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Multi-Millennial Genetic Resilience of Baltic Diatom Populations Disturbed in the Past Centuries

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Received: 27 February 2025 | **Revised:** 2 July 2025 | **Accepted:** 9 August 2025

Funding: This study was funded by the K314/2020 grant of the Collaborative Excellence Programme of the Leibniz Association.

Keywords: Baltic Sea | phytoplankton | population genomics | sedaDNA | *Skeletonema marinoi* | target capture

ABSTRACT

Little is known about the genetic diversity and stability of natural populations over millennial time scales, although the current biodiversity crisis calls for heightened understanding. Marine phytoplankton, the primary producers forming the basis of food webs in the oceans, play a pivotal role in maintaining marine ecosystems health and serve as indicators of environmental change. This study examines the genetic diversity and shifts in allelic composition in the diatom species *Skeletonema marinoi* over ~8000 years in the Baltic Sea by analyzing chloroplast and mitochondrial genomes. Sedimentary ancient DNA (sedaDNA) demonstrates the stability and resilience of genetic composition and diversity of this species across millennia in the context of major climate events. Accelerated change in allelic composition is observed from historical periods onwards, coinciding with times of intensifying human activity, like the Roman Empire, the Viking Age, and the Hanseatic Age, suggesting that anthropogenic stressors have profoundly impacted this species for the last two millennia. The data indicate a very high natural stability and resilience of the genomic composition of the species and underscore the importance of uncovering genomic disruptions caused by human impact on organisms, even those not directly exploited, to better predict and manage future biodiversity.

1 | Introduction

Human activities have had a profound impact on natural environments, resulting in the endangerment of a multitude of ecosystems, including marine environments (Goulletquer et al. 2014). Phytoplankton forms the basis of marine food webs, and, as crucial components of marine ecosystems, changes in this group are central to understanding ecosystem shifts (Panja et al. 2024). Among the phytoplankton, diatoms, which play a significant role in global biogeochemical cycles, are sensitive bioindicators (Benoiston et al. 2017), as the different species have specific requirements. *Skeletonema marinoi*, a prominent marine diatom species (Johansson et al. 2019), is influenced by different abiotic and biotic changes, like temperature, migration, and human activities (Boyd and Hutchins 2012). It is a dominant contributor to the Baltic Sea spring bloom (Kremp et al. 2024), which is a highly productive seasonal event essential for primary production and marine food webs in the region. For this species, changes in bloom timing (Hjerne et al. 2019) and optimal growth temperature (Hattich et al. 2024) have already been observed as a result of recent climate change. Additionally, previous studies have reported adaptive genetic alterations in *S. marinoi* in response to anthropogenic pressures, including eutrophication

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and metal pollution (Briddon et al. 2025). Investigation of marine phytoplankton response to current global changes is mostly based on taxonomic diversity, but recent studies show that diatoms also quickly adapt to environmental changes through acclimation and genetic adaptation on a population genomic level (Rynearson et al. 2022). In fact, intraspecific genomic variation is an important factor in the response and resilience of diatoms to environmental perturbations (Godhe and Rynearson 2017). Thus, investigating the genomic composition of diatom populations and its changes is crucial for understanding their adaptability to environmental changes.

Despite its relatively brief history, the Baltic Sea has undergone significant transformations, making it suitable for studies addressing organism responses to environmental changes. For the last ~10,000 years, these transformations include a transition between fresh and brackish water between ca. 9000 and 7000 calibrated years before present (years cal BP; 0 BP = 1950 Common Era) (Björck 2008), as the basin evolved from the freshwater Ancylus Lake into the more saline Littorina Sea. This shift was driven by glacial retreat, post-glacial rebound, and sea-level rise, which allowed a connection with the North Sea and a salinity increase. In addition, the region has experienced several distinct climate phases, including the Holocene Thermal Maximum (HTM; ~10,000–5500 years cal BP), the Late Antique Little Ice Age (LALIA; ~1400–1300 years cal BP), the Medieval Climate Anomaly (MCA; ~1150–650 years cal BP), the Little Ice Age (LIA; ~650–150 years cal BP) and the Contemporary Period (CP; since 0 years cal BP), all of which affected sea temperature, ice cover, salinity, and water circulation (Barbier 2010; Zillén et al. 2008). Due to its shallow enclosed nature and a steep salinity gradient, modern biodiversity is relatively low (Ojaveer et al. 2010). The Baltic Sea is currently under increasing pressure from human activities. Nutrient runoff from agriculture and wastewater has caused eutrophication, resulting in algal blooms and oxygen depletion at depth and in the seabed. Global warming exacerbates these effects by raising water temperatures and intensifying stratification, thereby limiting oxygen mixing. These changes strongly impact marine organisms, particularly phytoplankton such as diatoms, which are highly sensitive to environmental conditions and form the base of marine food webs (Reusch et al. 2018).

Undisturbed sediments serve as chronological and ecological archives, offering insights into past environmental changes and biodiversity shifts (Hochfeld et al. 2025), and providing long time series of phytoplankton dynamics. Phytoplankton archives in sediments include biomarkers, microfossils, (living) resting stages, and sedimentary ancient DNA (sedaDNA). These remains contain information on biodiversity and can reveal changes in adaptive traits (Ellegaard et al. 2020; Hattich et al. 2024). Here, we develop a time series of population-level responses of the diatom *S. marinoi* in the Baltic Sea, by employing a targeted approach to enrich chloroplast and mitochondrial genomes using hybridization enrichment. We focus on the organellar DNA, as organelles have a small genome size, are present in multiple copies per cell and thus this DNA is more concentrated in ancient samples, which improves the recovery and coverage of target sequences (Nguyen et al. 2023). This allows us to analