of the two are in discordant, as WBC spawn in early spring in the western area and EBC reach a peak spawning in the summer months in Bornholm Basin (Hüssy 2011; Hüssy et al. 2016).

Genetic evidence also supports this reproductive incompatibility, suggesting genetic isolation of EBC (Hemmer-Hansen et al. 2019; Weist et al. 2019). Even though historical hybrids in the 1980s were reported, indicating gene flows from EBC to WBC (Helmerson et al. 2023), current

genetic data show no ongoing hybridization. Especially for EBC, studies using whole genome data clearly demonstrate highly diverged genomes compared to any other Atlantic cod populations (Barth et al. 2019; Matschiner et al. 2022). Particularly, large inversions in LG2 and LG12 are linked to salinity and oxygen level and temperature, respectively, and under strong selection in EBC (Berg et al. 2015), which may be acting as a genetic barrier to reproduction.

The nearly complete reproductive isolation of EBC underscores its significance as a population adapting to the central Baltic Sea's unique environment. Living in an enclosed sea with reproductive barriers with neighbouring WBC, EBC seems to be undergoing a speciation event, which makes it an endemic species of the Baltic Sea. With an considerably low effective population size (N_e) compared to other cod populations (Matschiner et al. 2022), EBC faces severe threats from heavy fishing pressure, worsening environmental factors, including hypoxia and temperature changes, loss of spawning grounds, and a significant decrease in fish size. Having no genetic inflow, EBC may be experiencing a great risk of further decline of population fitness.

2. OBJECTIVES OF THESIS

In this thesis, combining available evidence of recent worsening of the EBC condition, population size structure and abundance, I hypothesised that evolutionary responses are detectable in a temporal population genomic data set that reflect the observed phenotypic changes. To test this, I took full advantage of the Baltic Sea Integrative Long-Term Data Series of EBC in Bornholm Basin, archived with otoliths, finclips and individual phenotype records. I conducted a whole-genome resequencing of the archived samples spanning five time points between 1996 and 2019, referred to as temporal populations hereafter. Along with the temporal scheme, the sampling was designed to encompass the most spectrum of phenotypic variations.

First, I investigated if there is any genomic differentiation in temporal populations. This hypothesis free approach, independent of the phenotype data, was to detect any genetic components undergoing selection or drift, if any, over the study period, even though the growth change was phenotypically the most evident pattern. Any selection acting upon the population would leave signatures in the genome, either at genome-wide level or in specific candidate regions.

Second, genome-wide association (GWA) analysis was conducted integrating phenotype and genotype data. To do this, since the conventional age reading has not been reliable for EBC, a newly developed method was employed to provide accurate age information for each sequenced individual. This allowed for the estimation of individual growth to confirm the expected change of a heritable trait under fishing pressure. Using individual growth performance index, GWA was carried out to identify specific responsible loci. These identified loci, linked to growth variation, were further analysed using temporal autocovariance to detect directional selection.

Lastly, I sought to overlay these two axes of time and phenotype by identifying the overlapping regions from the selection scan and GWA. This would validate directional shifts over time in the heritable components of growth in EBC. Biological relevance was explored in all intersecting outlier regions. Specific genes and enriched biological pathways under selection were described in detail in relation to growth.

This study represents the first to integrate information from whole-genome sequence data across multiple time points with the phenotype records from a wild marine population. The study highlights observed growth change over time, the corresponding evolutionary processes, and direct detection of selection through sequence comparisons of multiple time windows. The novel insights learned from this research implies evolutionary consequences of

overexploitation, thus highly relevant to fisheries management, and advance our understanding of the intricate dynamics shaping the EBC population.

3. MATERIALS AND METHODS

3.1. Sample Collections and DNA Extractions

In total 152 cod individuals were used in this study after excluding individuals which were identified as either a western Baltic cod from genetic analysis (9 samples), an outlier from growth analysis with measurement errors (1 samples), and of low sequencing quality (2 samples). Sampling was done in two different ways to cover the available time period and the full range of phenotype in the sampling pool (Figure 1). 1) A set of samples, called “random” hereafter, were randomly sampled along the length distribution for five catch years; 31 from 1996, 22 from 2002, 24 from 2008, 20 from 2014, and 20 from 2019. 2) As another set of samples, called “phenotype” hereafter, 19 smallest mature fish and 18 largest immature fish were selected from the catch year 1996-1998. As any age information of the archived samples was not available, neither sample based on the cohort nor on length at first maturity was possible. The rationale was that by sampling immature fish, which would be first mature in the following year if they had not been caught, and small, presumably young, mature fish, I attempted to cover as wide a range of phenotype variation as possible.

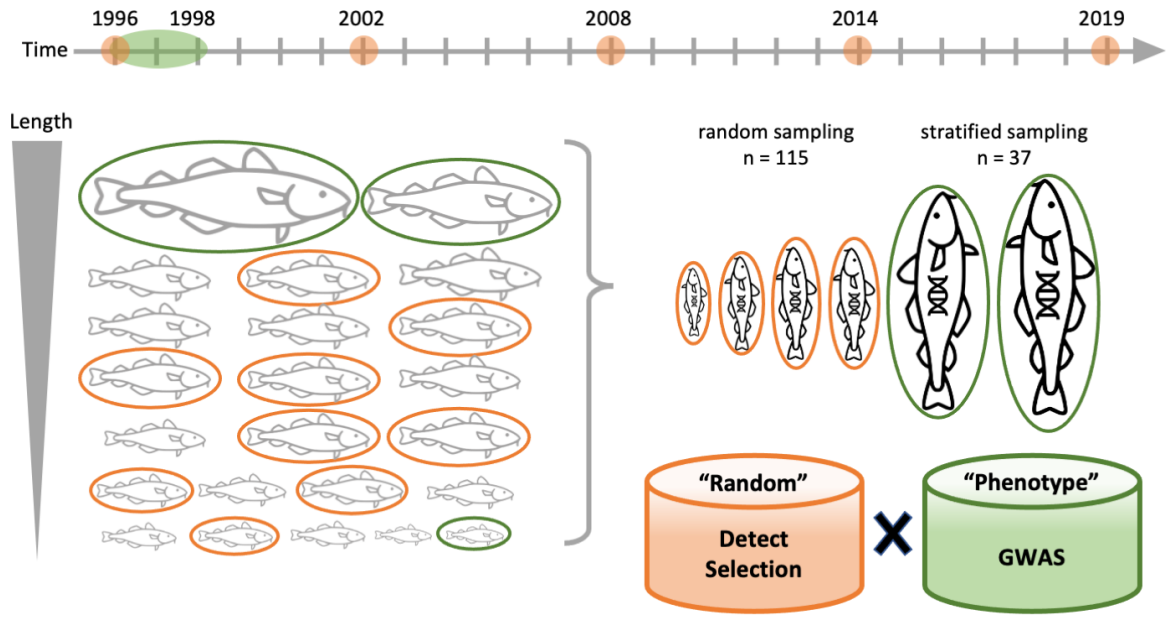


Figure 1. Study design combining temporal and phenotype sampling in Eastern Baltic cod, *Gadus morhua*
Samples from Baltic Sea Integrative Long-Term Data Series were strategically selected for sequencing in two separate approaches. First, random temporal sampling along the length distribution, coloured in orange, was conducted for five time points from 1996 to 2019. These 115 “random” samples were used to detect selection signals over time. In addition, stratified sampling, coloured in green, was conducted to cover the full phenotypic range of the sample pool. These additional 37 “phenotype” samples were included in a genome-wide association analysis.

Otoliths and finclips were collected in Baltic Sea Integrative Long-Term Data Series of the research division Marine Evolutionary Ecology at GEOMAR, carried out annually since 1996. They were taken on board from cod caught in Bornholm Basin, of which their phenotype data (e.g., body length, weight, maturity stage, and sex) was recorded (Supplementary Table 1). Otoliths were stored in paper bags in cabinets standing in the dark corridor in GEOMAR, but safely locked in. Finclips were stored in 100% ethanol at -20 degrees.

For genetic materials, DNA was extracted using otoliths from earlier years (1996-1998, 2002, and 2008) and fin clips from recent years, 2014 and 2019. Otoliths and finclips were always handled with tools (e.g., forceps) which were cleaned with ethanol 70% and sterilised in a Bunsen burner in between each individual sample to avoid cross contamination. The extraction procedure for both otoliths and finclips were conducted following the standard protocols from either DNeasy® Blood & Tissue Kit (Qiagen, Aarhus, Denmark) or NucleoSpin® Tissue Kit (Macherey-Nagel, Düren, Germany). Otoliths were fully submerged in the lysis buffer to lysate any remnant tissues then removed from the buffer. The lysate then was treated as in the manuals provided by the kits. Fin clips were cut into small pieces (up to 25mg), submerged in a lysis buffer, then continued following the protocols. The extracted DNA was purified using Qiagen QIAquick® PCR Purification Kit (Qiagen, Aarhus, Denmark). DNA quality was checked with standard electrophoresis in 1% agarose gel and the quantity was measured using NanoDrop^{tm} (Thermo Fisher Scientific^{tm}, Carlsbad, USA)

To validate cross contamination that might have occurred during the sample collection, archiving process, and DNA extraction, microsatellite (MSAT) analysis was done for DNA extracted from otolith samples. Four MSAT sites were used. A multiplex PCR was conducted with four primer pairs on a 96-well plate. The PCR product was mixed with Hi-Di^{tm} mix (Thermo Fisher Applied Biosystems^{tm}, Carlsbad, USA) with GeneScan^{tm} LIZ dye Size standard^{tm} (Thermo Fisher Applied Biosystems^{tm}, Carlsbad, USA). Capillary electrophoresis was done with the reaction mix using ABI PRISM 3100 Genetic Analyzer (Thermo Fisher Applied Biosystems^{tm}, Carlsbad, USA). The MSAT peaks were analysed using GeneMarker® software (Softgenetics, State College, USA). As the chosen MSAT loci typically show more than ten alleles per site in a population, when samples are mixed the likelihoods of encompassing the same allele at a single MSAT locus are small and are virtually zero if several such loci are combined. Thus, samples showing multiple peaks for any MSAT locus were identified as cross contaminated and subsequently excluded from the data set (see examples in Supplementary Figure 1).

3.2. Library Preparation and Sequencing

2x100 bp paired end library preparation for 16 samples from 1996 was done in the Ancient DNA Laboratory at the Institute of Clinical Molecular Biology (IKMB) as a pilot to check

if they should be treated specially like historic DNA samples. The details of the manual library preparation can be found in the method section in Krause-Kyora et al. 2018. For the finclip samples from 2014 and 2019, 2x150bp paired end libraries were prepared using Illumina DNA Prep kit (Illumina, San Diego, USA) by the Competence Centre for Genomic Analysis (CCGA) Kiel. These libraries (16 otolith samples from 1996 from pilot and 40 finclip samples from 2014 and 2019) were sequenced on Illumina 6000 S4 Flowcell (Illumina, San Diego, USA) by CCGA Kiel. In the end my collaborators and I have concluded that older otolith samples can be treated the same as the rest, yielding sequence data of comparable quality. Thus, rest of the samples, including “phenotype” samples from 1996-1998 and “random” samples of 1996, 2002 and 2008, were sent to Norwegian sequencing center (NSC) for 2x150 bp library preparation using Illumina Nextera DNA library preparation kit (Illumina, San Diego, USA) followed by sequencing on Illumina NovaSeq S4 Flowcell (Illumina, San Diego, USA).

3.3. Read Processing and Variant Calling

All sequenced reads from this study were processed together with published population data from Barth et al. 2018, to include 23 EBC, 22 WBC, and 24 North Sea cod samples, which were later partitioned out in the subsetting step of the workflow (workflow presented in Supplementary Figure 2). This was to identify WBC in our samples (data not included) as well as to conduct ancestry painting, which includes WBC and EBC individuals of known inversion status as reference (explained in *section 3.6*.). All sequenced reads were processed following the GATK best Practices workflow by Broad Institute (using GATK v4.1.9.0) (Van Der Auwera et al. 2013). All the detailed commands, parameters, and filtering options in the bioinformatics workflow are included in the provided scripts (referred to as script hereafter).

Fastq files with raw reads were transformed to uBam file format by FastqToSam then Illumina adapters are marked by MarkIlluminaAdapters (script 01 and script 02). The processed reads were mapped to the reference genome of Atlantic cod, gadMor3.0 (NCBI accession ID: GCF_902167405.1) using bwa v0.7.17 (script 03) (Li 2013). Mapped reads were marked for the duplicates by MarkDuplicates in Picard v2.23.8 (“Picard Toolkit” 2018) to produce final bam files (script 04). Quality control for read mapping was done using Qaulimap BAM QC v.2.2.2-dev (Okonechnikov, Conesa, and García-Alcalde 2016) and picard tool then summarised and visualised using MultiQC v1.10.1 (Ewels et al. 2016) (script 05). The median coverage of each individual ranged from 4x to 31x with a median of 12x for all samples. Two samples from 1996 were excluded based on their low mapping coverage below 4x.

Variants were first called per sample basis using GATK HaplotypeCaller to produce gvcf files, which were consolidated using GATK GenomicsDBImport (script 06 and 07). Then, GATK GenotypeGVCFs was used to jointly call variants across all samples (script 08). Only single

nucleotide polymorphisms (SNP) were selected for the further analysis (script 09_selectVariants.sh). Raw SNP variants were first hard filtered based on different qualities of variant sites according to best practices (detailed filters are included in the script 09_variantfiltrationSNPs.sh). Finally, only biallelic SNPs were selected and filtered again based on genotyping quality, missingness, read depths, and minor allele frequency (MAF) of 0.005 to produce the final variant call file in a vcf format containing 5,847,389 variants (script 09_variantfiltrationSNPs_gq_dp_ua_bial_miss_meanDP_hwe_maf.sh). When possible, this full set of variants based on MAF > 0.005 were used, although some analyses were carried out using 4,685,343 variants filtered with MAF>0.01 due to the processing time and resource limitation.

Further analyses were done with two separate sets of variants resulting from different partitioning of the total sample set (also partitioned from WBC and North Sea samples), as parts of the sampling was intentionally biased for “phenotype” samples as explained earlier. i) 115 of “random” samples were used for the rest of the analysis identifying signatures of selection over time. ii) A total of 152 samples including “random” and “phenotype” samples were used for genotype-phenotype association. The subset of the master vcf file was created using bcftools v1.2 (Danecek et al. 2021) then further was removed of fixed sites using GATK SelectVariants (v4.1.9.0) (script 09_subset_vcf.sh).

3.4. Population Statistics and Principal Component Analysis

To examine any temporal differentiation in EBC independent of phenotypic data, 115 “random” samples were used in computing Nucleotide diversity (π), between population nucleotide divergence (d_{xy}), and F_{st} and in principal component analysis (PCA). For calculating π and d_{xy}, I followed the guides provided by Pixy (1.2.7.beta1) (Korunes and Samuk 2021). A vcf file containing invariant sites was created, using GATK GenotypeGVCFs with option –all-sites followed by site filtering steps using GATK VariantFiltration with same criteria as in hard filtering of variants and followed by vcftools v0.1.16 (Danecek et al. 2011) on missingness and read depths (script 10_filter_all_callable_sites.sh). This filtered all-site file was combined with the final variant file to create the input vcf file for Pixy. A total of 81,462,138 records including invariant and variant sites, were used to calculate π for each catch year and pairwise d_{xy} in 50kb non-overlapping windows (script 10_pi_pixy.sh). For genome-wide nucleotide diversity for each temporal population, average π value for all windows was calculated according to the equation provided by Pixy (script 10_plot_pi_pixy.r).

PCA on the subset of SNPs (4,685,343 after filtering for MAF > 0.01) was carried out using the R package pcadapt v4.3.3 (Privé et al. 2020) (script 11_pca.r). The required input bedfiles were converted from vcf files using PLINK v1.9 (Purcell et al. 2007). Scree plots of total variance explained by each principal component (PC) were examined to decide up to which

PCs to investigate (Supplementary figure 3). When all sites are included, a unique clustering pattern driven by inversion status of individuals appeared (Figure 5(a) and Supplementary figure 4). Thus, sites within the inverted regions (identified as described in *section 3.6. Identifying inversion status*. were excluded to examine the remaining population structure.
Weir and Cockerham's F_{st} was calculated using vcftools v0.1.16 in 20kb windows (script 12_fst_20k.sh). Only weighted F_{st} was used for plotting and interpretation of the data. All plots were created in R (R Development Core Team, 2022) using the base "plot" function.

3.5. Genome-wide Temporal Covariance and Simulation

Genome-wide temporal covariance was calculated using a modified python script in Jupyter notebook based on the functions in cvtkpy (http://github.com/vsbuffalo/cvtk) published in Buffalo and Coop (2020) (script 13_temporal_covariance.ipynb). Error bars were calculated by bootstrapping covariance values, resampling blocks of loci 5000 times, using the bootstrap function provided by cvtkpy. As initial genome-wide temporal covariance showed an inconclusive pattern (see results in *section 4.2.),* I simulated a neutrally evolving population to compare the covariance values as a control. First, backward-in-time simulation was employed to create a population with matching diversity using msprime v1.2 (Baumdicker et al. 2022), with mutation rate 3.5e-9, recombination rate 3.11e-8, 5000 genomes, and a sequence length of 30Mb (script 14_sim_00_msprime_burnin.py and 14_sim_00_runburins_msprime.sh). With this population as a founding population, a forward-in-time simulation was conducted using SLiM v2 (Haller and Messer 2017) (script 14_sim_01_neutral_run_slim.sh and 14_sim_01_neutral.slim). Additional 100 generations were burned in at the beginning of the simulated time. From generation 101, 20 individuals were sampled from the simulated population for five generations, to imitate the sampling scheme of wild population. Final vcf file was created to calculate the covariance of the simulated temporal populations. This was replicated 100 times to create a distribution of patterns from neutrally evolving populations. For the calculation of temporal covariance, a custom script in R language was used which replicated the functions in cvtkpy (script 14_sim_02_calc_cov_sim.R).

3.6. Identifying Inversion Status

Four large (5-17 Mbp) chromosomal inversions in Atlantic cod species have been previously identified (Berg et al. 2015; Kirubakaran et al. 2016; Sodeland et al. 2016), three of which are polymorphic in the EBC population. I targeted these regions as candidate supergenes which may have undergone selection over the study period and examined how their frequency changed over time. With prior knowledge of inversions located in LG2, 7 and 12, PCA was done on subset vcf files of each chromosome. Three distinct clusters of individuals of different inversion status (homozygous ancestral, homozygous derived, and

heterozygous, “ancestral” status adopted from Matschiner et al. 2022) were observed, which was used for individual assignment. Then, F_{st} values were calculated among these three groups (each pairwise and global) and plotted to identify boundaries of the inversions (Supplementary Figure 5). These boundaries were used to subset the bedfiles to feed as input of local PCA analysis. The inversion status of individuals was verified again by visually examining local PCA plots for each inversion status (Figure 2) (script 11_pca.r). When ambiguous, the individuals were visually examined for their genotypes in IGV v2.12.0 (Thorvaldsdóttir, Robinson, and Mesirov 2013). The frequency of inversion, here ancestral orientation, was calculated and plotted over time using R.

To identify the individual status of double crossover, ancestry painting was carried out following a tutorial from a git repository of M. Matschiner (github.com/mmatschiner/tutorials/tree/master/analysis_of_introgression_with_snp_data). I used four homozygous individuals as reference points, two of ancestral homozygotes and two of derived homozygotes, and two “control” individuals of EBC, which are known to have crossovers based on Matschiner et al. (2021). SNP sites between positions 6.5Mb and 7.5Mb in LG12, (Note that the location is different than reported in Matschiner et al. as different reference genomes were used) which are fixed 80% in these reference individuals, allowing for 20% of missingness, were painted two different colours in EBC individuals (Supplementary Figure 6). Double crossover status, either ancestral/derived homozygous or heterozygous, was assigned by visual examination.

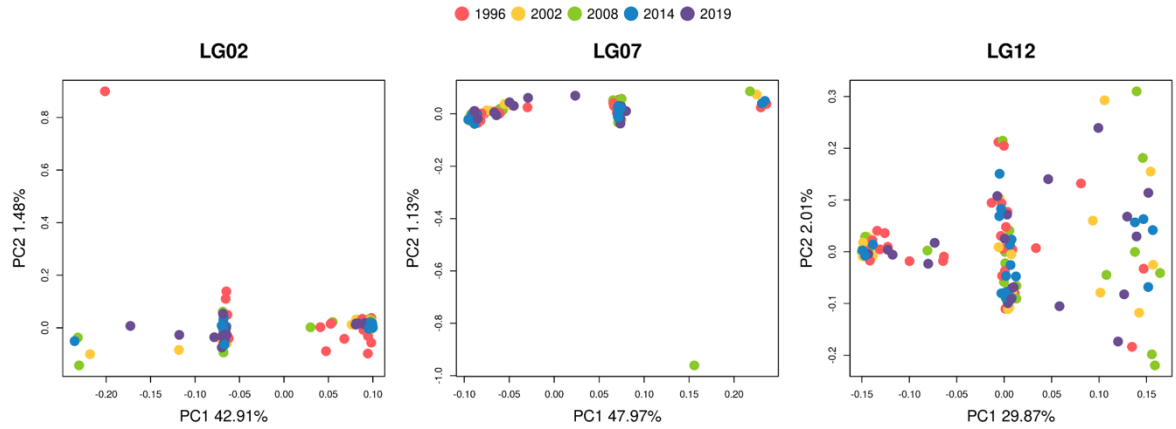


Figure 2 Principal component analysis on inverted chromosomal regions in LG02, LG07, and LG12 of the cod *Gadus morhua* genome
Local PCA was conducted using SNP sites within the inverted regions to identify individual inversion status. Three groups depending on the genotypes, ancestral and derived homozygotes on the sides and heterozygotes in the middle, are strongly clustered. Samples were assigned their status according to these clusters to calculate inversion frequency over time. Individuals are coloured according to the catch year.

3.7. Age Reading of Otoliths

As the conventional otolith reading method has not been reliable for EBC, a newly developed method was employed to acquire age information of the sequenced samples in order to model growth based on Hüssy et al. 2021. For chemical analysis, otoliths were embedded in Epoxy resin (Struers®) and cut to have exposed surface of the core and the rostral part. Trace element analysis were conducted by Laser Ablation Inductively Coupled Plasma Mass Spectrometry (LA-ICP-MS) to measure magnesium (^{25}Mg), phosphorus (^{31}P), and calcium (^{43}Ca), which exhibit seasonal variations in EBC (Hüssy et al. 2021; Heimbrand et al. 2020). Since the elements were read from the core of an otolith to the edge, the measured element traces represent the chemical characteristics of an individual's lifespan from the hatch to catch. With the measured element profile, a statistical analysis was carried out to determine the age. Chemical minima were identified using local polynomial regression function "loess" and "peaks" in R (R Development Core Team, 2022). The arguments were set based on the settings used in age reading of tag-and-recapture cod samples in previous studies (Hüssy et al. 2021). The numbers of minima in Mg and P, which suggest the fish's exposure to the coldest temperature of a year (February and March) (Hüssy et al. 2021), are counted as the age of an individual (Figure 3). When the two values disagreed, the element profiles were visually examined. This approach is not as stable for the signals near the otolith edge. Thus, visual assessment was conducted for the samples caught in the first quarter of a

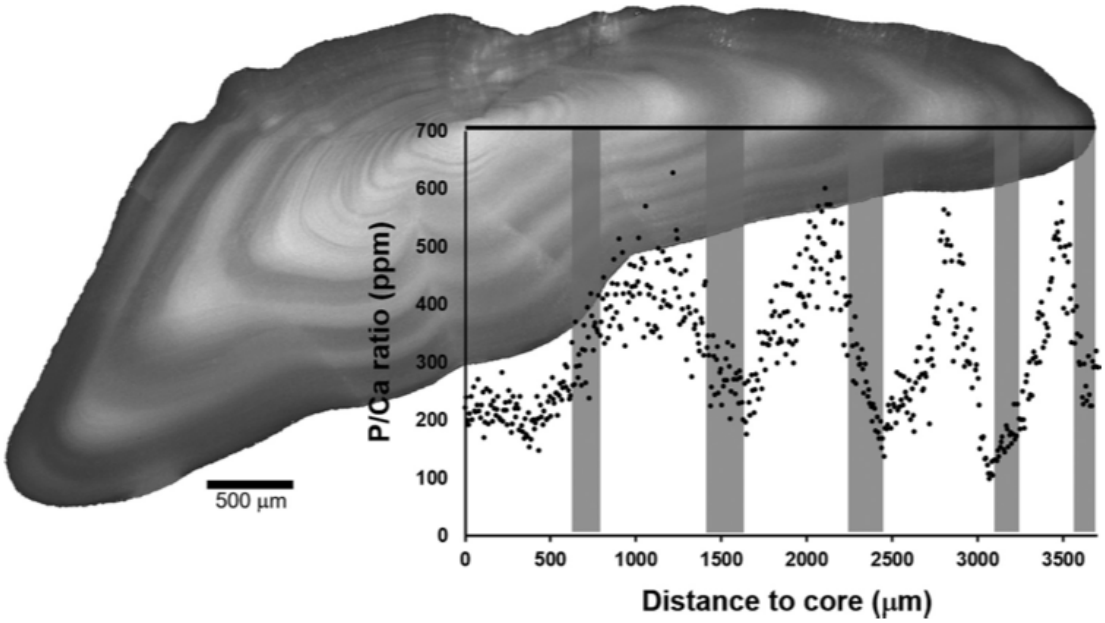


Figure 3. Otolith dissection and chemical banding for reading age in a Baltic cod
An otolith chemical analysis (Figure taken from Figure 2 in Hüssy et al. 2021) to identify the age of sequenced individuals were conducted. In this example, the phosphorus measurements in ratio of calcium of a 4-year-old test sample is shown, which was used to identify the best setting for the statistical processing of element profiles. The seasonal growth zones of otoliths are indicated in vertical grey areas in the plot as phosphorus to calcium elemental ratio upon mass spectrometry

year. As a result, annual chemical radii for each individual, total otolith radius, as well as the age at catch were extracted. The exact details of preparation of otoliths, procedures concerning LA-ICP-MS, and the statistical analysis can be found in Hüssy et al. 2021.

3.8. Modelling Individual Growth Rates

To acquire a heritable phenotype that may have been affected by fishing pressure, I modelled individual growth using the age information. Although it was recently confirmed that the growth of EBC has impaired over last decades (Mion et al. 2021), it is crucial to obtain the growth pattern of sequenced individuals to integrate genotypes and phenotype.

To fully utilise the hierarchical nature of the estimated otolith chemical annuli at age of fish individuals from different catch years, Bayesian hierarchical modelling was applied using R2jags v0.7.1 R package (Su and Yajima 2021) (script 15_growth_model.r). The von Bertalanffy growth function (von Bertalanffy 1957) was fitted to distance from core to chemical annuli at age:

$$L_a = L_\infty \ (1 - e^{-k(t_a - t_0)}),$$

where L_a is distance from otolith core to each chemical annulus, t_a is the estimated age at the annulus, $L\infty$ is asymptotic length, which is hypothetical length at age of infinity, k is a growth coefficient, and t_0 is hypothetical age at length equals 0. Three levels of hierarchy included measurements of annuli at age, nested in a fish individual, again nested in a group of a catch year. As a result, $L\infty$ and k parameters were estimated for each individual and each catch year. I took the most conservative approach of priors, applying gamma distribution for catch years and normal distribution for individuals with relaxed standard deviations (details in the script). 100,000 iterations were observed for three MCMC chains and the first 10,000 were discarded as burn-in. The median of Rhat values were 1.0036 and model convergence of the chains were visually examined in addition (Supplementary Figure 7). As an additional assessment of the model, residuals were calculated from estimated otolith length from the model and observed length of otolith annuli (Supplementary Figure 8). Here, the variance of residuals is larger for the first year which could be caused by the uneven number of observations that were fed to the model for each age. Nevertheless, the overall residuals remain near zero for all years. Back-calculation of fish length was conducted using an equation from Hüssy, Eero, and Radtke 2018, using biological intercepts specific for Baltic cod. Accordingly, L_0, which is the fish length at age 0, was set to 4.3 and O_0, the otolith length at age 0 was set to 0.01 (Details in the script).

3.9. Genome-wide association analysis (GWA)

To identify specific genomic regions responsible for growth variation in the EBC population, genome-wide association study was conducted. Growth performance was converted into an

index using the growth estimates, Φ = $log\ k\ +\ 2\ log\ L\infty$ (Moreau, Bambino, and Pauly 1986; Munro and Pauly 1983). Subsequently, this variable was subjected to a univariate nonlinear mixed model to identify loci associated with the growth change using GEMMA v0.98.3 (Zhou and Stephens 2012) (script 16_gwas.sh). A total of 679,584 SNPs were used after filtering for minor allele frequency of 0.05 and missingness of 0.1 as recommended by the developers. Genetic population structure was considered as a random effect and sex as covariates to incorporate and eliminate possible other contributing factors. Genomic inflation factors and QQ plots showed that systematic biases were adequately corrected from the other contributing factors (Supplementary figure 9). After correcting for multiple testing, using false discovery rate (Benjamini and Hochberg 1995), with the number SNPs sites not in linkage disequilibrium (174,541), there were no SNP sites with significant Wald test p-values observed (Discussed below in *section 5.1*). Instead, as an exploratory approach to identify the loci that are most likely to be associated with growth, I chose a cutoff which includes the most obvious peaks but excludes more spurious signals in the Manhattan plot. As results, SNP loci occupying the 0.05% tail of distribution of the p-values, 338 variants, were assigned as outliers for further analysis (referred to as “GWA outliers” hereafter).

3.10. Calculating and Bootstrapping Temporal Autocovariance of GWA outliers

To demonstrate the directional changes over time in allele frequencies of the GWA outliers which are accountable for the growth variations, temporal covariance of the outlier loci was calculated in R using a custom script replicating the cvtkpy functions. I used delta values of different time windows, lag-2 and lag-3, contrary to those with lag-1 provided in the package, which always uses consecutive time points to calculate the allele frequency changes. This was to avoid including a shared time point in calculating autocovariance which showed positive covariance values even in the simulated neutral populations. To assess the significance of observed covariance, a permutation test was conducted calculating temporal covariance values using 338 random loci sampled from all SNP sites in GWA analysis. The observed values were compared to the distribution of 1000 random permutations.

3.11. Gene Identification and Gene Ontology (GO) Term Analysis

To further assess the biological relevance of any outlier loci or windows from genomic analysis, two approaches were employed, 1) by searching for functional annotations in targeted genes for GWA outlier SNPs and 2) by gene ontology (GO) term enrichment analysis using a set of outlier. For 1), among the 338 SNPs assigned as GWA outliers, only regions with clustering outliers with flanking SNPs with low values (marked with red arrows in Figure 12) were examined in depth. Genes located at or within 5 Kb up- and downstream of the outliers were further searched for their biological functions in the literature (Table 1). The

search was carried out using the gene names or descriptions, targeted with or without key words, e.g., fish, growth, maturity, and reproduction to find the most relevant functions to this study. Genes were listed by cross referencing each SNP to annotated genes in the gadMor3.0 annotation database ("gmorhua_gene_ensembl") in Ensembl using the BioMart v2.54.1 R package (Durinck et al. 2005). Same database and workflow were used in identifying genes lying within F_{st} outlier windows and in overlapping windows of F_{st} and GWA outliers. With the listed sets of genes, enriched GO terms were identified using the GO terms provided in the annotations of the gadMor3.0 database as “universe.” The workflow was based on the vignette provided by GOstats v2.64.0 R package (Falcon and Gentleman 2007).

4. RESULTS

4.1. Temporal Genomic Differentiation

To investigate any temporal differentiation of EBC over the last 25 years (1996-2019), a set of SNPs in 115 “random” samples were used in population summary statistical approaches. First, nucleotide diversity (π) of 50kb windows along the genome as well as genome-wide value were calculated to explore if there are any significant differences among the temporal populations (Figure 4 (a)). Here, the genome-wide π were comparable among each other without a temporal pattern (ranging from lowest value of 0.0071 for 1996 to highest value of 0.0077 for 2008). Additionally, the windowed π values generally fluctuate along the genome without clear patterns among different catch years. This is likely due to the variation in level of genetic diversity from varying recombination rate along the chromosomes, e.g. centromere regions generally suppressed with recombination (Sardell and Kirkpatrick 2020; Tigano et al. 2021). Some divergence was observed at the beginning of LG2 and in the middle of LG7, which were most likely caused by the inverted regions (details in *section 4.3*). Absolute divergence between populations (d_{xy}) were computed comparing different catch years to the first time point 1996 in the same windows along the genome (Figure 4(b)). Overall pattern shows slightly yet consistently increased d_{xy} values as the time windows stretch further. As this pattern persists all along the genome, it indicates drift over time.

Lastly, principal component analysis (PCA) first showed a distinct clustering pattern according to the inversion genotype of samples (explained in *section 3.4*, Figure 5(a)). After removal of SNP sites within the inversions, no clusters based on the temporal populations remained (Figure 5(b)) This indicates that there is no population structure based on the catch year in the genome-wide level.

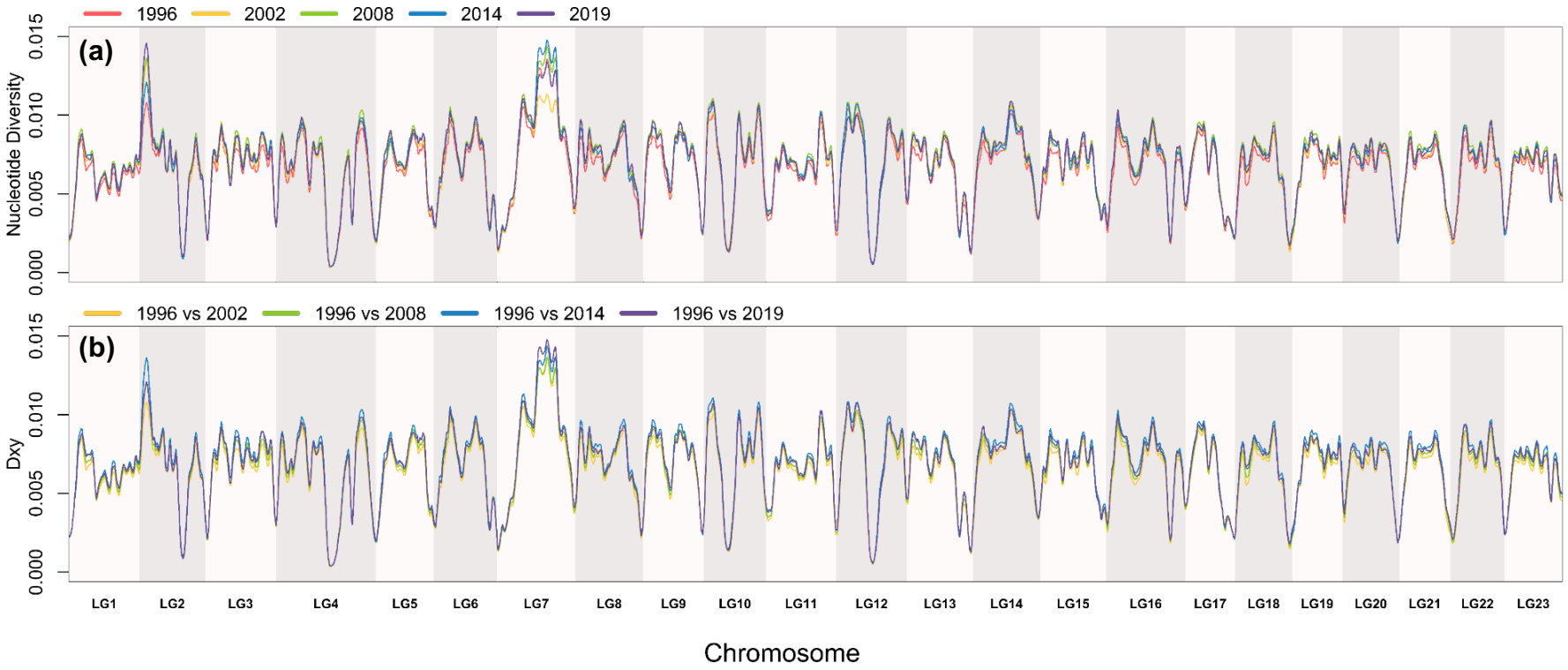


Figure 4. Population genetic statistics in 50Kb non-overlapping windows along the genome
(a) Nucleotide diversity (π) for each catch year and (b) absolute divergence between populations (d_{xy}) of first time point 1996 to all other years. Colours as in the legends above the plots. A total of 81,462,138 invariant sites and variant SNPs were used to calculate the values. For plotting, an R function "loess.smooth" was used to smooth the curves for visual ease.

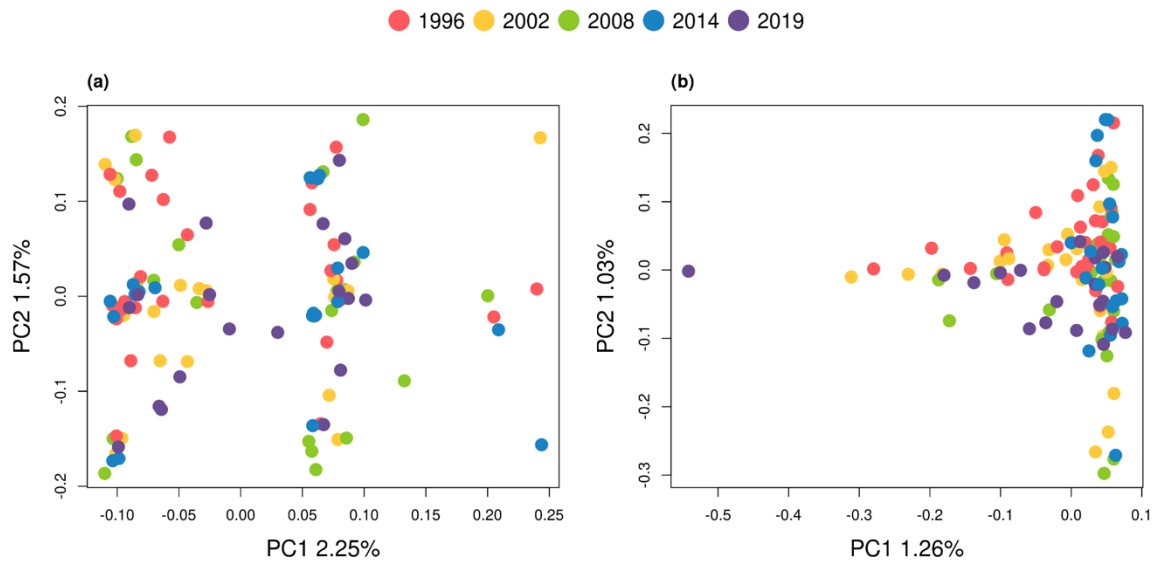


Figure 5. Principal component analysis of 115 "random" samples.
(a) Including all 4,685,343 SNPs (after filtering for MAF > 0.01). PC1 explains 2.25% of all variations in the genotypes and PC2 explains 1.57%. (b) Excluding sites in the inversions in LG2, 7, and 12. PC1 explains 1.26% of all variations in the genotypes and PC2 explains 1.03%. The clustering pattern observed in (a) disappears once the inversion is removed in (b). Each individual is coded in colour according to the catch years as in legend.

4.2. Genome-wide Temporal Autocovariance of Allele Frequency Changes

To detect genome-wide signals of directional selection, temporal autocovariance of allele frequency changes were calculated (Buffalo and Coop 2020; 2019). The theory predicts that the covariance of allele frequency changes over multiple time points should be positive, when there is directional selection, as opposed to drift, acting on genomes. This is due to the linkage disequilibrium over neutral loci to the focal site under selection, producing concurrent directional change in allele frequencies (Smith and Haigh 1974; Charlesworth, Harvey, and Barton 2000). The marked genome-wide pattern of positive covariance would disappear as generation continues, levelling down to zero, as the linkage disequilibrium breaks down over generations. The pattern of genome-wide covariance of temporal EBC populations showed positive values for deltas of three consecutive time points, the first off-diagonal cells in the covariance matrix (e.g. cov(Δ1996-2002, Δ2002-2008), then scale down to near zero for further time windows (Figure 6). These time intervals of significant change were somewhat inconclusive to interpret. Hence, as a validation step, I checked whether similar patterns of significant covariance would be detected by random processes as well. Accordingly, I set up a simulation of neutrally evolving populations to compute temporal covariances as a control. A Wright-Fisher model of neutral evolution was employed to create the simulated populations and the same sampling scheme was applied as the wild population to replicate the real situation. The resulting simulated covariance values were of comparable magnitude (around 0.02-0.03) than the actual results from the data set for the first off-diagonal covariances (Figure

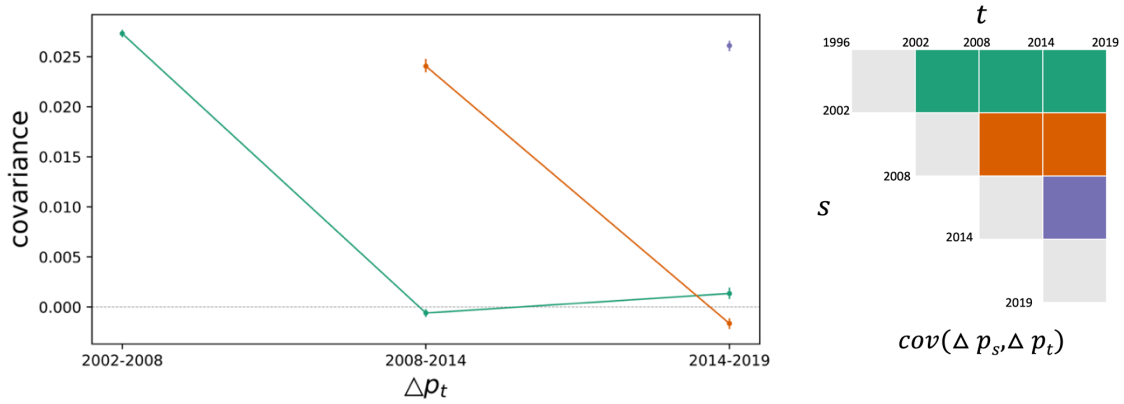


Figure 6 Genome-wide temporal covariance analysis on SNP polymorphism through time. Each line in the covariance plot represents the temporal covariance, cov(Δp_s, Δp_t), calculated using allele frequency changes in two time windows of *s* and *t*; the lines are coloured accordingly to rows of the temporal covariance matrix on the right side. The x-axis of the plot shows the later time windows in the calculation, Δp_t. For example, the three green points are, from left, cov(Δ1996-2002, Δ2002-2008), cov(Δ1996-2002, Δ2008-2014), and cov(Δ1996-2002, Δ2014-2019). Error bars of 95% confidence interval calculated by bootstrapping covariance are drawn as lines over each point.

7). These results show that the positive covariance values of three consecutive time points, as it is implemented right now, are unreliable for detecting real directional selection, for reasons that are beyond the scope of my thesis. Altogether, I can only state that I was unable to find evidence for directional selection at the genome-wide level using this approach, which is, however, no safe evidence for the absence of any selection. Having said this, temporal

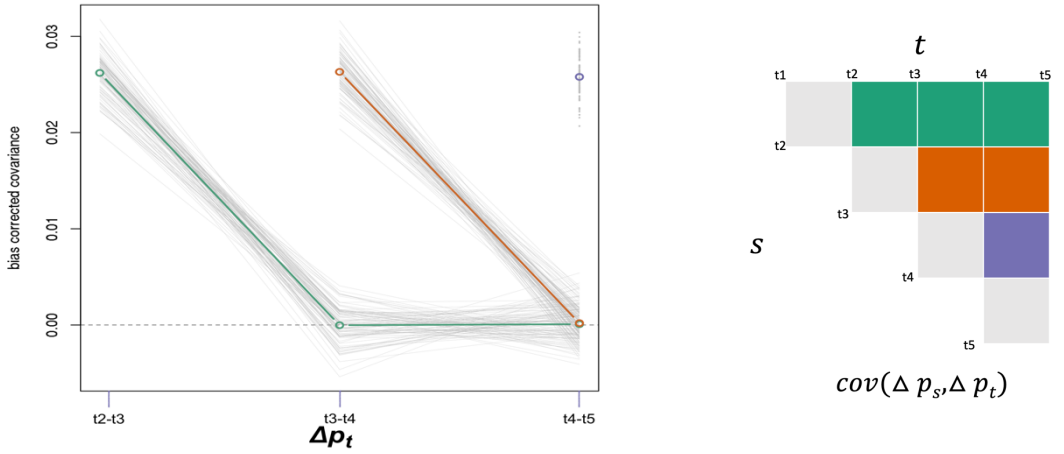


Figure 7 Simulated genome-wide temporal covariance through time in the absence of selection.
Similar to Figure 6, each line in the covariance plot represents the temporal covariance, cov(Δp_s, Δp_t), calculated using allele frequency changes in two time windows of *s* and *t*; the lines are coloured accordingly to rows of the temporal covariance matrix on the right side. The x-axis of the plot shows the later time windows in the calculation, Δp_t. Instead of the catch years, simulated generations (t1 - t5) were used. The median of all 100 simulated populations are plotted in colours and all temporal covariance values are plotted in grey lines to show random distribution of covariance values in a scenario of neutral evolution.

covariance results are in line with a lack of temporal differentiation found in genomic diversity (π) and in the PCA analysis.

4.3. Regions of Temporal Selection

In addition to the global patterns, I examined specific regions of interest to detect selection signals in a targeted approach. First, I computed F_{st} values in 20kb non-overlapping windows comparing 1996 and 2019 to scan for regions which have differentiated the most relative to the genome-wide average F_{st} (Figure 8). The windows with 5% highest F_{st} values, a total of 1466, were assigned as outlier windows. Pronounced signals of high F_{st} values in LG2 and LG12 as well as low values in LG7 were observed, which are caused by inversions in the region (followed up below). Apart from that, the highest F_{st} values were spread across the genome, some of which appear in peaks of clustered outliers. GO term enrichment analysis was conducted using 575 genes residing within the outlier windows (Supplementary Table 2). Several enriched GO terms were enriched in several sub-categories, which are highly related to the growth of a fish. For example, metabolisms and processing of macromolecules such as amino acids, fatty acids, and carbohydrates which in turn are key to any growth process. Fatty acid oxidation is strongly related to use of energy sources in response to feeding conditions (Turchini and Francis 2009; Stubhaug, Lie, and Torstensen 2007; J. Ø. Hansen et al. 2008) and cAMP biosynthesis is part of processing ATP, which is also critical in regulations of hormones involved in metabolism and reproductions (Takahashi and Ogiwara 2023; Miki, Van Heerden, and Fitzpatrick 1997). Also, regulation of TOR pathway, which is crucial in sensing growth hormone, nutrient or oxygen condition (Hietakangas and Cohen 2009; Dobrenel et al. 2016), was found to be enriched. As expected, some enriched biological pathways do not always show direct relevance to growth. Other highly represented clusters of GO term are in regard to developments such as gastrulation, convergent extension involved in axis elongation, and tissue morphogenesis. Interestingly, regulation of neural retina development together with melanosome transport, which is involved retinal pigmentation, may suggest temporal differentiation in the visual sensory system in EBC which is potentially relevant to depth adaptation, thus vertical movements (Berg et al. 2017; Pampoulie et al. 2015).

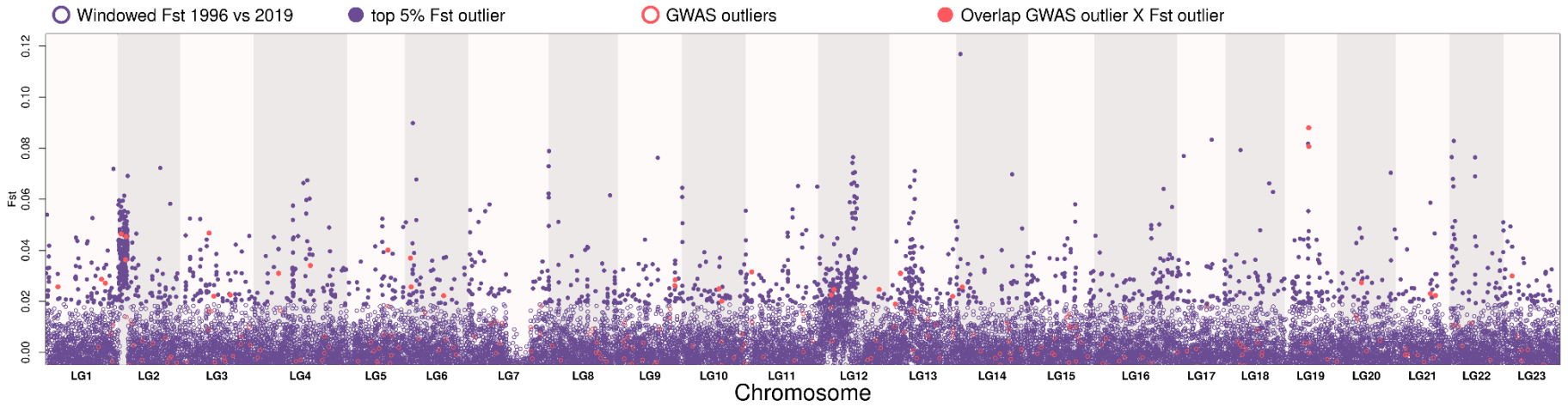


Figure 8. A Manhattan plot of F_{st} values in 20kb windows along the genome.
Pairwise F_{st} values of 1996 and 2019 in 20 Kb non-overlapping windows were calculated along the whole genome. Filled purple points indicate the highest top 5% of genome-wide F_{st} outlier windows. Windows where GWA outlier SNPs lie are marked as open red circles. When the windows with GWA outlier SNPs are also assigned as F_{st} outliers, they are highlighted as filled red circles.

As I observed highly conspicuous deviations in F_{st} and π values in the previously reported inverted regions in linkage group 2, 7 and 12 (Figure 4(a) and Figure 8), inversion frequencies for each temporal population were calculated. Interestingly, only the inversion in LG12 was decreasing in its frequency consistently over time (Mann-Kendall test for monotonic trend: p-value = 0.027) (Figure 9). Within this inversion, another block of inverted region, so called “double crossover” (DC), was reported to be private to the EBC population (Matschiner et al. 2022). The study emphasised the presence of a vitellogenin gene complex which is important in maintaining egg buoyancy (Sullivan and Yilmaz 2018). Thus, I tracked the frequencies of the DC region over time (yellow in Figure 9) Unlike the consistent decrease in the inversion frequency of LG12, frequency of the DC within only decreases until 2014 then picks up in 2019. So, it seems that while the large inversion in LG12 behaves under directional selection as a whole, the DC escapes from this pressure and is rather either drifting or under balancing selection on its own.

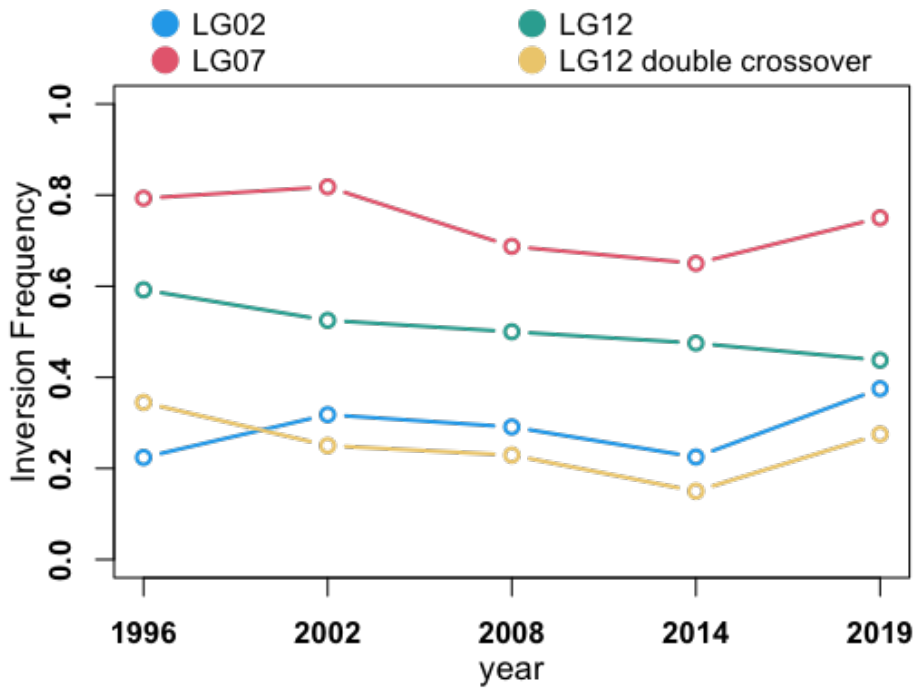


Figure 9. Inversion frequency changes over time.
The frequency of ancestral allele of each inverted region in LG02, LG07, and LG12, and the double crossover within LG12 are plotted over study period. The inversions in LG02 and LG07 display an inconsistent pattern. For the inversion in LG12, a monotonic decrease in frequency over time is observed that is statistically significant (Mann-Kendall test for monotonic trend: p-value = 0.027), whereas the frequency of double crossover within the region changes independently.

4.4. Temporal Changes in Growth Rates

To incorporate phenotype data to genotype information, a total of 152 fish individuals were successfully aged using archived otoliths. The oldest fish was 7 years old caught in 1996 and the oldest individuals from more recent years (2014 and 2019) were 5 years old (Supplementary Table 1). Using the distance from the core to each chemical annulus, von Bertalanffy growth parameters were estimated for each fish individual and each temporal population (Supplementary Table 3). The von Bertalanffy growth curves using estimated parameters for each temporal population are presented in Figure 10, along with observed otolith radius (=chemical annuli) at age. Fish from 1996 grow to become larger in the later age than fish from recent years, even though the rates of reaching a size tend to vary among temporal populations as well as among different ages. The median of estimated individual length at infinity, L_∞, decreased by 48% from 1996 to 2019, with a small inconsistency in 2008 (Figure 11(a)). More comprehensively, a stark decrease from 1150 mm in 1996 to 539 mm in 2019 in terms of L_∞ was predicted by back-calculating maximal fish length. Accordingly, growth coefficient k increases over the period with the same trend in 2008 in both group parameters and individual parameters (Figure 11(b)). A growth performance index (Φ) for each fish of

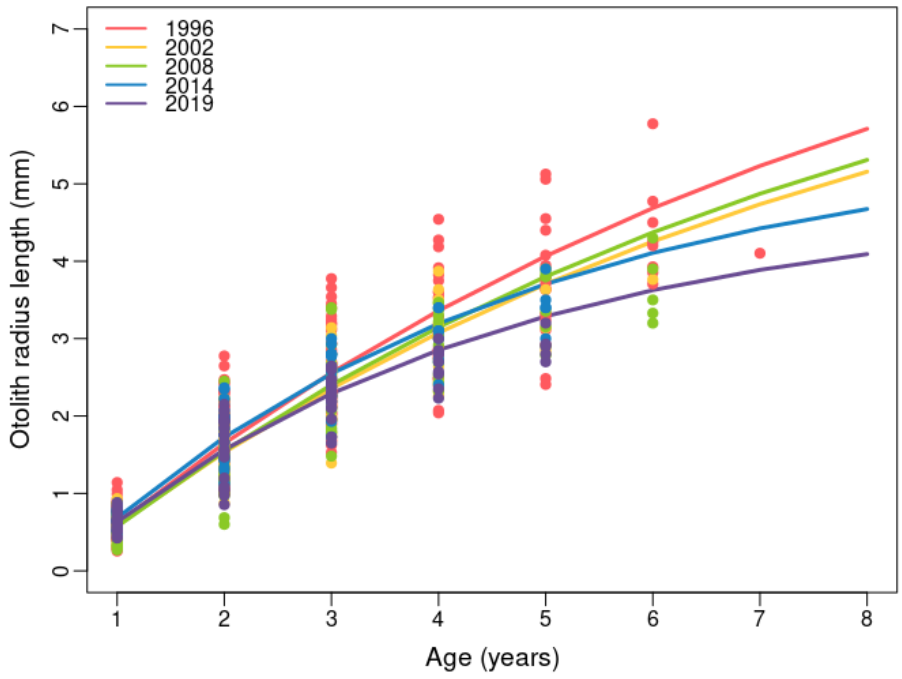


Figure 10. Estimated von Bertalanffy growth curves for each catch year. The von Bertalanffy growth curves are based on otolith readings (cf. Figure 3) and were plotted using estimated sets of parameters for each temporal population of "random" and "phenotype" samples. The group 1996 in this figure also includes "phenotype" samples (catch year from 1996-1998) as they are treated as one temporal population in the model. Each point depicts observed otolith radius to chemical annuli at age coloured based on the individuals' catch year.

different years, which summarises the growth (Moreau, Bambino, and Pauly 1986), showed a consistent decrease in time (Figure 11(c)). Additionally, the otolith radii at age 1 for all fish were back-calculated to body length and compared to examine any deviation in the juvenile growth of EBC in temporal trend (Figure 11(d)). Although mean distances to the first-year radii do not differ, the variance of the radii significantly reduced over time (Bartlett's test for variance, p-value = 0.02868). Overall, this supports the initial hypothesis that the population has shifted to grow slower and reach smaller size at later age during the study period of heavy fishing pressure. Furthermore, phenotypic diversity in juvenile growth has truncated (Figure 11(d)), with a removal of faster and slower growing individuals from the population.

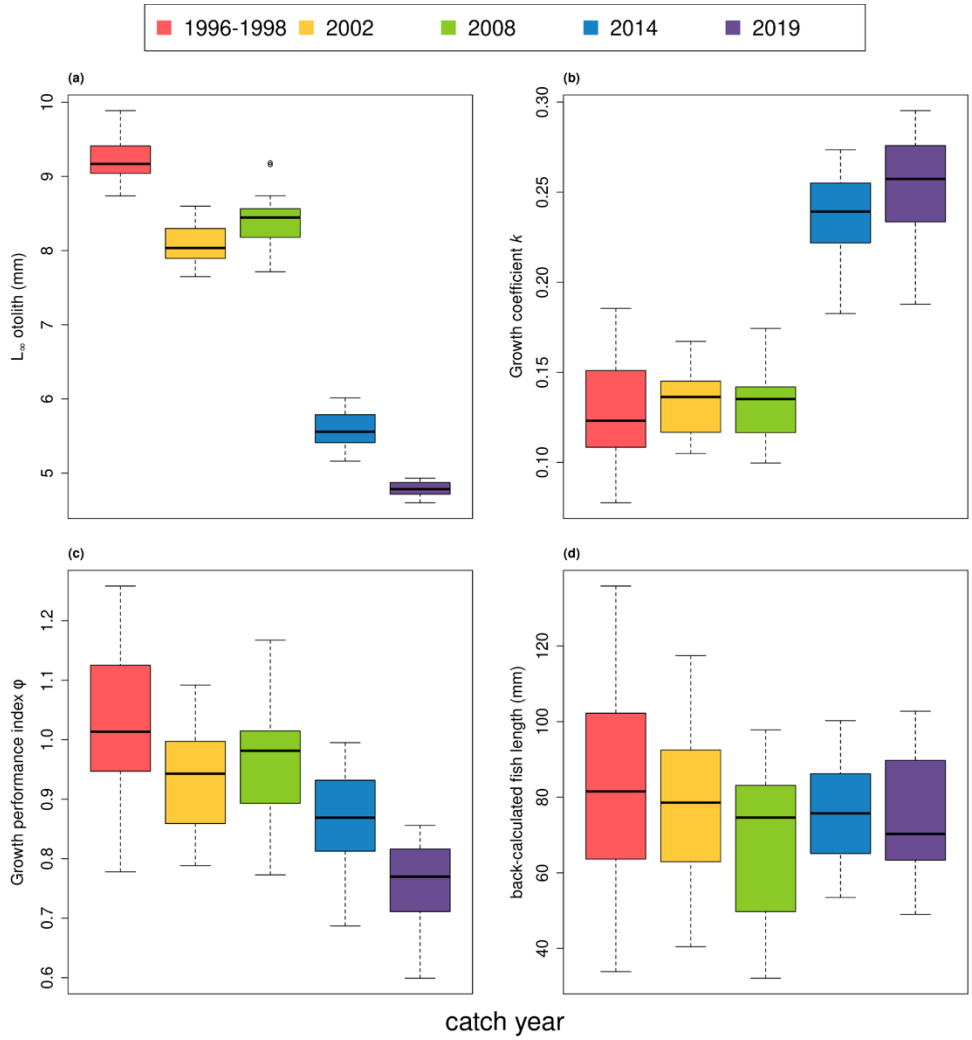


Figure 11. Boxplots of estimated individual von Bertalanffy growth parameters over time.
The individual level parameters were estimated in the growth model using "random" and "phenotype" samples. The posterior predictions of estimated parameters of individual level were grouped in temporal populations to calculate the median and the lower and higher whiskers. (a) L_∞, and (b) growth coefficient k, (c) growth performance index, Φ, and (d) otolith radii at age 1 of all fish. Colour codes are based on individuals' catch years as in the legend.

4.5. Genotype-Phenotype Association

I then conducted a genome-wide association (GWA) analysis, using the modelled growth of all individuals ("random" and "phenotype" samples) as phenotype (Figure 1). In a univariate linear mixed model, growth performance index (Φ) calculated with estimated von Bertalanffy growth parameters, was used as a phenotype and regressed against a total number of 679,584 biallelic SNPs as genotypes. A Manhattan plot showing the negative log of p-values of SNP sites showed relatively weak signals on an absolute scale (-logP < 7) while some regions clearly featured outlier peaks throughout the genome (Figure 12). The distribution of p-value in itself shows the polygenic nature of growth as well as the methodological character of GWA analysis (discussed in the *section 5.1*). Under a formal correction for multiple testing only a few regions would remain at p = 0.0127. As this study was designed as an explorative approach, an outlier status was instead assigned to 338 SNP loci that lie in the lowest 0.05% of the distribution of p-values.

Two approaches were employed to seek for biological relevance of the assigned outliers. First, regions with a peak of outliers, clustered adjacently to each other with flanking SNPs with low values, were examined in depth. Genes which span over 5 Kb up- and downstream of the outliers were listed as candidate genes linked to growth variations. Amongst these candidate genes, the three most evident peaks of outliers in LG3, LG6 and LG14 (marked with red arrows in Figure 12) contained genes which were most relevant to growth or maturity from functional annotation and literature search (Table 1): In linkage group 3 lie *ncapg*, which is differentially expressed in puberty in salmon (Crespo et al. 2019) and *fam184b*, which is associated with body weight at first egg in chicken (Fan et al. 2017), linkage group 6 included *pde4d* gene which showed response in the transcriptome of fast growth line in a rainbow trout (Cleveland, Gao, and Leeds 2020), and in linkage group 14 lie *mettl21e* which was linked to growth in pupfishes and intramuscular fat deposition in cattle (Fonseca et al. 2020; Patton et al. 2022).

Second, gene ontology (GO) analysis of 169 candidate genes showed significant enrichment of multiple biological pathways (Table 2). Diverse metabolic processes involving amino acids, glucose, and phosphate were significantly enriched, which is critical in growth of a fish (Pelletier et al. 1994; Finn and Fyhn 2010). Interestingly, ultradian rhythm, which is found to be important in diverse functions including growth, reproduction, and metabolism in fish (Zhdanova and Reebs 2006; Sánchez-Vázquez et al. 2019; Cowan, Azpeleta, and López-Olmeda 2017; Frøland Steindal and Whitmore 2019) was one of the top enriched pathways. Some GOs are seemingly only weakly connected to growth. Pathways involved in mitotic cell cycle and development (e.g., regulation of mitotic cell cycle, embryonic, myotome development) together with multicellular organismal water homeostasis, form a large part of the list. These pathways in common relate to a biological process called "oocyte maturation".

In fish, oocyte maturation takes place before ovulation and is necessary for a successful fertilisation (Nagahama and Yamashita 2008), which may be indirectly linked to growth.

Table 1. A list of genes intersecting or neighboring GWA outlier SNPs with its position and description.
A list of genes unique in the "ensembl_gene_id" located at or in 10 Kb surrounding regions of GWA outlier SNPs was subjected to a search for their functional annotations in the literature. Columns, ensembl_gene_id, chromosome_name, external_gene_name, description, start_position, and end_position, are annotations in the gadMor3.0 reference genome extracted from Ensembl database. When the external_gene_name were not provided by the database, search in the NCBI gene database or orthologs' name were filled in (NCBI Genes). Functional annotations of the genes in the most relavant context to this study, in column "known biological functions from literature", were listed by searching the gene names with or without keywords (e.g. fish, growth, weight, maturity, and reproduction) in the literature search. When there were no search results which showed direct or indirect biological relevance in the targeted context, they were marked as "Not found in literature". Some genes were catalogued with only weak matches to orthologs in other species in the database, thus marked as "NA (Not applicable)". Rows containing genes which are most relevant to this study are highlighted in grey.

ensembl_gene_id	external_gene_name	chromosome_name	known biological functions from literature	description	start_position	end_position	References
At the outlier loci							
ENSGMOG00000032747	HEPACAM	3	cell-adhesion, cell motility, cancer suppressor gene	carcinoembryonic antigen-related cell adhesion molecule 6-like [Source:NCBI gene (formerly Entrezgene);Acc:115540996]	13790699	13856484	Moh and Shen 2009; Arstikaitis, Gagné, and Cyr 2014
ENSGMOG00000015953	mnd1	3	meiotic arrest, recombination	meiotic nuclear divisions 1 homolog (S. cerevisiae) [Source:NCBI gene (formerly Entrezgene);Acc:115540214]	20677607	20683019	NCBI
ENSGMOG00000012895	NA	3	NA	NA	21756782	21778636	
ENSGMOG00000016255	haspin	3	mitosis, ciritical larval growth and survival in zebrafish	histone H3 associated protein kinase [Source:NCBI gene (formerly Entrezgene);Acc:115540151]	25267491	25278374	Gallo 2016
ENSGMOG00000016202	ncapg	3	DEGs in salmon puberty	non-SMC condensin I complex, subunit G [Source:NCBI gene (formerly Entrezgene);Acc:115540152]	25305001	25318049	Crespo et al. 2019
ENSGMOG00000007843	PDE4D	6	transcriptomic response bred line for fast growth in rainbow trout	phosphodiesterase 4D, cAMP-specific [Source:NCBI gene (formerly Entrezgene);Acc:115545011]	16947270	17078303	Cleveland, Gao, and Leeds 2020
ENSGMOG00000013441	trpm1b	9	retina pigment development	transient receptor potential cation channel subfamily M member 1-like [Source:NCBI gene (formerly Entrezgene);Acc:115550405]	21730570	21750419	Kastenhuber et al. 2013
ENSGMOG00000037198	ciart	9	Transcriptional changes in the process of reproductive hormone affecting circadian rythm in zebrafish.	circadian-associated transcriptional repressor-like [Source:NCBI gene (formerly Entrezgene);Acc:115550867]	21823470	21831852	Zhao, Castiglioni, and Fent 2015
ENSGMOG00000017135	coro1ca	13	Not found in literature	coronin, actin binding protein, 1Ca [Source:NCBI gene (formerly Entrezgene);Acc:115556521]	25841273	25924738	
ENSGMOG00000008588	ercc5	14	higher rate of malformations and decreased embryo viability in fish.	excision repair cross-complementation group 5 [Source:NCBI gene (formerly Entrezgene);Acc:115558732]	21543979	21552546	Dey et al. 2023
ENSGMOG00000016695	PPFIBP2 (orthologs)	14	human fetal abnormality	PPFIA binding protein 2a [Source:ZFIN;Acc:ZDB-GENE-070705-277]	22269074	22285193	Carss et al. 2014
ENSGMOG00000018629	kcnk2b (ortholog)	21	increased expression during puberty in zebrafish	NA	4143319	4168663	Loganathan et al. 2017
ENSGMOG00000013114	snx17	21	intracelluar protein transport, in a conserved genomic region (together with atraid) associated with miR-133b involved in oogenesis in a tilapia	sorting nexin 17 [Source:NCBI gene (formerly Entrezgene);Acc:115534617]	4307230	4333109	Ma et al. 2021

5 Kb up- and down-stream							
ENSGMOG00000026566	NA	3	NA	NA	13810816	13811780	
ENSGMOG00000015878	TMEM131L	3	Not found in literature	transmembrane 131 like [Source:NCBI gene (formerly Entrezgene);Acc:115540213]	20642815	20676221	
ENSGMOG00000030622	NA	3	NA	NA	25275974	25276992	
ENSGMOG00000036363	fam184b	3	chicken body weight at first egg	family with sequence similarity 184 member B [Source:NCBI gene (formerly Entrezgene);Acc:115540150]	25280244	25303554	Fan et al. 2017
ENSGMOG00000022331	lcorl	3	Differential expression related to the length of the neonate at birth in human	ligand dependent nuclear receptor corepressor-like [Source:NCBI gene (formerly Entrezgene);Acc:115540149]	25319776	25337592	Hatem et al. 2022
ENSGMOG00000036563	NA	13	NA	NA	25928210	25928944	
ENSGMOG00000033950	cenpq	14	Not found in literature	centromere protein Q [Source:NCBI gene (formerly Entrezgene);Acc:115559135]	21398766	21402387	
ENSGMOG00000025157	gmo-mir-155	14	Not found in literature	gmo-mir-155 [Source:miRBase;Acc:MI0036008]	21410103	21410161	
ENSGMOG00000003226	ephrin-B2a-like	14	angiogenesis	ephrin-B2a-like [Source:NCBI gene (formerly Entrezgene);Acc:115559324]	21411256	21419004	
ENSGMOG00000025102	trmt10c	14	Not found in literature	tRNA methyltransferase 10C, mitochondrial RNase P subunit [Source:ZFIN;Acc:ZDB-GENE-041114-12]	21536364	21543958	
ENSGMOG00000035263	blzf1	14	heart function, development in medaka	basic leucine zipper nuclear factor 1 [Source:NCBI gene (formerly Entrezgene);Acc:115558734]	21538764	21543958	Gierten et al. 2023
ENSGMOG00000030760	mettl21e	14	linked to growth in pupfishes, intramuscular fat deposition in cattle	methyltransferase like 21e [Source:NCBI gene (formerly Entrezgene);Acc:115558735]	21552352	21557877	Patton et al. 2022, Fonseca et al. 2020
ENSGMOG00000024865	NA	14	differentially expressed in response to temperature in stickleback, also generally skeletal muscle development related	protein-lysine methyltransferase METTL21C-like [Source:NCBI gene (formerly Entrezgene);Acc:115558577]	21560583	21565349	Metzger and Schulte 2018
ENSGMOG00000013100	atraid	21	bone differentiation	all-trans retinoic acid-induced differentiation factor [Source:NCBI gene (formerly Entrezgene);Acc:115534618]	4334479	4337000	

Table 2. A list of enriched gene ontology (GO) term using all 338 GWA outlier SNPs.
A total of 679,584 SNPs were used in GWA analysis with individual growth performance index, Φ, as a phenotype. The top 5% of the SNPs with lowest p-values, total 338 sites, were assigned an outlier status. The genes intersecting with these outlier loci were subjected to gene ontology (GO) enrichment test to identify any biological functions that correlate to growth performance. P values are adjusted using false discovery rate. Only biological process was presented among GO categories for the analysis.

GO.term	GO.name	p.value.adjusted
GO:0006468	protein phosphorylation	0.04040673037
GO:0090235	regulation of metaphase plate congression	0.04040673037
GO:0007624	ultradian rhythm	0.04040673037
GO:0043412	macromolecule modification	0.04040673037
GO:0032012	regulation of ARF protein signal transduction	0.04040673037
GO:0050891	multicellular organismal water homeostasis	0.04040673037
GO:0009794	regulation of mitotic cell cycle, embryonic	0.04040673037
GO:0006011	UDP-glucose metabolic process	0.04040673037
GO:0046373	L-arabinose metabolic process	0.04040673037
GO:0140673	co-transcriptional chromatin reassembly	0.04040673037
GO:0034080	CENP-A containing chromatin assembly	0.04040673037
GO:0070285	pigment cell development	0.04040673037
GO:0001667	ameboidal-type cell migration	0.04073455525
GO:0071705	nitrogen compound transport	0.04078593448
GO:0006796	phosphate-containing compound metabolic process	0.04436890185
GO:0032968	positive regulation of transcription elongation by RNA polymerase II	0.04436890185
GO:0061055	myotome development	0.04436890185
GO:0051303	establishment of chromosome localization	0.04436890185
GO:0048070	regulation of developmental pigmentation	0.04436890185
GO:0071702	organic substance transport	0.04436890185
GO:0006325	chromatin organization	0.04436890185
GO:0060236	regulation of mitotic spindle organization	0.04436890185
GO:0007076	mitotic chromosome condensation	0.04436890185
GO:0006857	oligopeptide transport	0.04436890185
GO:0006546	glycine catabolic process	0.04436890185
GO:0098727	maintenance of cell number	0.04436890185
GO:0006611	protein export from nucleus	0.04436890185
GO:0097324	melanocyte migration	0.0464646647
GO:0007030	Golgi organization	0.0464646647
GO:0035825	homologous recombination	0.0464646647
GO:0007131	reciprocal meiotic recombination	0.0464646647
GO:0006891	intra-Golgi vesicle-mediated transport	0.0464646647
GO:0008053	mitochondrial fusion	0.0464646647
GO:1901564	organonitrogen compound metabolic process	0.04969126382
GO:0098813	nuclear chromosome segregation	0.04969126382
GO:0030198	extracellular matrix organization	0.04969126382

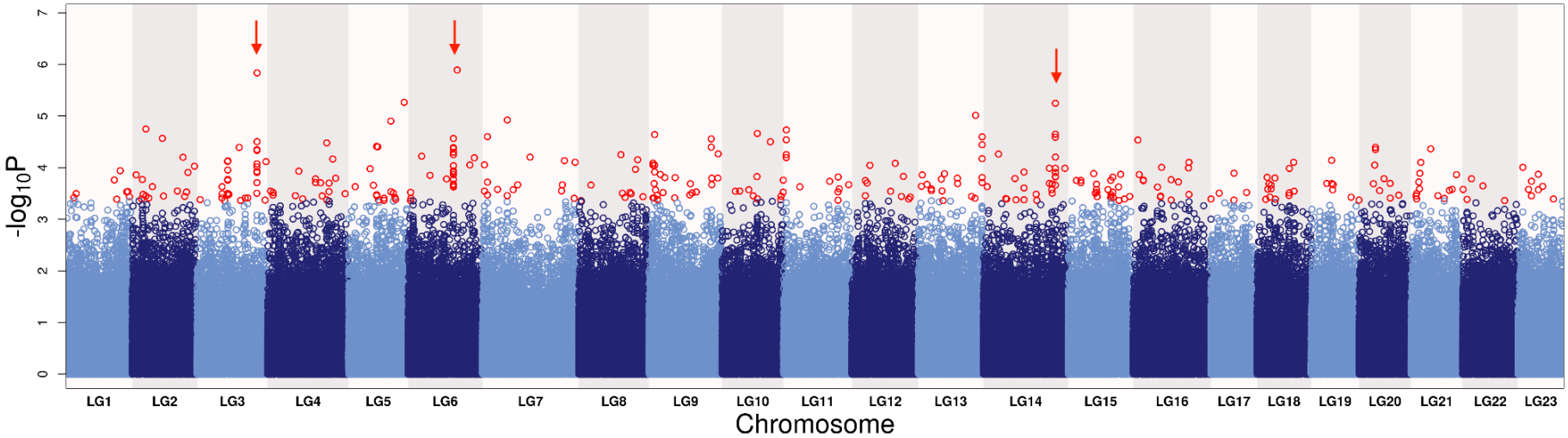


Figure 12. A Manhattan plot of -logP values in genome-wide association (GWA) analysis.
A total of 152 samples were subjected to GWA using the sequenced genotypes, 679,584 SNPs (>0.05 MAF), and estimated growth performance index as phenotype. Negative log transformed Wald test p-values for each SNP were plotted along the genome. Outlier status was assigned for 338 SNPs with lowest 0.05% p-values (in red circles). The cutoff for outliers were selected based on the visual examination of this Manhattan plot, so as to include distinctive peaks with clustering outliers and at the same time exclude spurious outliers consisting of single SNPs only.

4.6. Integration of Selection Scans and GWA analysis

I next examined the interesting overlap between my two principal results, the selection scans and GWA analysis, in order to substantiate the selected component of growth in EBC. The integration of these two independent results aims to study whether regions identified as outliers in GWA have preferentially undergone selection through time. First, I calculated covariance values for the GWA outliers to observe directional change in their allele frequency. Specifically, lag-2 (i.e. cov(Δ1996-2008, Δ2002-2014) and cov(Δ2002-2014, Δ2008-2019)) and lag-3 (i.e. cov(Δ1996-2014, Δ2002-2019)) autocovariance (as illustrated in the right column of Figure 13) were calculated, to avoid problem of shared time point as mentioned

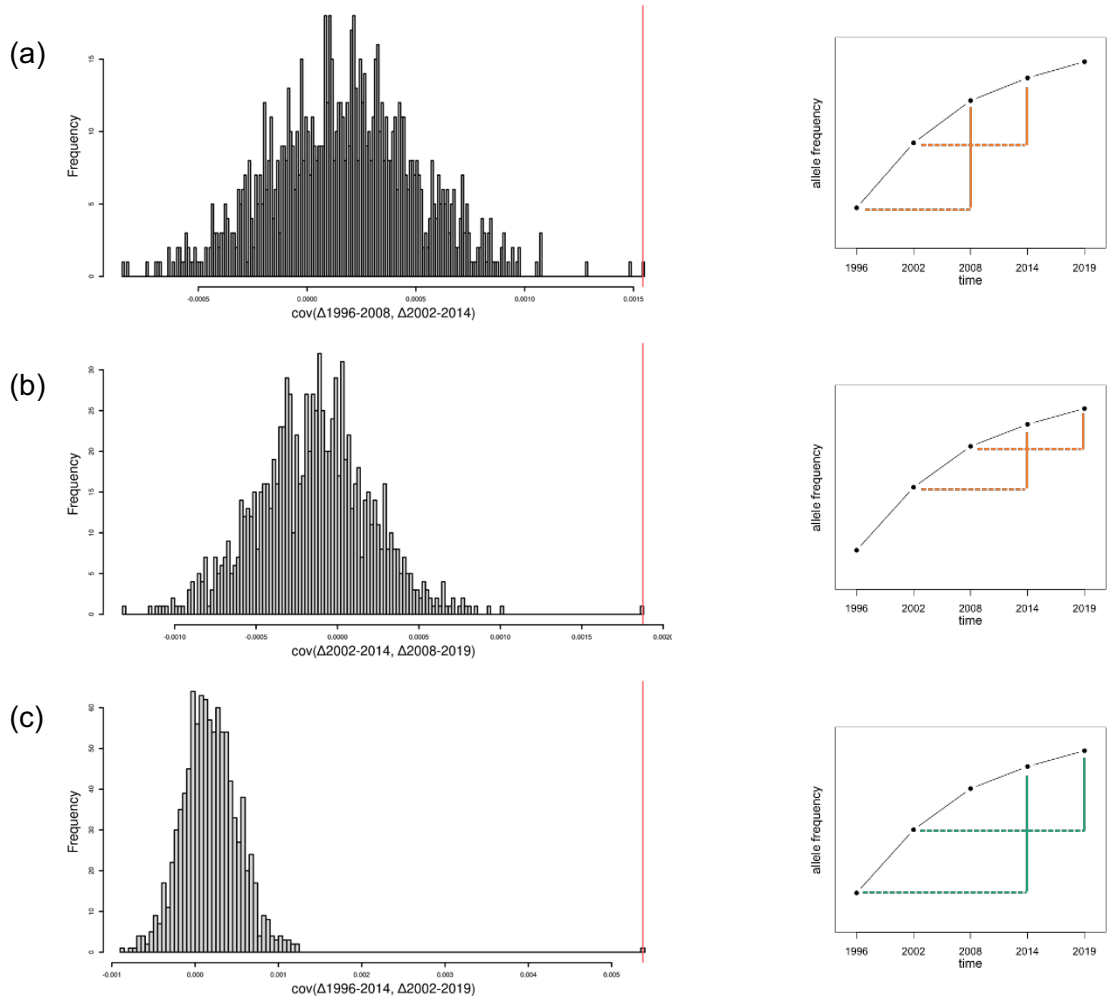


Figure 13. Frequency distribution of lag-2 and lag-3 temporal covariance of randomly permuted 338 SNPs compared to GWA outliers.
To detect signals of directional selection of GWA outliers which are correlated to growth performance, temporal covariance of allele frequency of the outliers were calculated and compared to values from randomly permuted 338 SNPs. The lag-2 and lag-3 time windows were used for calculating covariance to avoid shared time points, as in the right side of each histogram visualised with a hypothetical allele frequency change. The frequency distribution of covariance of 1000 permutations of random SNPs are presented. The covariance was calculated in lag-2 time windows, namely cov(Δ1996-2008, Δ2002-2014) in (a) and cov(Δ2002-2014, Δ2008-2019) in (b), and lag-3 time window, cov(Δ1996-2014, Δ2002-2019) in (c). The red vertical lines depict the corresponding real covariance values of GWA outlier SNPs.

above. Temporal covariances of allele frequency changes of 338 outlier SNPs exhibited remarkably high values of 0.00154 and 0.00187 for lag-2 and 0.00537 for lag-3 (Red lines in Figure 13). A custom-made randomization test generated an expected null-distribution against which the observed values were tested (Figure 13). Conducting 1000 permutations of random 338 SNPs sites to calculate covariances, the observed GWA outliers display much higher values than the null-distribution. This result strongly supports that the GWA outliers, highly correlated to the growth performance collectively, experienced a selection pressure and responded to change their frequency in a directional manner over time.

Secondly, I analysed how GWA outliers intersect with F_{st} outlier windows. Among the windows of the top 5% of F_{st} values, 33 windows overlapped with the GWA outliers (Figure 6). Again, to test the statistical significance of this overlap, a null distribution was produced with a custom-made randomization test which the observed values can be compared to. Based on 5000 random permutations, wherein 339 random SNPs were chosen to overlap with the outlier windows, the observed number exceeded the higher tail of the expected distribution (Figure 14). This signifies that loci associated with growth performance are predicted to reside in the regions of highest F_{st} between 1996 and 2019.

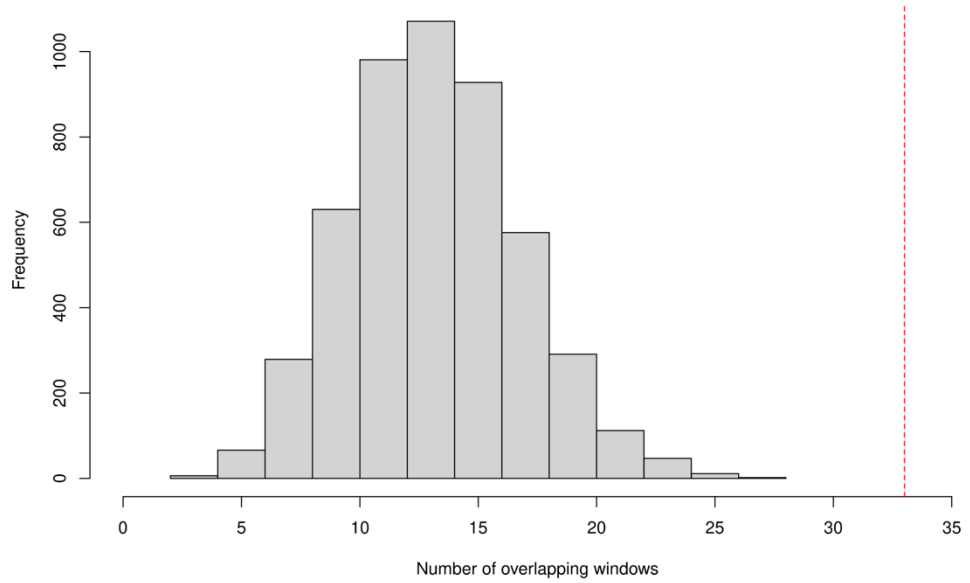


Figure 14. Frequency distribution of the number of randomly overlapping windows of F_{st} and GWA outliers.
A custom-made null model was used to assess the significance of the observed number of overlaps among F_{st} outlier windows and GWA outlier SNPs. To this end, 5000 random permutations of 338 SNPs were overlapped to F_{st} outlier windows. When a GWA outlier SNP (or a randomly chosen SNP in a permutation) resides within a F_{st} outlier window (20 Kb), this window counts as an overlapping outlier window. The null distribution of the number of overlapping outlier windows is presented with the red dashed line presenting the observed number of overlapping windows at 33 in real data.

These two lines of evidence, the positive temporal covariance values of GWA outliers and their significant overlap with high F_{st} windows, strongly indicate the impact of directional selection on the genetic factors under growth variations in EBC.

The significance of these overlapping regions was further explored through GO term enrichment test on overlapping F_{st} windows (Table 3). This is to ensure a nuanced examination more than merely the subset of enriched GO terms of entire GWA outliers. Similar to the GWA results, multiple pathways involved in protein metabolism, meiotic cell cycle, ultradian rhythm and water homeostasis were enriched. Interestingly, “folic acid-containing compound biosynthetic processes” was among the newly listed. Folic acid deficiency in diet has direct implications in fish growth (John and Mahajan 1979; Lin, Lin, and Shiau 2011; Miao et al. 2013; Hardy and Kaushik 2021). The dietary requirement of folic acid in fish emphasises its role in not only growth performance but also diverse functions such as immune responses (Trichet 2010; Badran and Ali 2021) Lastly, the biological process of “response to heat” is indeed highly linked to growth traits in fish. Warmer temperatures as the Baltic sea has been experiencing (Meier et al. 2022), critically impacts the species throughout the lifespan from larva to adult stage (Oomen et al. 2022; Righton et al. 2010) and dynamically interlinked with other environmental factors such as oxygen (discussed below). Thus, it may suggest that the selected slow growth trait was also mediated or accompanied by shifts in heat response over time.

Table 3. A list of enriched GO term using genes within F_{st} windows that overlap with GWA outlier SNPs.
To identify loci which are highly correlated with growth performance and selected over time, the intersections of F_{st} outlier windows and GWA outlier SNPs were investigated. When a GWA outlier SNP resides within an F_{st} outlier window, this window was counted as an overlapping outlier window. Any genes residing within this overlapping outlier windows were subjected to gene ontology (GO) enrichment test to identify any biological functions that correlate to growth performance and at the same time differentiated the most over time. P values are adjusted using false discovery rate. Only biological process was presented among GO categories for the analysis.

GO.term	GO.name	p.value.adjusted
GO:0007624	ultradian rhythm	0.01203089399
GO:0050891	multicellular organismal water homeostasis	0.01442325268
GO:0034080	CENP-A containing chromatin assembly	0.01442325268
GO:0006546	glycine catabolic process	0.02048356121
GO:0035825	homologous recombination	0.02098495744
GO:0007131	reciprocal meiotic recombination	0.02098495744
GO:0009396	folic acid-containing compound biosynthetic process	0.02214772591
GO:0009408	response to heat	0.02678127453
GO:0000122	negative regulation of transcription by RNA polymerase II	0.0330299368
GO:0009069	serine family amino acid metabolic process	0.03431805692
GO:0140013	meiotic nuclear division	0.03509647983

GO:1901606	alpha-amino acid catabolic process	0.03509647983
GO:0042558	pteridine-containing compound metabolic process	0.03509647983
GO:0061982	meiosis I cell cycle process	0.03509647983
GO:0051321	meiotic cell cycle	0.04643225312
GO:0001755	neural crest cell migration	0.04698068426

5. DISCUSSION

This study identifies, for the first time according to my knowledge, a number of genomic regions with associated gene functions that are linked to growth impairment and at the same time seem to be under directional selection in an exploited marine fish population, Eastern Baltic cod. Temporal selection was likely driven by strong and documented overfishing that ultimately led to the life-history change by fisheries induced evolution. Being an uncontrolled study undertaken based on field samples taken from a natural environment that is changing in many other parameters, these results have to be taken with a grain of salt and require further rigorous testing. At the very least, however, I consider the regions and genes identified here as hypothesis generating starting points for further studies.

The most novel findings of this study come from the identification of loci responsible for growth performance, marked as GWA outliers, demonstrating clear evidence of selection. The outlier SNPs collectively exhibit significantly positive temporal autocovariances of allele frequency changes and an excess number of overlaps with regions of high F_{st}. The combination of a selection test and GWA used here is a powerful implementation of detecting an adaptive polygenic trait (Barghi, Hermisson, and Schlötterer 2020), which have responded to a selective pressure. Notably, this study pioneers the application of temporal autocovariance theory to disentangle directional selection from drift (Buffalo and Coop 2020; 2019) in the field samples spanning over multiple time points. Although the method itself needs further validation in diverse field sample designs (discussed in *section 5.2*), the exceptionally high covariance values suggest directional selection acting upon the identified GWA outlier SNPs. Furthermore, as F_{st} of the first and last temporal populations (1996 vs. 2019) represent the most differentiated windows in the genome, the extreme number of overlaps indicates that the GWA outlier regions are amongst the most differentiated over the study period.

Several enriched GO pathways for the overlapping regions of GWA and F_{st} outliers suggest that the selected gene functions are causally linked to altered growth in EBC (Table 3). Light manipulation to trick ultradian rhythm, thus the long term seasonality, is a very common method to control growth and maturity in fish aquaculture including Atlantic cod (Skulstad et al. 2013; Taranger et al. 2010; Karlsen et al. 2006; Hansen et al. 2001). Depending on the applied photoperiod, sexual maturation can be controlled, either postpone or advance, which is tightly entangled to somatic growth of a fish (Hansen et al. 2001; Davie, Porter, and Bromage 2003). In addition, water homeostasis is an important in egg hydration during oocyte maturation process to make floaty eggs, which is one of the major evolutionary acquisitions for pelagic teleost fish (Fyhn et al. 1999). Oocyte maturation takes place before ovulation and is necessary for a successful fertilisation (Nagahama and Yamashita 2008). Specific

hypotheses directly connecting oocyte maturation and growth are currently lacking in the field. Nevertheless, it is well conceivable that the timing of spawning, through control of oocyte maturation, may be critical for successful reproduction, as maturation process is highly affected by energy allocation (Roff 1993), thus tightly linked to somatic growth in a fish's lifespan.

In spite of the obvious, functionally validated links to growth from candidate loci, there seems to be a general lack of congruency in the gene contents or the GO pathways compared to previous studies that experimentally addressed the genomic effects of size selective selection. Therkildsen et al. (2019) resequenced samples from the seminal study of Conover and Munch (2002) that subjected Atlantic silversides to 5 generations of upwards and downward selection with respect to body size. They listed enriched GO terms from highly differentiated loci accompanied by body size changes under different harvest regimes. Here, I found no intersection to my own results, which is perhaps not surprising given that the study itself observed highly divergent genomic responses across replicates under the same treatment. Additionally in Uusi-Heikkila (2015), the genes selected by fishing pressure in an experimental setting were not present among the genes listed as outliers in this study. Lastly, the *vgll3* and *six6* genes that are of high effective size in age at maturity in salmonids species (Barson et al. 2015; Ayllon et al. 2015), a tightly linked yet different life history trait, were not found to be significant in any of my analyses. This lack of consistent patterns of identified genes and pathways in different studies of FIE indicate that there are heterogeneous responses in the genome level either under same phenotype changes, growth, or under same selective pressure, size-selective fishing.

5.1. Complications in Detecting the Basis of Polygenic Traits

There are two layers of complexity in detecting the genetic basis of growth here. One, growth is a highly complex trait intricately linked to multiple life history traits and diverse biological pathways at the phenotypic level. Biologically, a multitude of factors influencing either energy acquisition or allocation contribute to a fish's growth (comprehensively reviewed in Enberg et al. 2012. Energy acquisition involves processes such as sensing, behaviours, feeding, and digestion, while allocation encompasses basic metabolism for maintenance, such as immune response, in addition to morphological developments, and energy storage. Most importantly in the context of this study, allocation to reproduction, such as gonad development, mating and parental care, creates a trade-off between somatic growth and reproduction. And this complexity is yet disregarding the extrinsic effects of environmental factors a fish faces during its lifetime (discussed in *section 5.4*). Nevertheless, as the growth performance index (Munro and Pauly 1983) using von Bertalanffy parameters is derived from bioenergetics of fish (Essington, Kitchell, and Walters 2001; von Bertalanffy 1957), it serves as a

comprehensive summary indicative of a fish's overall growth pattern and potential (Moreau, Bambino, and Pauly 1986).

The second layer of complexity arises from the highly polygenic nature of somatic growth, with possibly hundreds of loci with small effects governing the expression of the quantitative trait (Fisher 1919; Wellenreuther and Hansson 2016; Silventoinen et al. 2003). Exemplifying from human GWA studies of stature, hundreds of common and rare variants collectively explained up to 45% of the variance (Bergey et al. 2018; Marouli et al. 2017; Yang et al. 2010). Most of these SNPs do not show direct biological relevance, as the causal variants can be spatially associated instead of located in the vicinity of the SNPs (Schierding et al. 2016; Schierding, Cutfield, and O'Sullivan 2014). Furthermore, these findings were acquired using a large sample size up to thousands of subjects. In fish, GWA studies on growth traits, mostly in the interest of species of economic importance, reported a relatively small number of significant SNPs, even using a relatively large sample size (Gutierrez et al. 2015; Omeka et al. 2022; N. Li et al. 2018; Sandoval-Castillo, Beheregaray, and Wellenreuther 2022). For example, in Gutierrez et al. 2015, one marker of chromosome wide significance was found using 480 Atlantic salmon individuals, with no clear functional annotation of the gene in the vicinity. Notably, the lack of overlap in genes or pathways among these studies again signifies the complex nature of a quantitative trait with multiple intrinsic processes involved.

Overall, the power of GWA highly depends on the study design, sample size, marker density, effect size of responsible loci, and the linkage disequilibrium and dependency among them, particularly in the context of quantitative traits (Watanabe et al. 2019). In this study, a low sample size of 152 and polygenic and highly plastic nature of growth may explain the absence of genome-wide significance of any SNPs after multiple testing correction. Despite this, the Manhattan plot of -logP values reveals clear peaks of local maxima, which are distinct from spurious signals of noise, indicative of robust genomic signals even within the constraints of a small sample size. Notably, this is the first study to conduct GWA on growth performance in Atlantic cod and marks a promising starting point, underscoring the potential significance of the identified genes and biological pathways in understanding growth variations. Building on this foundation, subsequent steps with validation with genomic prediction, possibly across populations with different growth patterns can be undertaken (Barghi, Hermisson, and Schlötterer 2020). Moreover, alternative methodological approaches can be considered to cross validate results and reduce false positives (Bernatchez 2016). For example, random forest algorithm may complement GWA, as it is especially well suited for complex genomic architecture and when genomic loci outnumber sample size (Chen and Ishwaran 2012).

5.2. Overall Patterns of Temporal Genomic Change

The absence of a discernible genome-wide pattern contradicted my initial predictions. Non-significant change of nucleotide diversity, a lack of clustering pattern in PCA, and genome-wide covariance patterns resembling neutral population suggest that the genomes as a whole did not undergo detectable evolution over the study period, at least not at the resolution provided by the methods employed. The non-significant changes may be attributed to many loci with very small effects, resulting in a minor impact on the overall genome wide pattern, similar to rationale behind the absence of statistical significance in GWA. In addition, heterogeneous response of the genome, utilising standing genetic variations through different biological processes, may have been driving the changes in phenotype (Crespel et al. 2021). As a corollary, these results are also reassuring, in that the premise of this study, namely that EBC is a closed, self-sustained gene pool without immigration of divergent genotypes, is supported. The genome-wide covariance method, which depends on the linkage disequilibrium among casual and neutral loci, may be manifesting its challenges with large marine population size where linkage breaks down faster. Moreover, the possibility of other traits undergoing selection or drift in different directions than the targeted trait, could potentially obscure the genome-wide signal of size selective fishing in wild populations. For example, in EBC, an opposing selection pressure against small female body size can be hypothesized. This is because larger females produce larger and more buoyant eggs that permit them to float higher in the water column (Nissling and Vallin 1996), away from the near-bottom where the oxygen conditions are worsening. Thus, further testing on different wild populations is necessary for the method, as it was only validated in the experimental populations and simulations without sampling processes (Buffalo and Coop 2020).

Absence of evidence of overall pattern does not equate to evidence of absence of selection. Despite the lack of overall pattern, evident non-random signals were observed when targeting specific regions, the inverted region of LG 12 and the candidate loci of GWA. Against the background of no overall change in genomic patterns (Figure 5) this directional change in the frequency of inversion in LG12 clearly suggests selection in parallel to the apparent decline of growth rates. Although no GO term was found significantly enriched for genes located within the inverted region of LG12, the ancestral homozygous status of individuals, together with body size, had a correlation to lower survival rate in a specific environment (Barth et al. 2019). This implies potential functional importance of the inversion in adaptation for Atlantic cod species. In the meantime, the frequency of double crossover (DC) within the inversion region seems to be fluctuating independently of the large inversion. Interestingly, this region is densely packed with genes including three vitellogenin genes, which is crucial for creating buoyancy of eggs for the survival and successful spawning in EBC (Nissling and Westin 1991). In this context, I speculate that the heavy selection pressure acts upon the inversion as a

whole, but is relaxed for the crucial set of genes in the DC by broken linkage disequilibrium. This then also might explain the hypothesis of the opposite selection pressure on body size of females mentioned above.

5.3. Application of Temporal Covariance Analysis to a Wild Fish Stock under Exploitation

This study employed temporal covariance values and F_{st} statistics as methods for detecting whether the selection signal of GWA outliers exceeded expectations of a custom generated null-expectation. Directional selection, in contrast to drift, leaves a positive temporal autocovariance of allele frequency changes over multiple time points due to the linkage disequilibrium among neutral and causal loci (Buffalo and Coop 2020; 2019). To the best of my knowledge this study is the first to utilise temporal covariance methods for a temporal genomic dataset with multiple time points from the wild, but also in combining covariance tests to complement phenotype associations. In addition, by calculating lag-2 and lag-3 covariances to avoid shared time points, two pairs of time windows could be treated as replicates, allowing for independent observations of allele frequency changes and strengthening the robustness of the results. The approaches applied here together with study design represent the best available in the field in detecting very recent and possibly ongoing selection. This is because currently available selection scans tend to pick up sweep signals that had happened in deeper evolutionary history (selection scans reviewed in Weigand and Leese 2018; Vatsiou, Bazin, and Gaggiotti 2016). And the sweep signature itself, even so-called soft sweeps, mostly rely on the fixation of the selected alleles, which is not suitable for detecting ongoing selection as this case. Given the absence of genome-wide signature of selection, subtle ongoing selection encompassing many loci could be only detected by direct observation of allele frequency changes in targeted regions.

5.4. Potential Other Causes of Growth Performance Declines in EBC

Even though I have provided evidence for a heritable component of the observed growth performance decline in EBC, possibly induced by fishing pressure, the observed dramatic change of growth may also be attributed to components of other non-genetic factors. Marked environmental conditions during the study time interval pose alternative, but non-exclusive, plausible causes for the observed change. In this section, I will discuss these factors in detail with mechanisms involved in each case as well as the interplays among them. Though each factor cannot fully explain the individual and population level growth impairment on its own, complex dynamics together with feedback loop may extend the genetic component of growth variation of EBC.

5.4.1. Environmental Conditions and Phenotypically Plastic Responses in Growth Rates

Growth is a profoundly plastic trait affected by various factors such as feeding and physiological conditions. Of particular concern for EBC in their growth and condition is extensive hypoxia, which has intensified fivefold over the past decades (Conley et al. 2009; Zillén et al. 2008). Lack of oxygen, in its direct impact, triggers physiological stress response and alters feeding behaviours in cod (Brander 2020; Chabot and Dutil 1999; Herbert and Steffensen 2005). Otolith chemistry analysis revealed that growth and condition decreased as exposure to hypoxia increased over a fish's lifetime, irrespective of sex and age (Limburg and Casini 2019; 2018). Indirectly, hypoxia has impacted the reduction in the spatial range of prey items, both benthic for young cods and pelagic for older cods (Casini et al. 2016; Neuenfeldt et al. 2020; Eero et al. 2012). The spatial mismatch of cod and prey items was exacerbated by habitat compression of EBC themselves (Casini et al. 2016). Eventually higher density caused by spatial reduction further feeds into negative feedback of intraspecific competition of resources and affects growth impairment.

Analysis on stomach contents of EBC by Neuenfeldt et al. (2020) showed critically low feeding level which leads to poor condition. Here, natural mortality results from the poor condition and death by starvation, which would lead to truncated size structure of the population. Similarly to the feedback loop from hypoxia, density-dependent response is expected with increased smaller sized individuals. At the population level, growth is then arrested. In addition, increase of predator abundance, specifically grey seal, as well as its parasite infestation in cods are suspected to affect the condition, thus natural mortality, to impact the overall size distribution (Mehrdana et al. 2014; Horbowy, Podolska, and Nadolna-Ałtyn 2016; Marnis et al. 2019). Lastly, increased inter-species competition with flounders over benthic preys over last decades also might have contributed to the low condition level of cod in the Baltic Sea (Orio et al. 2020; Haase et al. 2020).

Temperature is one of the critical factors influencing body size in fish which populates the major concern in the context of climate change (Forster, Hirst, and Atkinson 2012; Pauly and Cheung 2018; Cheung et al. 2013). In Atlantic cod, ambient temperature and growth rates generally show a positive relationship (Purchase and Brown 2001; Brander 1995; Neuheimer and Grønkjær 2012; Pedersen and Jobling 1989; Denechaud et al. 2020). However, thermal conditions for cod growth are intricate, with a thermal threshold causing performance drops (Righton et al. 2010) and shifting optimal temperatures based on fish age and size (Björnsson, Steinarsson, and Árnason 2007; Björnsson, Steinarsson, and Oddgeirsson 2001). The actual availability of the optimal temperature is not always met in the wild, and further confounded by migratory behaviour as well as other environmental factors (Righton et al. 2010). Surprisingly, in EBC, a specific focus on the temperature effect on the current worsening of growth or

condition has been largely overlooked. The reason might be that EBC shows unusually low growth rates compared to other stocks experiencing similar ambient temperature (McQueen et al. 2019), which implicates the overpowering effect of other factors. Nevertheless, considering the consistent rise of surface and bottom temperature in Bornholm Basin over recent decades (Barghorn, Meier, and Radtke 2023; Stockmayer and Lehmann 2023), EBC may be experiencing indirect temperature impact, such as more frequent thermal shock (Righton et al. 2010) and reduced vertical habitat volume (Freitas et al. 2016). In addition, since the higher growth rate in warmer temperature emerges through higher metabolic requirements (Brett 1956), when paired with oxygen and food limitations experienced by EBC, the negative impact can be intensified.

5.4.2. Integrated Impacts of Overexploitation and Environmental Factors on Growth Dynamics

Impacts of overexploitation and size-selective fishing extend beyond the deterioration of population functioning and productivity on its own by exacerbating risks of collapse under environmental change (Brander 2007; Perry et al. 2010). Demographically, overexploitation reduces the phenotypic variations of a population along with its abundance, and thus increases its sensitivity to stochastic climate events. For example, increased adult mortality alters demographic structure, thus affecting spawning and recruitment potentials (Rouyer et al. 2011; Perry et al. 2010; Rogers and Dougherty 2019). Furthermore, fishing-induced habitat loss or formation of homogenised or patchy subpopulations result in a diminished buffer or supply under adverse environmental conditions in case of interconnected populations (Morrongiello et al. 2021; Ottersen, Hjermann, and Stenseth 2006). Especially in the context of ocean warming, harvesting can curtail the diversity of individual responses to temperature changes, thereby restricting a population's adaptive capacity (Morrongiello, Sweetman, and Thresher 2019). Conversely, environmental changes, such as hypoxia and warming, can affect fishing dynamics, e.g. by changing behaviour and physiology of a fish, rendering them more susceptible to harvest pressure (Thambithurai and Kuparinen 2023). The Baltic Sea is one of the most heavily affected by climate change (Reusch et al. 2018). Therefore, persistent overfishing that EBC had experienced were potentially compounded by the adverse environmental conditions and collectively shaped the current appalling state of the population (Eero et al. 2023; Birgersson 2022).

5.5. Long Term Trend in EBC Growth and Size Outside My Study Period

This study focuses on the period from 1996 to 2019 and provides a contemporary snapshot of the long-term population dynamics of EBC. However, it is crucial to acknowledge another historical phase of altered size distribution dating back to the 1940s, where cod

exceeding 50 cm became increasingly scarce (Eero, Köster, and MacKenzie 2008; Zeller et al. 2011). Growth has fluctuated, with an increase during the 1960s to 1980s, followed by a noticeable decline from the 1990s to the present (Mion et al. 2021). As discussed earlier, various environmental factors and overexploitation likely have been shaping the stock conditions over time, possibly with alternating causality (Eero et al. 2011; Mion et al. 2021). For example, hypoxia, a usual suspect, appears unlikely as the primary driver of EBC's poor condition in the 1940s-50s due to better oxygen status (Eero et al. 2011). Most notably, a long term data series undoubtedly shows a synchronous trend between the fishing pressure and L95 in EBC, but the link uncoupled since the 2000s (Eero et al. 2023). Thus, the direct causes and evolutionary responses shaping the growth trend warrant further investigation within a longer timeframe. Nevertheless, this study, focusing on the critical period marked by a steep decline and lowest point in growth, strongly suggests that the evolutionary changes in EBC growth under persistent overexploitation partially have a genetic basis.

5.6. Darwinian Debt: Understanding Evolutionary Responses and Implications in Fisheries Management

Examples abound that overexploitation will cause evolutionary change, but these responses are always highly context dependent. Depending on the life history traits under selection and their genomic architecture, strength, length, and types of selection pressure together with natural selection by various environmental factors may be reinforcing or counteracting the trait evolution in a convoluting manner. This study showcases EBC as an evolving population with stunted growth potentially caused by heavy exploitation in context of dynamic plays of adverse environmental factors. Here, an inherent lag in evolutionary response, referred to as "Darwinian debt" (Ulf Dieckman in an interview by Cookson, *Financial Times*) may be contributing to the delay of recovery. That is, heavy fishing exerts selective pressure, as evidenced by the observed genetic changes, with multigenerational effects on the entire population, compromising growth potentials and population resilience (Anderson et al. 2008; Ahti, Kuparinen, and Uusi-Heikkilä 2020). In fact, even with the current implementation of moratorium, the length at maturity has not recovered in EBC (Eero et al. 2023). Moreover, the growth changes itself can initiate a trophic cascade effect through prey-predator interaction, which impacts the ecosystem at large (Frank et al. 2005; Soudijn et al. 2021). Importantly, this impact will persist, as the shifted evolutionary trajectory creates resistance to reverting to the original status (Enberg et al. 2009; Dunlop, Heino, and Dieckmann 2009), which emphasises the persistent ecological repercussions of past overexploitation beyond a single population. This understanding urges a comprehensive examination of long-term consequences and the need for effective conservation measures.

DISCUSSION

Successful management plans for EBC, as well as any other strongly size selective fisheries, must incorporate evolutionary aspects into their framework. Approaches such as introducing F_{evol} (Hutchings 2009) or integrating evolutionary processes into economic assessments of management plans (Schenk, Zimmermann, and Quaas 2023; Eikeset et al. 2013) should be considered. Then, management plans explicitly addressing evolutionary perspectives should be implemented, e.g. changing the gear selectivity and phenotype regulations, fishing grounds, introduction of marine protected areas (Dunlop et al. 2009; Jørgensen et al. 2007) for evolving EBC. Having said that, the impact of such measures on fisheries management may be limited at this stage as the damage has already been done. At present, the evolutionary debt has been substantially owed and despite the current moratorium, the stock recovery falls short of expectations due to concurrent contribution of ecological and environmental factors to stock condition (Eero et al. 2023). Whether this lack of recovery is already one consequence of the Darwinian debt remains to be seen and is certainly a very interesting research question. In order to enable recovery of EBC, along with reverting the genetic change itself, ecological factors such as the magnitude of overexploitation, natural mortality, and density dependent dynamics surely play major roles in harvest-induced evolution (Hutchings and Kuparinen 2021; Pelletier and Coltman 2018). Therefore, a holistic understanding of multiple factors in the EBC population is imperative for devising effective conservation and management strategies.

6. FUTURE RESEARCH DIRECTIONS

In delineating future research directions, this study unveils key methodological insights, underscoring strengths and caveats. First, it is demonstrated that effective combination of two independent methods, phenotype-genotype associations and selection scan, mutually enhances their analytical power as well as overall robustness of the results. While these methods proved complementary to each other, each method could be further strengthened through cross-validations. For instance, to reinforce the genotype-phenotype associations, genomic prediction using GWA outlier SNPs can be applied, also extending to other populations for a validation. Moreover, the detection of selection could benefit from employing analysis of cross population EHH (extended haplotype homozygosity), which is more sensitive to the ongoing selection with alleles yet to be fixed (Sabeti et al. 2007). The application of multiple methods to detect selection over drift helps mitigate false positive rates significantly (Leigh et al. 2021).

Second, a critical aspect illuminated by this study is the pivotal role of the long-term sampling through a monitoring scheme. Temporal collection of genetic samples coupled with phenotypic records proved to be very powerful tools for studying evolution in action. Further expanding this dataset through additional sampling, both preceding and succeeding the study period, would be highly interesting. This extension not only serves to perpetuate and validate the current findings, but also offers insights into the future implications for fisheries management.

Lastly, this study prompts a call for more comprehensive research into FIE. The observed genetic changes lack direct causality in this study, even though strong circumstantial evidence is suggested. The regions and genes identified should be best viewed as generated hypotheses for further thorough testing. Hence, more case studies with long term monitoring of wild populations and experimental approaches in order to disentangle various processes, for example, environmental influence from fishing effects, are necessary to understand the full picture of FIE.

CONTRIBUTION STATEMENTS

This work was done in a collaboration with other researchers listed as below.

Thorsten Reusch (GEOMAR), as my supervisor, conceived the research ideas and plans and was involved in interpretation of results and discussions.

Reid Brennan (GEOMAR) was involved in resolving bioinformatics issues and interpretation of results and discussions.

Erika Kokubun, a master student who I supervised, participated in extracting DNA and microsatellite analysis.

Karin Hüssy (Technical University of Denmark) conducted the chemical age reading analysis of the otolith described in *section 3.7*.

Tonny B. Thomsen and Benjamin D. Hereida (The Geological Survey of Denmark and Greenland) conducted LA-ICP MS for measuring element profiles in age reading protocol.

Sissel Jentoft (University of Oslo) was involved in developing the research plans including sequencing strategy and supported bioinformatics analysis and interpretation of results.

Cecilia Helmerson (University of Oslo) supported with scripts and insights to analyse inversion boundaries and identify inversion status of individuals.

Jan Dierking (GEOMAR) supported by introducing the time series data collection and dried otoliths and providing the established microsatellite protocols.

Ben Krause-Kyora (Christian-Albrechts University Kiel) conducted the pilot library preparation for 16 samples from 1996 using ancient DNA protocol to check any sign of damage in DNA before continuing to sequencing.

Jannina Fuss (Christian-Albrechts University Kiel) sequenced the samples processed in CCGA Kiel.

DATA AND CODE AVAILABILITY

The scripts and metadata used in this study are archived in a GEOMAR Gitlab repository (https://git.geomar.de/kwi-young-han/my-awesome-project.git)

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APPENDIX I. SUPPLEMENTARY TABLES

List of Supplementary Tables

Supplementary Table 1. All samples used in this study and metadata.

Supplementary Table 2. A list of enriched GO terms for outlier windows F_{st} between 1996 and 2019.

Supplementary Table 3. Estimated von Bertalanffy growth parameters for individual fish, catch years and all samples.

Supplementary Table 1. All samples used in this study and metadata.
A total of 154 samples were subjected to sequencing and growth modelling. Two of them were excluded in any genetic analysis due to their low sequencing depth. "Otolith radius in mm" is the length from otolith core to the edge and "distance_min_x" are the distance from the core to the chemical annuli (minima) for each age estimate. "chemAge" is the estimated age from the age reading protocol. "sample.type" shows the assignment of the sample type "random" and "phenotype" according to the sampling design described in *section 3.1*. The samples were grouped into "bins" according to the catch year in growth modelling. The "phenotype" samples from 1996-1998 were grouped together with "random" samples from 1996 in "bin1". For all the genetic analysis, "SequencingName" were used and matched with "fishID" for metadata.This table is also provided in the Git repository.

fishID	catch.year	length in mm	sex	maturity	otolith radius in mm	chemAge	distance_min_1	distance_min_2	distance_min_3	distance_min_4	distance_min_5	distance_min_6	distance_min_7	sample.type	bins	SequencingName
AL097_334	1996	420	F	1	3.211704	3	0.7882197	1.9999617	3.10577	NA	NA	NA	NA	pheno	bin1	104-104-AL097-334_S50_L004
AL097_430	1996	260	M	4	2.3528964	3	0.4396807879	1.319046909	2.270547	NA	NA	NA	NA	pheno	bin1	75-75-AL097-430_S21_L004
AL097_552	1996	410	M	1	3.30582	4	0.6611660184	1.385672	2.231428877	2.786335818	NA	NA	NA	pheno	bin1	83-83-AL097-552_S29_L004
AL099_189	1996	460	F	1	4.317564	7	0.8161973752	1.466789481	2.259326806	2.850775876	3.31210568	NA	NA	pheno	bin1	39-39-AL099-189_S39_L004
AL099_326	1996	270	M	5	2.1646641	3	0.4941093	1.423503	2.01172563	NA	NA	NA	NA	pheno	bin1	64-64-AL099-326_S10_L004
AL099_328	1996	400	F	1	2.9293566	3	0.5646945	2.1999582	2.70583023	NA	NA	NA	NA	pheno	bin1	102-102-AL099-328_S48_L004
AL099_344	1996	310	M	5	2.5175976	3	0.399993	1.2470361	2.35289643	NA	NA	NA	NA	random	bin1	65-65-AL099-344_S11_L004
AL099_35	1996	890	F	6	5.450875	5	0.49018495	1.39213	2.86269	4.27443	5.058725	NA	NA	random	bin1	J32532-_L1_S1_L002
AL099_37	1996	1040	F	6	5.929299	6	0.70587	2.776419	3.6587559	4.5410901	5.1251896	5.7754189	NA	random	bin1	J32533-_L1_S2_L001
AL099_577	1996	570	F	6	3.835218	3	0.7005473147	2.64784067	3.775258	NA	NA	NA	NA	random	bin1	100-100-AL099-577_S46_L004
AL099_591	1996	350	M	7	2.541129	4	0.4845875811	1.004636149	1.678331314	2.475258	NA	NA	NA	random	bin1	22-22-AL099-591_S22_L004
AL099_597	1996	530	M	6	4.258746	4	1.047039	2.294076	3.5411103	4.185647	NA	NA	NA	random	bin1	38-38-AL099-597_S38_L004
AL099_600	1996	340	M	6	3.199941	4	0.329406	1.2588003	2.105844	2.847006	NA	NA	NA	random	bin1	47-47-AL099-600_S47_L004
AL099_602	1996	270	M	6	2.4705438	3	0.7529295	1.2352734	1.5293817	NA	NA	NA	NA	pheno	bin1	53-53-AL099-602_S53_L004
AL099_613	1996	580	F	6	3.92934	3	0.623517	2.4705417	3.450258	NA	NA	NA	NA	random	bin1	J32535-_L1_S3_L002
AL099_621	1996	630	M	7	4.599915	6	0.4138730706	1.064247408	2.38273266	3.068580604	3.783991621	4.245165247	NA	random	bin1	61-61-AL099-621_S7_L004
AL099_630	1996	430	M	6	3.517578	3	0.5665854198	1.085960329	2.679497306	NA	NA	NA	NA	random	bin1	4-04-AL099-630_S4_L004
AL099_636	1996	620	M	7	4.8430445	5	0.6666505	1.1764455	2.1372095	3.1450465	4.0783495	NA	NA	random	bin1	J32536-_L1_S4_L002
AL099_78	1996	560	M	6	4.411681	6	0.45097045	1.1176255	1.68624	2.4901455	3.313661	3.7058095	NA	random	bin1	J32534-_L1_S2_L002

AL101_105	1996	570	F	7	4.623444	5	0.6015187318	2.193776675	3.290665614	3.915776082	4.550167	NA	NA	random	bin1	70-70-AL101-105_S16_L004
AL101_114	1996	580	F	7	4.599912	6	0.823515	1.435269	2.141136	2.8411237	3.646989	4.5	NA	random	bin1	99-99-AL101-114_S45_L004
AL101_185	1996	590	M	6	4.282269	6	0.4507659285	1.328570843	2.052166361	2.882524952	3.6298459	4.2	NA	random	bin1	20-20-AL101-185_S20_L004
AL101_214	1996	540	F	8	3.164646	4	0.6978097159	1.564543397	2.323111806	3.1	NA	NA	NA	random	bin1	J32537-_L1_S5_L002
AL101_287	1996	460	M	7	3.682284	4	0.482346	0.988218	2.5058343	3.6	NA	NA	NA	random	bin1	J32538-_L1_S6_L002
AL101_288	1996	550	F	6	4.388151	7	0.5946012489	1.117850348	1.95028967	2.473538466	3.24652009	3.853009118	4.102741642	random	bin1	J32539-_L1_S8_L001
AL101_344	1996	430	F	7	3.670518	4	1.1411547	1.741143	2.8352406	3.6	NA	NA	NA	random	bin1	J32542-_L1_S9_L002
AL101_422	1996	560	F	7	3.905811	5	0.835278	1.470564	2.1764283	2.7528929	3.71757858	NA	NA	random	bin1	J32543-_L1_S10_L002
AL101_423	1996	480	F	7	3.435228	3	0.8470425	1.8940806	3.24699558	NA	NA	NA	NA	random	bin1	J32544-_L1_S11_L002
AL101_430	1996	540	F	7	4.25874	6	0.5323416666	1.005538617	1.940091808	2.489621822	3.111246793	3.927502105	NA	random	bin1	77-77-AL101-430_S23_L004
AL101_434	1996	430	M	7	2.9175936	5	0.462548792	1.079270837	1.897623088	2.039940722	2.407611293	NA	NA	random	bin1	25-25-AL101-434_S25_L004
AL101_442	1996	800	F	7	5.305779	6	0.6735619839	1.890701522	2.812416969	3.521431169	3.94683969	4.774019609	NA	random	bin1	J32545-_L1_S12_L002
AL101_504	1996	460	F	7	3.70581	4	0.5701255101	1.045227073	2.316130644	3.539523029	NA	NA	NA	random	bin1	26-26-AL101-504_S26_L004
AL101_523	1996	650	F	7	4.599912	5	0.6148993755	1.288922183	2.636967799	3.748516972	4.4	NA	NA	random	bin1	J32546-_L1_S13_L002
AL101_546	1996	500	M	1	3.449085	4	0.6470439	1.5058527	2.6843898	3.28437795	NA	NA	NA	pheno	bin1	76-76-AL101-546_S22_L004
AL101_595	1996	470	M	7	3.352878	4	0.2833422798	1.097950431	2.184092526	3.093147742	NA	NA	NA	random	bin1	69-69-AL101-595_S15_L004
AL101_623	1996	220	M	6	2.235252	3	0.3882306	1.1764512	1.8940839	NA	NA	NA	NA	pheno	bin1	95-95-AL101-623_S41_L004
AL101_679	1996	510	F	7	3.4313135	4	0.2941162	1.2744875	2.0391795	2.8234765	NA	NA	NA	random	bin1	J32547-_L1_S14_L002
AL111_235	1997	270	M	5	2.3293683	2	0.7645091697	2.126296225	NA	NA	NA	NA	NA	pheno	bin1	81-81-AL111-235_S27_L004
AL111_28	1997	430	F	1	3.423462	4	0.5212224352	1.149051534	2.025651062	3.008856348	NA	NA	NA	pheno	bin1	67-67-AL111-28_S13_L004
AL114_826	1997	340	F	5	3.30582	3	0.8649636474	2.322368675	3.2	NA	NA	NA	NA	pheno	bin1	13-13-AL114-826_S13_L004
AL114_868	1997	350	F	4	3.246996	3	0.8176741991	2.287117683	3.128492023	NA	NA	NA	NA	pheno	bin1	5-05-AL114-868_S5_L004
AL114_937	1997	350	F	6	3.376407	3	0.8487897867	2.416796168	3.2	NA	NA	NA	NA	pheno	bin1	45-45-AL114-937_S45_L004
AL129_106	1998	400	F	1	2.9528847	4	0.399993	1.4823252	2.2234863	2.76465522	NA	NA	NA	pheno	bin1	18-18-AL129-106_S18_L004
AL129_148	1998	350	F	4	2.778504	5	0.4823439	1.0470411	1.623498	2.0726367	2.48439267	NA	NA	pheno	bin1	19-19-AL129-148_S19_L004

AL129_243	1998	240	M	6	2.1528984	2	0.4163059375	1.760383449	NA	NA	NA	NA	NA	pheno	bin1	42-42-AL129-243_S42_L004
AL129_266	1998	300	F	4	2.5293633	3	0.5343765927	1.033124708	1.971240748	NA	NA	NA	NA	pheno	bin1	50-50-AL129-266_S50_L004
AL129_339	1998	400	F	1	2.9881758	3	0.8267653782	1.759833805	2.326756389	NA	NA	NA	NA	pheno	bin1	15-15-AL129-339_S15_L004
AL129_369	1998	350	F	4	2.8705353	3	0.5551164224	1.665348665	2.23227125	NA	NA	NA	NA	random	bin1	23-23-AL129-369_S23_L004
AL129_377	1998	410	M	1	3.15288	5	0.611754	1.1646843	1.729377	2.388189	2.91759021	NA	NA	pheno	bin1	62-62-AL129-377_S8_L004
AL129_389	1998	410	F	1	2.8352403	2	0.4016601013	2.043735052	NA	NA	NA	NA	NA	pheno	bin1	3-03-AL129-389_S3_L004
AL129_401	1998	410	F	1	2.9764101	2	0.6640568246	2.430933466	NA	NA	NA	NA	NA	pheno	bin1	90-90-AL129-401_S36_L004
AL129_419	1998	270	M	6	2.4234843	3	0.5438058898	1.525022739	2.116114997	NA	NA	NA	NA	pheno	bin1	86-86-AL129-419_S32_L004
AL129_467	1998	270	M	6	2.2470147	3	0.5468895363	1.47423065	2.033013177	NA	NA	NA	NA	pheno	bin1	36-36-AL129-467_S36_L004
AL129_47	1998	400	F	1	3.30582	4	0.6493552721	1.157034585	2.160588787	2.739108187	NA	NA	NA	pheno	bin1	28-28-AL129-47_S28_L004
AL129_87	1998	350	F	4	2.8117119	2	0.8779157876	2.325297341	NA	NA	NA	NA	NA	pheno	bin1	34-34-AL129-87_S34_L004
AL130_199	1998	260	M	6	2.5528887	3	0.5964681468	1.049787613	2.290440306	NA	NA	NA	NA	pheno	bin1	98-98-AL130-199_S44_L004
AL130_206	1998	230	M	6	2.5293633	2	0.9928371908	2.115683232	NA	NA	NA	NA	NA	pheno	bin1	88-88-AL130-206_S34_L004
AL130_223	1998	420	F	1	3.176409	3	0.7851854841	2.010541617	2.938476416	NA	NA	NA	NA	pheno	bin1	8-08-AL130-223_S8_L004
AL130_244	1998	330	F	6	2.9881803	2	0.9249138092	2.027694449	NA	NA	NA	NA	NA	pheno	bin1	78-78-AL130-244_S24_L004
AL130_429	1998	410	F	1	3.129351	3	0.4978527531	1.967698629	2.939692628	NA	NA	NA	NA	pheno	bin1	48-48-AL130-429_S48_L004
AL130_440	1998	520	F	1	3.576402	3	0.6750192331	1.78820314	3.398767277	NA	NA	NA	NA	pheno	bin1	91-91-AL130-440_S37_L004
AL130_68	1998	420	F	1	3.23523	3	0.8549463871	2.113527618	2.680282951	NA	NA	NA	NA	pheno	bin1	46-46-AL130-68_S46_L004
AL133_100	1998	450	F	1	3.552873	3	0.8882189846	2.214623884	3.173899831	NA	NA	NA	NA	pheno	bin1	97-97-AL133-100_S43_L004
AL133_116	1998	340	F	6	2.9528862	3	0.6522451519	1.482374658	2.644552459	NA	NA	NA	NA	pheno	bin1	27-27-AL133-116_S27_L004
AL133_119	1998	320	F	6	2.6117169	3	0.6522451519	1.197758119	2.644552459	NA	NA	NA	NA	pheno	bin1	71-71-AL133-119_S17_L004
AL133_136	1998	470	F	1	3.399936	4	0.8854023731	1.605527096	2.679811202	3.175636356	NA	NA	NA	pheno	bin1	24-24-AL133-136_S24_L004
AL207_131	2002	390	M	7	2.9881758	5	0.6284651135	1.209496947	1.968402221	2.407140865	2.845879599	NA	NA	random	bin2	87-87-AL207-131_S33_L004
AL207_143	2002	410	F	7	2.9293536	4	0.3543567045	1.098505905	1.759972496	2.64036229	NA	NA	NA	random	bin2	107-107-AL207-143_S53_L004
AL207_146	2002	440	F	7	3.764634	4	0.694104	1.3882092	2.5528917	3.2	NA	NA	NA	random	bin2	101-101-AL207-146_S47_L004

AL207_149	2002	520	F	6	4.035219	6	0.5427495625	0.8731188615	1.392270316	2.312582686	3.138505331	3.763845804	NA	random	bin2	73-73-AL207-149_S19_L004
AL207_151	2002	640	F	6	4.117569	4	0.741164	2.164665	3.1411167	3.87051285	NA	NA	NA	random	bin2	55-55-AL207-151_S1_L004
AL207_197	2002	640	M	9	4.211685	4	0.599988	1.5	2.5764198	3.4822851	NA	NA	NA	random	bin2	57-57-AL207-197_S3_L004
AL207_20	2002	440	F	7	3.364644	4	0.5999913	1.6587927	2.270547	3	NA	NA	NA	random	bin2	51-51-AL207-20_S51_L004
AL207_231	2002	390	F	7	3.517578	4	0.7224642069	1.871302639	2.534550964	3.387294944	NA	NA	NA	random	bin2	106-106-AL207-231_S52_L004
AL207_249	2002	420	M	7	3.69405	4	0.647049	1.3646817	2.5999524	3.44699532	NA	NA	NA	random	bin2	33-33-AL207-249_S33_L004
AL207_25	2002	340	F	8	2.91759	3	0.858807	1.8117303	2.68230021	NA	NA	NA	NA	random	bin2	66-66-AL207-25_S12_L004
AL207_413	2002	430	F	7	3.894045	5	0.7338329108	1.810910549	2.603922628	3.065524183	3.633654307	NA	NA	random	bin2	72-72-AL207-413_S18_L004
AL207_462	2002	340	M	7	3.317583	4	0.6611543444	1.711921929	2.59739611	3.187715182	NA	NA	NA	random	bin2	40-40-AL207-462_S40_L004
AL207_473	2002	280	M	7	2.3764248	3	0.532034494	1.265062102	2.199079989	NA	NA	NA	NA	random	bin2	60-60-AL207-473_S6_L004
AL207_490	2002	340	M	6	2.9432226	3	0.8782172608	1.685232469	2.136207452	NA	NA	NA	NA	random	bin2	49-49-AL207-490_S49_L004
AL207_504	2002	300	M	7	2.7646581	4	0.5220840928	1.340798843	1.791689375	2.444288742	NA	NA	NA	random	bin2	16-16-AL207-504_S16_L004
AL207_516	2002	410	F	5	3.211704	4	0.7058661	1.788198	2.2823076	3.01170594	NA	NA	NA	random	bin2	108-108-AL207-516_S54_L004
AL207_539	2002	370	M	7	2.9999472	4	0.3188930824	1.027539658	1.99602551	2.740107833	NA	NA	NA	random	bin2	89-89-AL207-539_S35_L004
AL207_561	2002	320	M	7	3.69405	4	0.6941085	1.2588	2.4352512	3.50581758	NA	NA	NA	random	bin2	29-29-AL207-561_S29_L004
AL207_61	2002	360	F	7	3.376407	4	0.5194484002	1.35	2.184042542	3.104879284	NA	NA	NA	random	bin2	56-56-AL207-61_S2_L004
AL207_625	2002	410	M	7	3.752868	4	0.3433214951	2.048094775	3.042544295	3.634480872	NA	NA	NA	random	bin2	93-93-AL207-625_S39_L004
AL207_691	2002	270	M	6	2.36466	2	0.9340402522	1.927195885	NA	NA	NA	NA	NA	random	bin2	94-94-AL207-691_S40_L004
AL207_91	2002	300	M	8	2.5528917	4	0.5936973173	1.270509752	1.733591673	2.256044477	NA	NA	NA	random	bin2	30-30-AL207-91_S30_L004
AL318_200	2008	350	M	5	3.188178	4	0.3081526075	0.687416774	1.481498318	2.69039754	NA	NA	NA	random	bin3	58-58-AL318-200_S4_L004
AL318_234	2008	350	F	5	3.258759	6	0.5925007683	1.007250974	1.824903442	2.322606469	2.784755696	3.2	NA	random	bin3	63-63-AL318-234_S9_L004
AL318_29	2008	420	F	5	3.905808	6	0.270582	0.599988	1.8470214	2.541126	3.352875	3.9	NA	random	bin3	14-14-AL318-29_S14_L004
AL318_9	2008	240	M	5	2.2587816	3	0.4139116985	0.9697372029	1.785736611	NA	NA	NA	NA	random	bin3	105-105-AL318-9_S51_L004
AL320_1003	2008	480	F	5	3.517581	4	0.3316183982	1.136999585	2.250310503	3.3	NA	NA	NA	random	bin3	21-21-AL320-1003_S21_L004
AL320_1067	2008	310	M	5	2.847	3	0.8778179102	1.51839758	2.669068386	NA	NA	NA	NA	random	bin3	43-43-AL320-1067_S43_L004

AL320_1172	2008	310	M	7	2.8352403	3	0.7473292852	1.969170141	2.6	NA	NA	NA	NA	random	bin3	37-37-AL320-1172_S37_L004
AL320_132	2008	490	M	5	4.117566	5	0.3775425303	1.156218583	2.465818032	3.374278542	3.9	NA	NA	random	bin3	2-02-AL320-132_S2_L004
AL320_153	2008	310	M	5	2.5175976	3	0.6264462774	1.666575662	2.269380261	NA	NA	NA	NA	random	bin3	7-07-AL320-153_S7_L004
AL320_263	2008	300	M	5	2.847006	3	0.4863638243	1.589579793	2.6	NA	NA	NA	NA	random	bin3	1-01-AL320-263_S1_L004
AL320_331	2008	430	F	6	3.670518	6	0.6941019	1.4470317	2.0705454	2.5058325	3.1528773	3.5	NA	random	bin3	17-17-AL320-331_S17_L004
AL320_335	2008	490	M	5	4.505796	6	0.447054	1.247034	2.0940774	2.9175948	3.7999287	4.3	NA	random	bin3	31-31-AL320-335_S31_L004
AL320_379	2008	350	M	5	3.599931	3	0.75	2.45	3.4	NA	NA	NA	NA	random	bin3	6-06-AL320-379_S6_L004
AL320_398	2008	420	F	5	3.576399	6	0.6963977649	1.192131415	1.794099079	2.431479987	2.903610626	3.328529286	NA	random	bin3	44-44-AL320-398_S44_L004
AL320_487	2008	240	F	5	2.3881875	3	0.3294024	1.3293867	1.9646661	NA	NA	NA	NA	random	bin3	41-41-AL320-487_S41_L004
AL320_5	2008	370	F	5	3.235227	4	0.5058714	1.2235044	2.117601	3.03523188	NA	NA	NA	random	bin3	35-35-AL320-5_S35_L004
AL320_532	2008	390	F	5	3.094062	3	0.5646987	1.9881987	2.79995067	NA	NA	NA	NA	random	bin3	9-09-AL320-532_S9_L004
AL320_772	2008	430	F	5	3.505815	3	0.6514159446	2.226670653	3.375530361	NA	NA	NA	NA	random	bin3	10-10-AL320-772_S10_L004
AL320_865	2008	270	M	6	2.7293613	3	0.7541682573	1.831546336	2.5	NA	NA	NA	NA	random	bin3	12-12-AL320-865_S12_L004
AL320_879	2008	400	F	6	3.775266	4	0.494109	1.4940825	1.941141	3.1399809	NA	NA	NA	random	bin3	52-52-AL320-879_S52_L004
AL324_1047	2008	510	M	6	4.035219	5	0.6489411397	1.581052027	2.383374686	3.457073306	3.85	NA	NA	random	bin3	103-103-AL324-1047_S49_L004
AL324_1064	2008	440	M	6	3.870516	4	0.8048787446	1.941175432	2.923599148	3.468076549	NA	NA	NA	random	bin3	74-74-AL324-1064_S20_L004
AL324_1151	2008	480	F	8	4.105803	5	0.63528	1.8940794	2.5411272	3.2234691	3.8	NA	NA	random	bin3	32-32-AL324-1151_S32_L004
AL324_652	2008	220	M	6	2.2470147	2	0.7568868586	2.005097484	NA	NA	NA	NA	NA	random	bin3	80-80-AL324-652_S26_L004
AL435_298	2014	320	F	5	2.8940655	3	0.6286303753	2.348460953	2.8	NA	NA	NA	NA	random	bin4	J35428-S1-_L1_S125_L002
AL435_334	2014	310	M	5	2.8705371	3	0.8065983966	1.991122238	2.8	NA	NA	NA	NA	random	bin4	J35413-S1-_L1_S110_L002
AL435_403	2014	320	M	5	3.976395	5	0.7433609596	1.486723725	2.595865011	3.398224796	3.9	NA	NA	random	bin4	J35419-S1-_L1_S116_L002
AL435_413	2014	270	M	6	2.741127	4	0.7594484835	1.756220117	2.183408262	2.7	NA	NA	NA	random	bin4	J35426-S1-_L1_S123_L002
AL435_634	2014	390	F	5	3.023472	3	0.4742735811	2.07493539	3	NA	NA	NA	NA	random	bin4	J35414-S1-_L1_S111_L002
AL435_636	2014	410	M	5	3.494052	5	0.7764564	1.7529093	2.2470129	2.8234758	3.4	NA	NA	random	bin4	J35427-S1-_L1_S124_L002
AL435_721	2014	330	F	7	3.023472	4	0.8536846452	1.659944381	2.371347043	3	NA	NA	NA	random	bin4	J35424-S1-_L1_S121_L002

AL435_725	2014	310	M	6	2.5646601	2	0.7293984	2.36466204	NA	NA	NA	NA	NA	random	bin4	J35434-S1-_L1_S131_L002
AL435_730	2014	330	M	6	3.07053	3	0.6588114	1.141155	2.564661	NA	NA	NA	NA	random	bin4	J35423-S1-_L1_S120_L002
AL437_245	2014	320	M	6	2.8352403	3	0.7088129519	1.937410822	2.646223894	NA	NA	NA	NA	random	bin4	J35406-S1-_L1_S103_L002
AL437_251	2014	290	M	6	2.5646544	3	0.6470451	1.835256	2.39995323	NA	NA	NA	NA	random	bin4	J35395-S1-_L1_S92_L002
AL437_264	2014	320	M	6	3.294054	4	0.5213653754	1.421896367	2.606803913	3.1	NA	NA	NA	random	bin4	J35407-S1-_L1_S104_L002
AL437_288	2014	350	F	5	3.129351	3	0.6588099	2.2234857	2.92935297	NA	NA	NA	NA	random	bin4	J35396-S1-_L1_S93_L002
AL437_505	2014	230	M	6	2.1058419	3	0.6470508	1.2940959	1.92937512	NA	NA	NA	NA	random	bin4	J35398-S1-_L1_S95_L002
AL437_562	2014	430	F	6	3.563544	4	0.5210818746	1.338224334	2.79376555	3.4	NA	NA	NA	random	bin4	J35425-S1-_L1_S122_L002
AL437_573	2014	460	F	6	3.729339	5	0.793224895	1.988981835	2.770365723	3.1	3.5	NA	NA	random	bin4	J35399-S1-_L1_S96_L002
AL437_579	2014	420	F	5	2.9528877	3	0.566954701	1.996152263	2.8	NA	NA	NA	NA	random	bin4	J35397-S1-_L1_S94_L002
AL437_582	2014	320	F	5	3.223467	5	0.5214416408	1.113990801	1.730242567	2.405749341	3	NA	NA	random	bin4	J35432-S1-_L1_S129_L002
AL437_601	2014	340	F	6	3.446994	5	0.6278031271	1.445134023	2.262461899	2.736272713	3.4	NA	NA	random	bin4	J35405-S1-_L1_S102_L002
AL437_611	2014	310	F	5	3.282297	4	0.7764591	1.9764387	2.4940734	3.1	NA	NA	NA	random	bin4	J35433-S1-_L1_S130_L002
AL521_566	2019	300	M	5	2.3999532	3	0.7684568129	1.761544264	2.2	NA	NA	NA	NA	random	bin5	J35415-S1-_L1_S112_L002
AL521_726	2019	280	M	5	2.7764181	5	0.5339250681	0.8542825901	1.649239937	2.230626713	2.7	NA	NA	random	bin5	J35416-S1-_L1_S113_L002
AL521_847	2019	380	M	5	3.152883	5	0.5058723	1.0352757	1.72938	2.541129	2.92935663	NA	NA	random	bin5	J35420-S1-_L1_S117_L002
AL521_865	2019	270	M	5	2.6587704	3	0.6381021358	2.15065042	2.6	NA	NA	NA	NA	random	bin5	J35421-S1-_L1_S118_L002
AL522_473	2019	230	M	6	1.9785411	2	0.6056997595	1.836523718	NA	NA	NA	NA	NA	random	bin5	J35403-S1-_L1_S100_L002
AL522_510	2019	290	F	5	2.5646601	3	0.6263930347	1.938266975	2.3	NA	NA	NA	NA	random	bin5	J35418-S1-_L1_S115_L002
AL522_511	2019	250	M	6	2.741127	4	0.7148181803	1.199241196	2.27442566	2.7	NA	NA	NA	random	bin5	J35404-S1-_L1_S101_L002
AL522_519	2019	360	M	7	3.22347	5	0.7999857	1.8705519	2.4234837	2.811714	3.2	NA	NA	random	bin5	J35400-S1-_L1_S97_L002
AL522_531	2019	330	F	5	2.9293536	4	0.8386457811	1.535552474	2.374197954	2.85	NA	NA	NA	random	bin5	J35431-S1-_L1_S128_L002
AL522_532	2019	280	F	5	2.6705391	3	0.6617258696	2.06789564	2.469656008	NA	NA	NA	NA	random	bin5	J35411-S1-_L1_S108_L002
AL522_543	2019	220	M	6	2.1764298	2	0.5708696617	1.926680718	NA	NA	NA	NA	NA	random	bin5	J35401-S1-_L1_S98_L002
AL522_547	2019	370	F	7	2.8352403	4	0.6761882658	1.565906436	2.277681154	2.8	NA	NA	NA	random	bin5	J35402-S1-_L1_S99_L002

AL522_561	2019	300	F	5	2.43525	3	0.6029011425	1.66684797	2.246103743	NA	NA	NA	NA	random	bin5	J35408-S1-_L1_S105_L002
AL522_564	2019	300	M	6	3.011706	5	0.6639975875	1.470283612	2.098707352	2.572997001	2.9	NA	NA	random	bin5	J35409-S1-_L1_S106_L002
AL522_579	2019	320	F	5	2.8234746	3	0.7646895	2.0117226	2.62347654	NA	NA	NA	NA	random	bin5	J35412-S1-_L1_S109_L002
AL522_593	2019	330	F	7	2.6929806	3	0.5207789457	1.087076907	2.113984798	NA	NA	NA	NA	random	bin5	J35422-S1-_L1_S119_L002
AL522_594	2019	300	F	5	2.7646524	3	0.5576724108	1.95780449	2.645997957	NA	NA	NA	NA	random	bin5	J35429-S1-_L1_S126_L002
AL522_613	2019	270	M	5	2.3646681	3	0.8823399	1.9176096	2.18819544	NA	NA	NA	NA	random	bin5	J35410-S1-_L1_S107_L002
AL522_624	2019	300	F	5	2.8352343	5	0.4370949496	1.051398175	1.96103226	2.350880647	2.8	NA	NA	random	bin5	J35430-S1-_L1_S127_L002
AL522_682	2019	410	F	5	3.199944	4	0.4235259	0.9764517	2.4705456	3	NA	NA	NA	random	bin5	J35417-S1-_L1_S114_L002

Supplementary Table 2. A list of enriched GO terms for outlier windows F_{st} between 1996 and 2019.

F_{st} values in non-overlapping 50Kb windows along the genome was calculated for 1996 and 2019 to identify regions that are the most differentiated over time. The windows with highest 5% F_{st} were assigned as outlier windows. The genes residing in these outlier windows were subjected to gene ontology (GO) enrichment test to identify any biological functions that have differentiated over time. P values are adjusted using false discovery rate. Only biological process was presented among GO categories for the analysis.

GO.term	GO.name	p.value.adjusted
GO:0006468	protein phosphorylation	0.02754635203
GO:0006541	glutamine metabolic process	0.02797620132
GO:0019217	regulation of fatty acid metabolic process	0.02797620132
GO:0016079	synaptic vesicle exocytosis	0.02797620132
GO:0031998	regulation of fatty acid beta-oxidation	0.02797620132
GO:1990504	dense core granule exocytosis	0.02797620132
GO:0006171	cAMP biosynthetic process	0.02797620132
GO:0034220	ion transmembrane transport	0.02870276413
GO:0019395	fatty acid oxidation	0.04186881996
GO:0042157	lipoprotein metabolic process	0.04212093394
GO:0051301	cell division	0.04212093394
GO:0061074	regulation of neural retina development	0.04212093394
GO:0033077	T cell differentiation in thymus	0.04212093394
GO:0006044	N-acetylglucosamine metabolic process	0.04212093394
GO:0006432	phenylalanyl-tRNA aminoacylation	0.04212093394
GO:0070509	calcium ion import	0.04212093394
GO:0062012	regulation of small molecule metabolic process	0.04212093394
GO:0007166	cell surface receptor signaling pathway	0.04212093394
GO:0030178	negative regulation of Wnt signaling pathway	0.04212093394
GO:0006814	sodium ion transport	0.04212093394
GO:0005975	carbohydrate metabolic process	0.04212093394
GO:0007264	small GTPase mediated signal transduction	0.04212093394
GO:0140013	meiotic nuclear division	0.04212093394
GO:0007169	transmembrane receptor protein tyrosine kinase signaling pathway	0.04212093394
GO:0009190	cyclic nucleotide biosynthetic process	0.04212093394
GO:0060027	convergent extension involved in gastrulation	0.04212093394
GO:0006796	phosphate-containing compound metabolic process	0.04212093394
GO:0030968	endoplasmic reticulum unfolded protein response	0.04212093394
GO:0030098	lymphocyte differentiation	0.04212093394
GO:0061982	meiosis I cell cycle process	0.04212093394
GO:0001702	gastrulation with mouth forming second	0.04212093394
GO:0050794	regulation of cellular process	0.04212093394
GO:0010033	response to organic substance	0.04212093394
GO:0009081	branched-chain amino acid metabolic process	0.04212093394
GO:0007099	centriole replication	0.04212093394
GO:0035567	non-canonical Wnt signaling pathway	0.04212093394
GO:0032007	negative regulation of TOR signaling	0.04212093394
GO:0021952	central nervous system projection neuron axonogenesis	0.04212093394
GO:0055074	calcium ion homeostasis	0.04212093394
GO:0009062	fatty acid catabolic process	0.04212093394
GO:0050769	positive regulation of neurogenesis	0.04212093394
GO:0042110	T cell activation	0.04212093394
GO:0035967	cellular response to topologically incorrect protein	0.04212093394
GO:0030433	ubiquitin-dependent ERAD pathway	0.04212093394
GO:0060028	convergent extension involved in axis elongation	0.04212093394

GO:0016579	protein deubiquitination	0.04285964063
GO:0030001	metal ion transport	0.04285964063
GO:0007154	cell communication	0.04331273079
GO:0048729	tissue morphogenesis	0.04501724582
GO:0048585	negative regulation of response to stimulus	0.04538697515
GO:0009247	glycolipid biosynthetic process	0.04719048324
GO:0023052	signaling	0.04719048324
GO:0065004	protein-DNA complex assembly	0.04790241745
GO:0090162	establishment of epithelial cell polarity	0.04790241745
GO:0035825	homologous recombination	0.04790241745
GO:0007131	reciprocal meiotic recombination	0.04790241745
GO:0006040	amino sugar metabolic process	0.04790241745
GO:0006801	superoxide metabolic process	0.04790241745
GO:0098655	cation transmembrane transport	0.04790241745
GO:0048285	organelle fission	0.04790241745
GO:0023057	negative regulation of signaling	0.04790241745
GO:0010648	negative regulation of cell communication	0.04790241745
GO:0051716	cellular response to stimulus	0.04790241745
GO:0023061	signal release	0.04790241745
GO:0032402	melanosome transport	0.04790241745
GO:0006284	base-excision repair	0.04790241745
GO:0036211	protein modification process	0.04790241745
GO:0043632	modification-dependent macromolecule catabolic process	0.04790241745
GO:0006511	ubiquitin-dependent protein catabolic process	0.04790241745

Supplementary Table 3. Estimated von Bertalanffy growth parameters for individual fish, catch years and all samples.
The Bayesian hierarchical model estimates parameters of nested levels at the same time. Here, three estimated von Bertalanffy parameters L∞, length at infinity, k, a growth coefficient, and t0, hypothetical length at age 0, were estimated for all samples, for each bin, based on the catch years, and for each individual. The individual parameters were used to calculated growth performance, Φ, which was used in genotype-phenotype association analysis.

	L∞	k	t0
All	7.4265107	0.1785009186	0.45453227
group parameters			
bin1	9.197300231	0.128748689	0.4674114129
bin2	8.07270249	0.1346183828	0.4368796201
bin3	8.355492139	0.1339595874	0.4697016901
bin4	5.601883356	0.2381987686	0.4521721634
bin5	4.794222888	0.2540789252	0.4417218798
Individual parameters			
AL097_334	9.450599562	0.1520235359	0.4475552977
AL097_430	9.087302412	0.1130445062	0.4992249003
AL097_552	8.991693021	0.1089703578	0.4471818953
AL099_189	8.87386943	0.1081162503	0.4034060656
AL099_326	9.001873984	0.1064093858	0.4727587402
AL099_328	9.294134062	0.1440551036	0.458454618
AL099_344	9.107911539	0.1144948398	0.5125570973
AL099_35	9.862030975	0.1545818366	0.6151723101
AL099_37	9.338815522	0.179830962	0.4050394258
AL099_577	9.886988158	0.1854323845	0.4736466419
AL099_591	8.922809483	0.08965639297	0.4861141298
AL099_597	9.519168066	0.1661813843	0.388586572
AL099_600	9.04811865	0.1077003178	0.5133851482
AL099_602	8.865169484	0.08686046859	0.4291770037
AL099_613	9.703720402	0.1723847808	0.4776966284
AL099_621	9.153721997	0.1159366327	0.5329026519
AL099_630	9.179612099	0.1220113227	0.510800712
AL099_636	9.269059273	0.1181639864	0.5105184667
AL099_78	9.017167028	0.09577655554	0.5042855393
AL101_105	9.300229768	0.155219942	0.4468083347
AL101_114	9.174572274	0.1124477676	0.4484334979
AL101_185	9.131668638	0.1103295181	0.5051449708
AL101_214	9.07790325	0.1186426579	0.4450988971
AL101_287	9.339071435	0.1272314452	0.5661345765
AL101_288	8.941416968	0.09725037072	0.4703341392
AL101_290	9.408169079	0.1379044579	0.5625363926
AL101_332	9.081519588	0.1115161007	0.5328694771
AL101_344	9.221909288	0.1375316857	0.377767302
AL101_422	9.036769493	0.1108161478	0.4243746867
AL101_423	9.507684883	0.154410608	0.4506158986
AL101_430	9.042936003	0.09719637536	0.4990055604
AL101_434	8.737914906	0.07886077014	0.4409890429
AL101_442	9.086019789	0.134018513	0.423991964
AL101_504	9.271457586	0.1230483967	0.5372382919
AL101_523	9.441536901	0.1366415583	0.5338619759
AL101_546	9.17519508	0.1277895548	0.4689240648
AL101_595	9.14239765	0.1131475528	0.5551555344
AL101_623	8.956316965	0.09746956772	0.4959048311
AL101_679	9.043583385	0.1060935329	0.5175851339
AL111_235	9.461991327	0.15358678	0.4465150743
AL111_28	9.07518508	0.1083889961	0.5008817759

AL114_826	9.526137235	0.1609316128	0.4221965564
AL114_868	9.475413075	0.1582214552	0.4294103049
AL114_937	9.532596612	0.1626247699	0.4209297711
AL129_106	9.002026372	0.1097054651	0.4810656196
AL129_148	8.794570505	0.07754371282	0.4536293287
AL129_243	9.245132909	0.1332643984	0.5029691637
AL129_266	8.950702232	0.09715883083	0.4819860694
AL129_339	9.109785129	0.1231829907	0.4162388817
AL129_369	9.09230404	0.1182275187	0.4620745171
AL129_377	8.851164347	0.08940231367	0.4486286454
AL129_389	9.416035586	0.1482700369	0.5093214217
AL129_401	9.662875585	0.1686834452	0.4689490516
AL129_419	9.040034327	0.1117776739	0.4653045182
AL129_467	9.010387282	0.1080124261	0.4631736665
AL129_47	9.002389964	0.1044357431	0.4646519995
AL129_87	9.591999296	0.1638570041	0.4284949264
AL130_199	9.058881759	0.1082911369	0.4867830913
AL130_206	9.47053881	0.1548214306	0.4071403752
AL130_223	9.374073623	0.1471718248	0.4393894005
AL130_244	9.408045541	0.1498888662	0.4189800309
AL130_429	9.406646004	0.1473586536	0.4953509983
AL130_440	9.583337471	0.1582945219	0.4978265952
AL130_68	9.249965364	0.1408448746	0.4081199343
AL133_100	9.49050287	0.1579455583	0.4210616173
AL133_116	9.200936866	0.1280703676	0.4736767546
AL133_119	9.163756832	0.1232225343	0.4880580957
AL133_136	9.117893336	0.1259574667	0.4129214144
AL207_131	7.649680902	0.1081416354	0.4202711597
AL207_143	7.795216507	0.1114914491	0.4674499961
AL207_146	8.161805783	0.138122074	0.4347289713
AL207_149	7.89575326	0.105939195	0.4810880663
AL207_151	8.598745009	0.1671428625	0.4109410267
AL207_197	8.306722064	0.1450613559	0.4501820786
AL207_20	8.02409794	0.1322939132	0.4251877645
AL207_231	8.245481996	0.1461482888	0.4120184535
AL207_249	8.29965245	0.1428372343	0.4499806396
AL207_25	8.297817071	0.1490380849	0.4018941439
AL207_413	8.011895365	0.1381896123	0.3946931393
AL207_462	8.177615271	0.1419191474	0.4198506593
AL207_473	7.936805647	0.1243798414	0.4476587427
AL207_490	7.984126882	0.1316682425	0.3958273588
AL207_504	7.721832776	0.1101414055	0.4334560669
AL207_516	8.026537311	0.1345181681	0.4081450666
AL207_539	7.871298514	0.1167095049	0.4777288743
AL207_561	8.267333165	0.1404821668	0.4525514602
AL207_61	8.045089124	0.1303392316	0.4531575304
AL207_625	8.516871434	0.1609191553	0.4573959705
AL207_691	8.375366546	0.1543463303	0.3911525867
AL207_91	7.652973621	0.1049047922	0.4250222648
AL318_200	8.004324218	0.1055665781	0.6565550876
AL318_234	7.713886643	0.09961048103	0.4345559428
AL318_29	8.296078913	0.1150727245	0.7374793351
AL318_9	7.904237062	0.104625754	0.5302913157
AL320_1003	8.518634158	0.133939944	0.6414515207
AL320_1067	8.470923633	0.1378787445	0.3915099997
AL320_1172	8.534894472	0.1434299212	0.3859437223

AL320_132	8.582672465	0.1386076274	0.6260217212
AL320_153	8.291394134	0.1303608222	0.4312805614
AL320_263	8.546185505	0.1403667817	0.5117499617
AL320_331	7.763856655	0.1113906249	0.3479169119
AL320_335	8.449163894	0.1279784037	0.5855312028
AL320_379	9.183784065	0.1743276474	0.4148729795
AL320_398	7.755807895	0.1029128544	0.3921064958
AL320_487	8.090126178	0.11787785	0.5356935788
AL320_5	8.270666667	0.125019782	0.527420293
AL320_532	8.739423257	0.1513249592	0.4638133059
AL320_772	9.15779552	0.1719636176	0.4647211654
AL320_865	8.446664257	0.1387328548	0.3884157674
AL320_879	8.265953535	0.126381176	0.505030336
AL324_1047	8.444693844	0.1370481296	0.4576930795
AL324_1064	8.589451741	0.1481852295	0.3686268299
AL324_1151	8.32059804	0.1364180702	0.3853341051
AL324_652	8.731817382	0.1512966595	0.4038428104
AL435_298	5.864809261	0.2652378212	0.4475483427
AL435_334	5.787893591	0.2559622744	0.4412232761
AL435_403	5.749631241	0.2394476233	0.4614281932
AL435_413	5.29856728	0.2187984678	0.4363076765
AL435_634	5.91046528	0.2627780346	0.467530867
AL435_636	5.352833388	0.2234446852	0.437419918
AL435_721	5.453864234	0.229488045	0.4387939227
AL435_725	6.01337452	0.2734623517	0.4443419378
AL435_730	5.47145833	0.2201121101	0.4649564816
AL437_245	5.699779538	0.2478242769	0.4472282347
AL437_251	5.547323367	0.2348889923	0.4491953529
AL437_264	5.561382498	0.229835008	0.469202689
AL437_288	5.9140313	0.2658132443	0.4494727246
AL437_505	5.214409517	0.1973634758	0.453997777
AL437_562	5.736571089	0.2388926366	0.478075704
AL437_573	5.475800125	0.2460417728	0.4290892014
AL437_579	5.789128394	0.254111154	0.4596674789
AL437_582	5.161057285	0.1825767766	0.4649460912
AL437_601	5.365783609	0.2146789286	0.4558613664
AL437_611	5.551650309	0.2405733583	0.436009765
AL521_566	4.785374419	0.2576090993	0.4200144405
AL521_726	4.599358919	0.187787258	0.4622705359
AL521_847	4.673541333	0.2088844679	0.4659267746
AL521_865	4.931469905	0.2952174229	0.4286036625
AL522_473	4.860981505	0.2732937974	0.4394298411
AL522_510	4.828798825	0.2692200531	0.4311532453
AL522_511	4.739056117	0.2372747965	0.4437710032
AL522_519	4.737025053	0.2642862543	0.4062924007
AL522_531	4.780649417	0.2570631968	0.4215520795
AL522_532	4.885994957	0.2850281813	0.4258320717
AL522_543	4.886445622	0.2783876422	0.4406260105
AL522_547	4.763554709	0.2521552246	0.436198989
AL522_561	4.783560822	0.2544689779	0.4399686355
AL522_564	4.647066793	0.229708281	0.4300718671
AL522_579	4.912403487	0.2922403256	0.4199102108
AL522_593	4.693241561	0.2201993833	0.4616249098
AL522_594	4.923511456	0.2888315373	0.4431665049
AL522_613	4.792925566	0.2659231351	0.4057731667
AL522_624	4.62913837	0.2064427007	0.4635240498

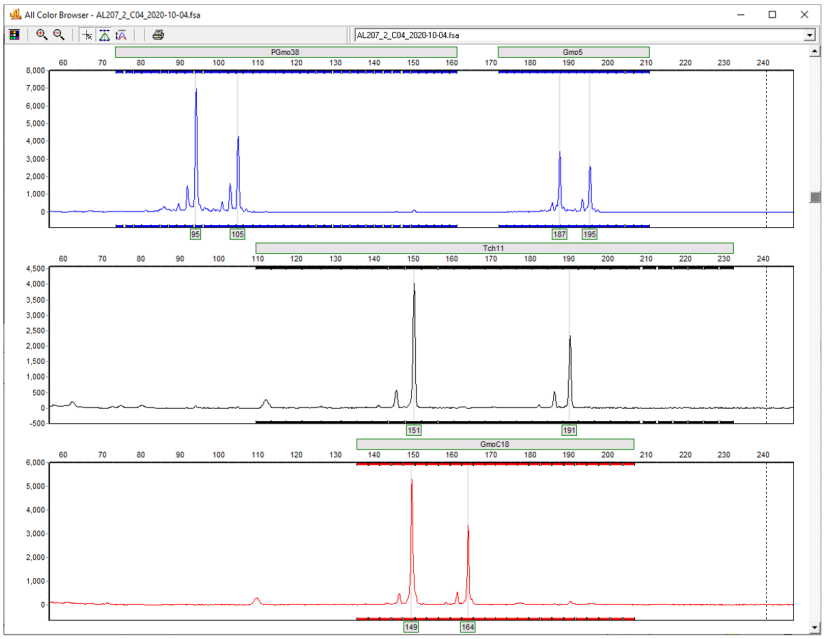
AL522_682	4.845561151	0.2483105756	0.4853192219

APPENDIX II. SUPPLEMENTARY FIGURES

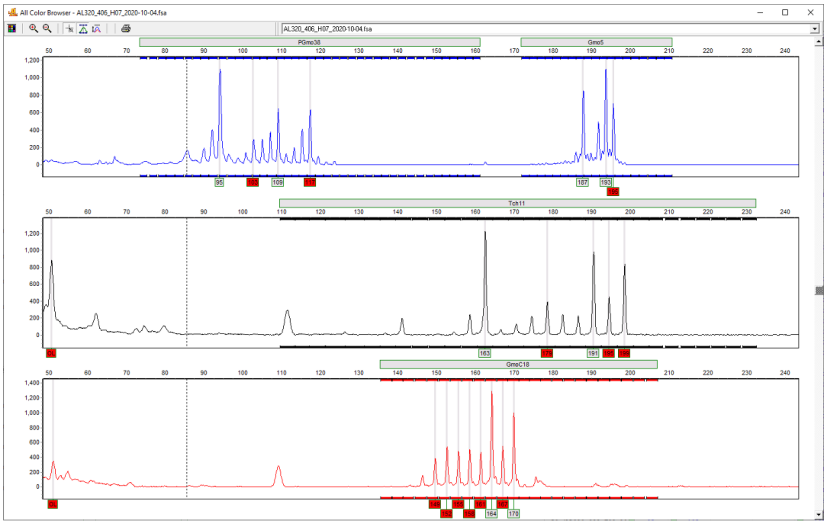
List of Supplementary Figures

Supplementary Figure 1. Segregation and electrophoretic visualization of microsatellite (MSAT) alleles in clean and contaminated samples.
Four MSAT loci, (PGmo38 and Gmo5 blue; Tch11 black; GmoC18 red) were used to identify cross-contaminated samples. Prior knowledge of each MSAT length range in the resolution of 1bp was used to bin allele sizes using the GeneMarker® software. **(a)** An example MSAT panel of a clean sample. Each locus shows two clear peaks, indicating a heterozygous status, marked with grey vertical lines. For example, in PGmo38 (left side of blue panel), a peak at 95bp and the other at 105bp appear as two different alleles in the locus. The smaller peaks before the highest peak in each allele is a typical noise pattern from a characteristic of MSAT analysis, called “stutter band”. The signal derives from incomplete products of multiplex PCR cycles, thus always smaller than the signal from complete products. **(b)** An example of contaminated samples. When more than two individuals with different MSAT genotypes are mixed in the DNA samples, three or more peaks appear as shown. For example, in Gmo5 (right side of the blue panel), three peaks are identified. As stutter bands are always smaller and increasing towards the real peaks, the last peak at size 195 bp (marked in red box) is likely to be a real signal of an additional allele. The other MSAT sites also show more than three peaks even after considering stutter patterns. All MSAT sites of all individuals were examined manually to confirm and edit the automatic peak detection of the software. Samples with more than three peaks in at least one MSAT were excluded in the selection process.

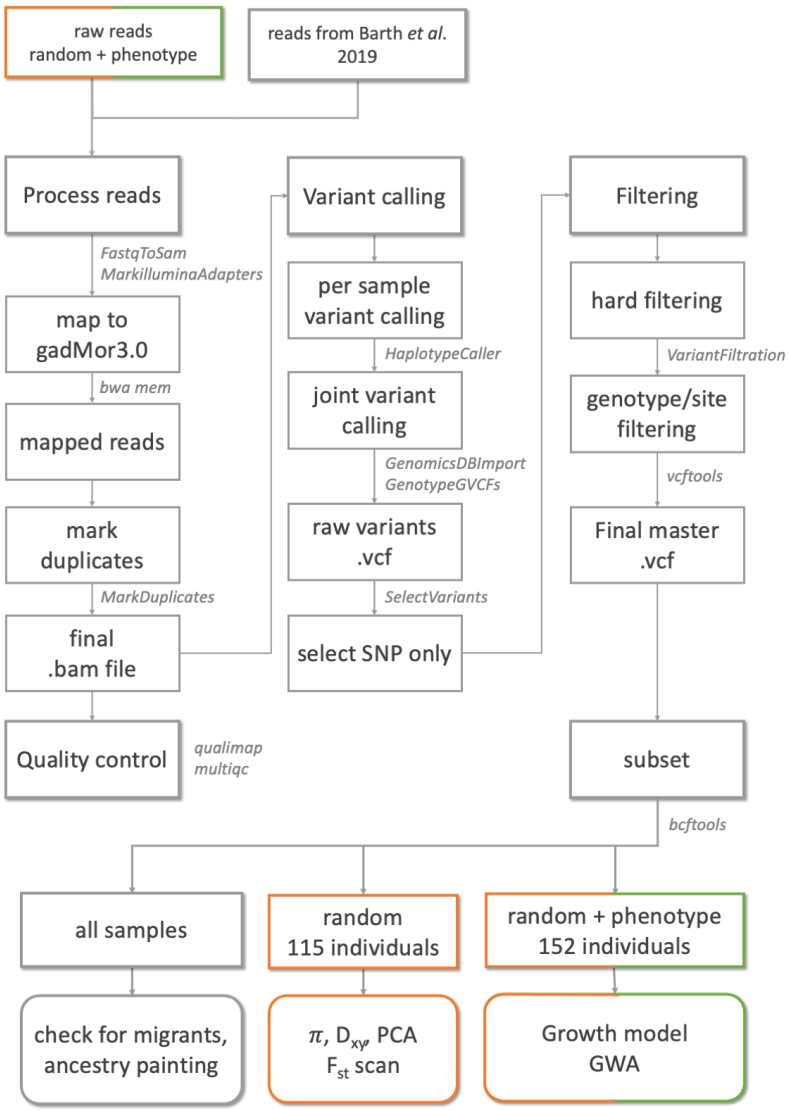
(a)



(b)

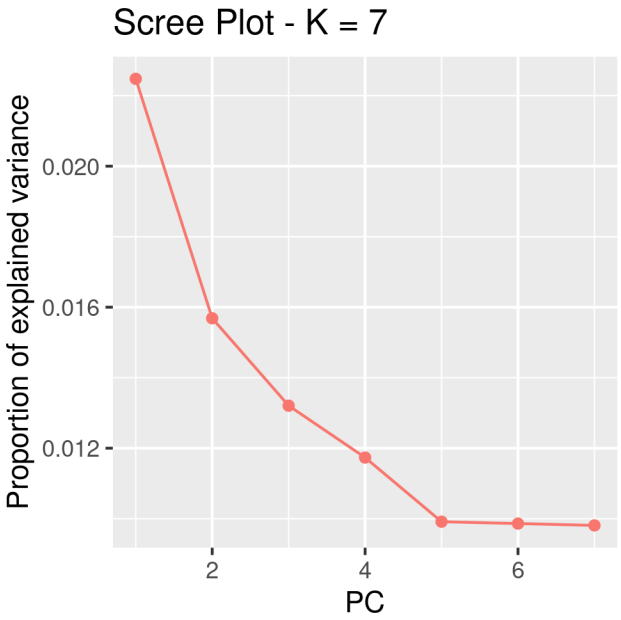


Supplementary Figure 2. A flowchart of bioinformatic analyses from raw reads to variant files. Using raw reads sequenced in this study ("random" coloured in orange and "phenotype" coloured in green) as well as publicly available reads of Eastern and Western Baltic cod individuals as input (Barth *et al.* 2019), the bioinformatics workflow follows three major steps, namely processing reads, variant calling and filtering of SNPs. The mapped *.bam* file was subjected to a quality check to exclude samples with low mapping quality. As sampling design (presented in Figure 1) included two different approaches, covering temporal and phenotypic ranges, the final master *.vcf* file was further subsetted to be streamed in different analyses. The softwares used in each step are written in italics.

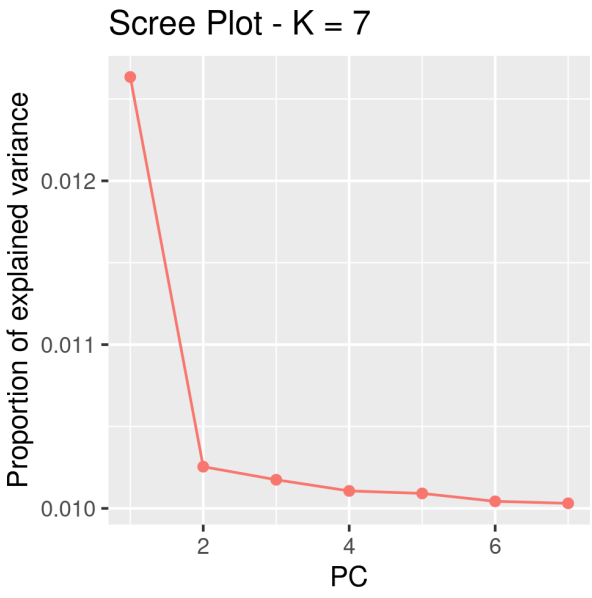


Supplementary Figure 3. Scree plots of principal component analysis.
Proportions of variance explained by each principal component (PC) are plotted for **(a)** PCA using all SNPs and **(b)** PCA using SNPs excluding inverted regions. Based on this plot, k=7 was chosen as the number of PCs to compute. All 7 PCs were investigated to confirm the lack of population structure based on the catch years (data not included), thus first two PCs were used to create PCA plots in Figure 5.

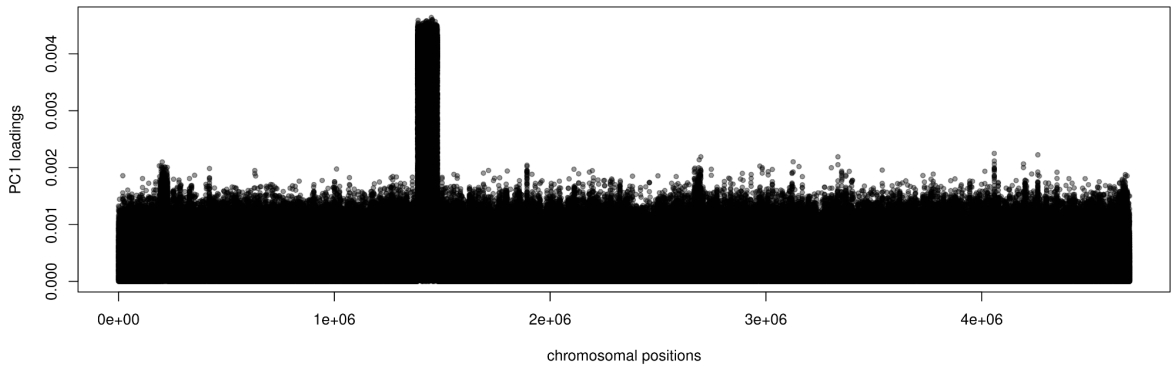
(a)

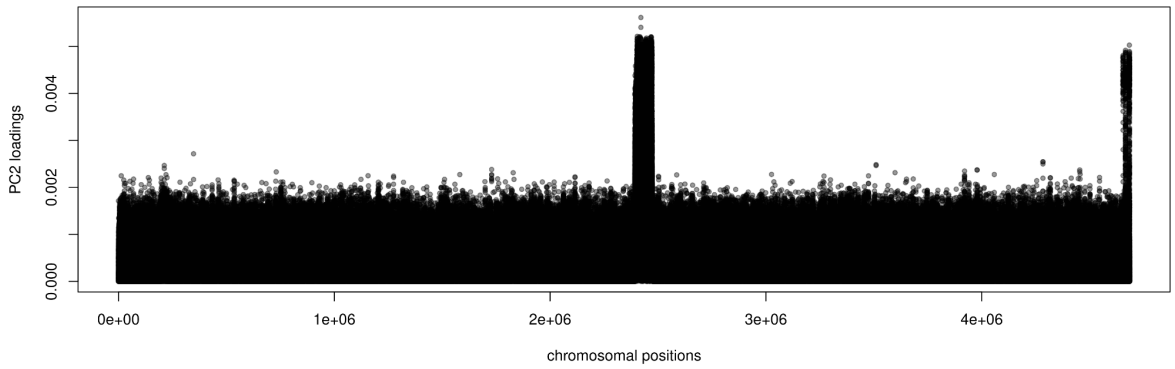


(b)



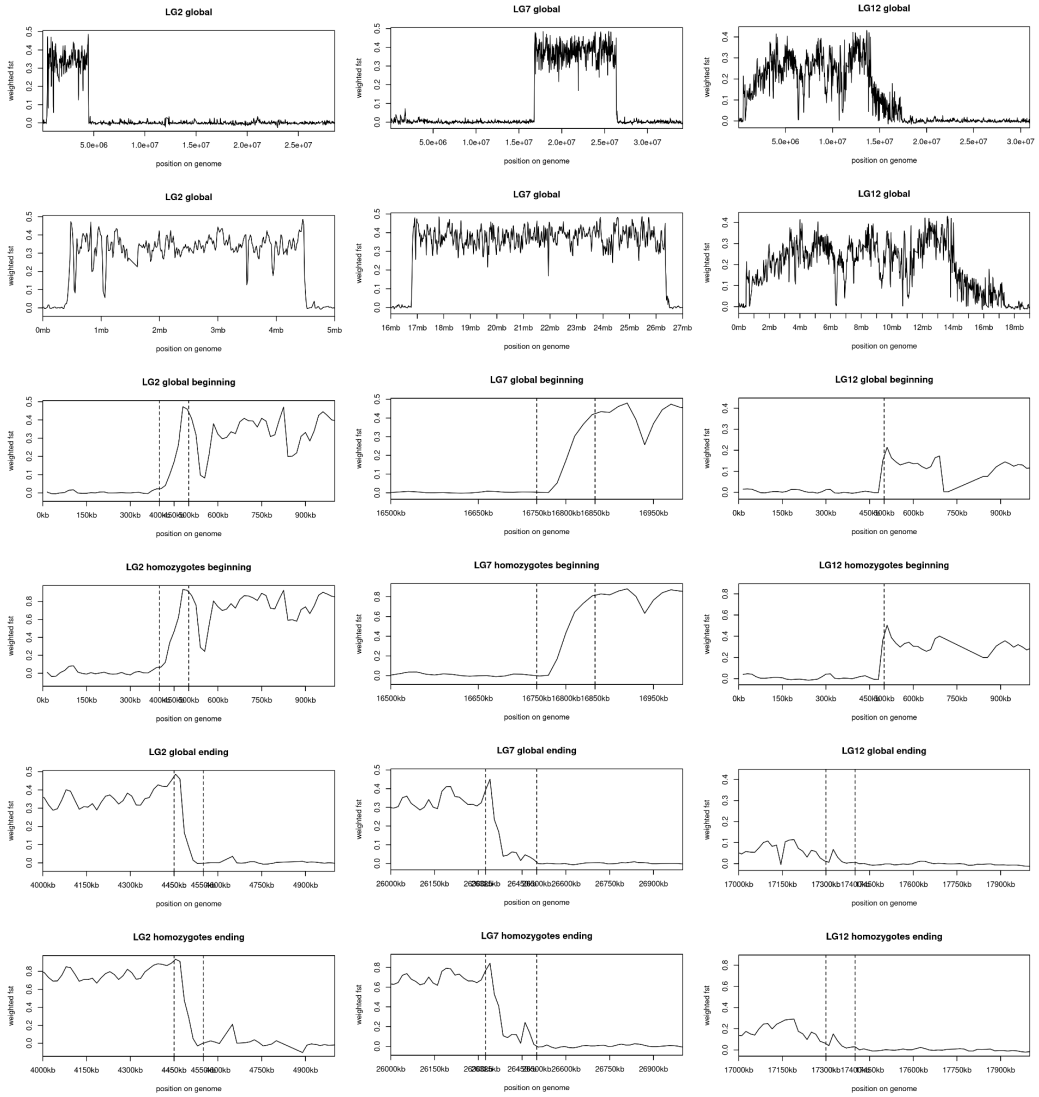
Supplementary Figure 4. PC loadings of PCA including inversions in Figure 5(a)
Loadings of each variant that affect PC values were plotted. X-axis is the genomic position of each variant with chromosomes sequentially placed. The pillar-like pattern in this plot created by strong loadings from a constrained region (inversion area) is a typical pattern appearing in a PCA of genotype data including inversions. This shows that the distinct clustering pattern in Figure 5(a) is driven by inverted regions in the genome. The PC1 values (top) are driven by the inverted region in LG07. PC2 values (bottom) are driven by inversion in LG12 (pillar at the center) as well as by some SNPs in unplaced scaffolds of reference genome (far right).





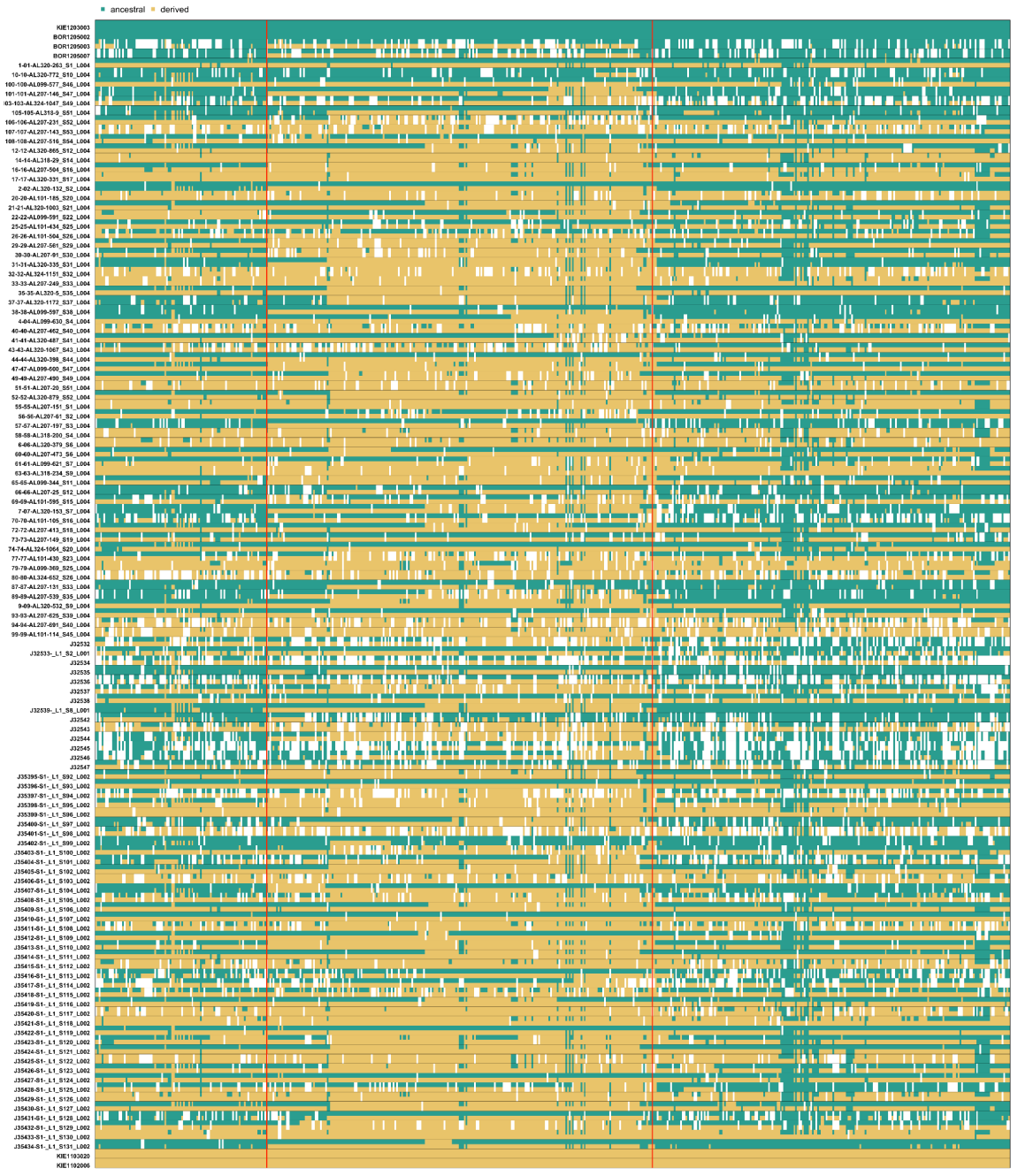
Supplementary Figure 5. Global and pairwise F_{st} on groups of individuals based on the inversion status (LG2, LG7, and LG12 in each column).

To determine the boundaries of inversion referenced to the reference genome gadMor3.0, F_{st} values in 30Kb overlapping windows (in 15 Kb steps) were computed using groups of individuals of different inversion status. After plotting the global F_{st} values over the whole chromosome (row 1), approximate coordinates were chosen to zoom in (row 2) to decide the beginning and end of the inverted regions (row 3 and 5). The pairwise F_{st} of two groups of homozygotes (ancestral and derived status) were also investigated to confirm the consistency of signals (row 4 and 6). Two locations were visually selected in the beginning and the end of inversions (Dashed vertical lines in row 3-6) to either include or exclude the regions depending on the downstream analysis conducted.

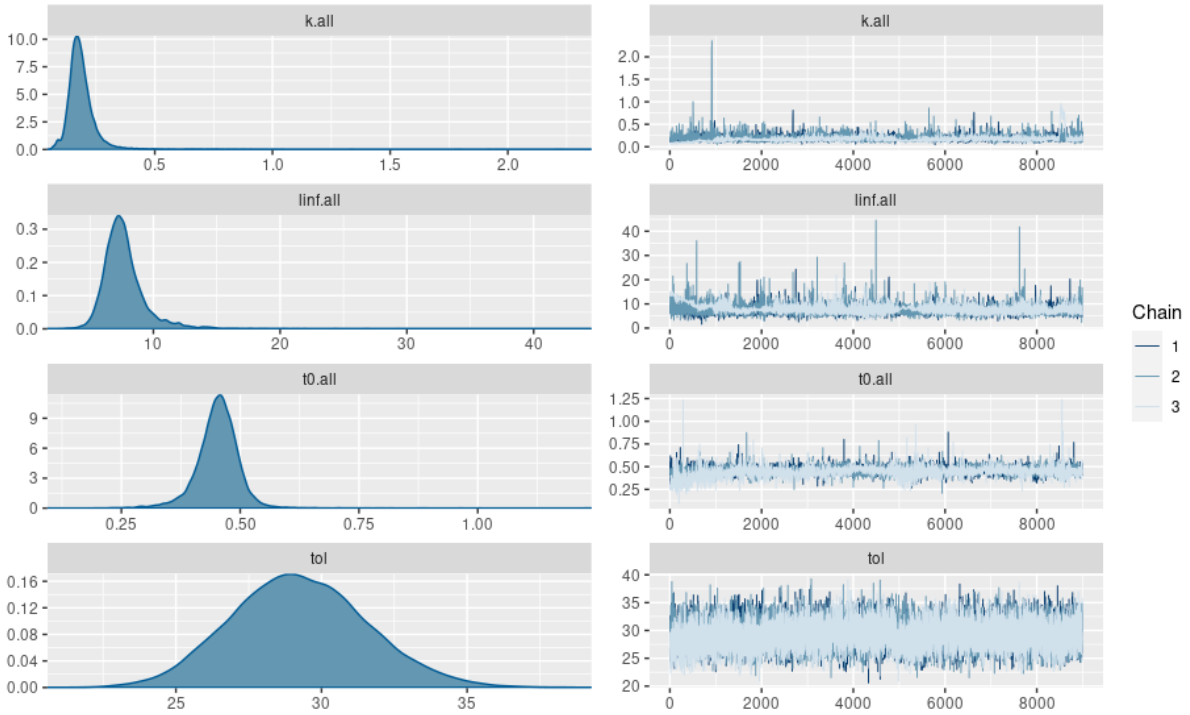


Supplementary Figure 6. Ancestry painting in double crossover region within the inversion in LG12.

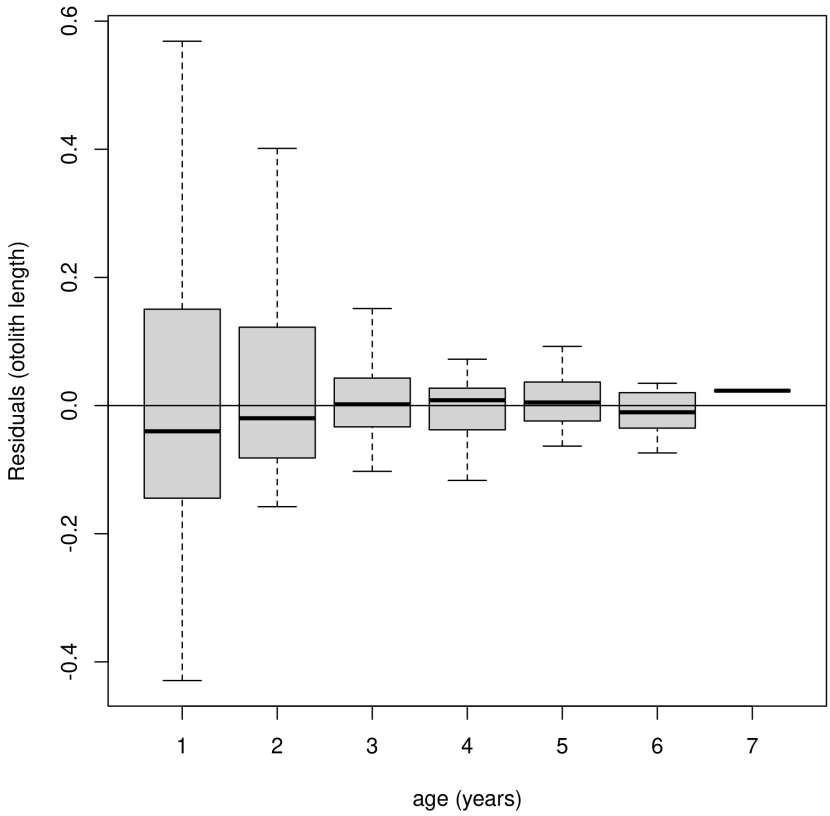
To identify the double-crossover status of each individual, all “random” samples were examined by ancestry painting analysis, using four samples (homozygotes ancestral: KIE1203003, BOR1205002 and homozygotes derived: KIE1202006, KIE1203020 from Barth et al. 2019) as reference of ancestral and derived homozygotes and two EBC (BOR1205003, BOR1205007; identified in Matschiner et al. 2021) as reference of double crossover. SNP sites between 6.5 and 7.5Mb within LG12 (reference to garMor3.0) which are fixed 80% in two sets of references were painted depending on the allelic status of ancestral or derived (green and yellow respectively as in legend), allowing for 20% of missingness in the data. The double crossover region is visually identifiable with higher frequency of derived alleles (marked with red vertical lines across all samples). With two rows of genomes in each individual, the genotype status were assigned in three sections, before, at and after the double crossover region. Sample names in the plot correspond to the sequencing names in Supplementary Table 1.



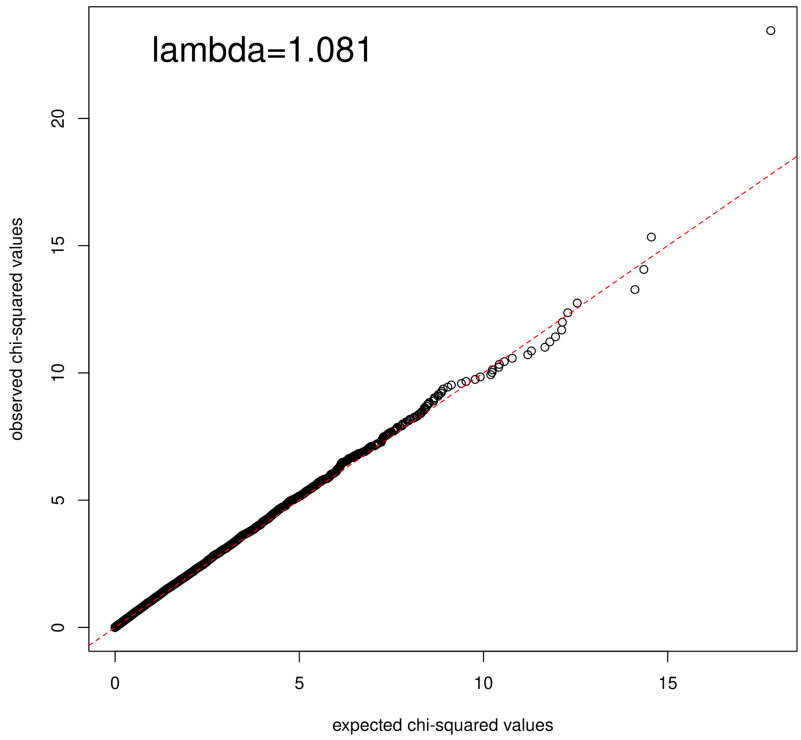
Supplementary Figure 7. Posterior distributions and model convergence of three Markov chain analyses to estimate von Bertalanffy parameters.
The posterior distributions of four parameters used in the growth model (only three von growth parameters for all samples; *k.all, linf.all*, and *t0.all* and error *tol* are shown), in the left column, and corresponding trace plots of simulated three Markov chains over 100,000 iterations with a thinning rate of ten, in the right column, are plotted. Each chain starting from different initial values have converged adequately at the beginning of the iterations, indicating the robustness of model fit.



Supplementary Figure 8. Residuals of estimated otolith lengths for each age class.
The residuals were calculated as (estimated otolith radii at age-observed otolith radii at age) / (observed otolith radii at age), matching the number of observations of each age class to assess the model fit. The discrepancy in variance of residuals in each age class is likely to come from the differences in the number of data points available in input (154 observations for age 1 and 1 observation for age 7).



Supplementary Figure 9. QQ plot of expected and observed chi-squared p-values of the GWA. The observed chi-squared p-values of the GWA were plotted against chi-squared expected p-value distribution in a quantile-quantile (QQ) plot. The genomic inflation factor (= lambda), i.e., the median of chi-squared observed p-value divided by expected median of chi-squared p-value, was calculated. The overall fit of the expected versus the observed with a slight deviation at the highest end indicates an adequate correction of confounding factors during the GWA analysis.



Affidavit

I hereby declare that I have written this thesis entitled:

Evidence for fisheries induced evolution at the genome level in a heavily exploited fish stock, the Eastern Baltic cod (*Gadus morhua*)

with the help of my supervisors and co-authors stated in the contribution statements using only the aids and sources indicated and in compliance with the rules of good scientific practice of the German Research Foundation. Any concepts or quotations applicable to these sources are clearly attributed to them.
This thesis has not been submitted to any other body as part of an examination procedure and is my only and so far first doctoral procedure.
The study conducted in this thesis has not yet been published in any peer-reviewed scientific journal for a publication.
An academic degree has never been withdrawn.

……

Kwi Young Han
Kiel, 09 January 2024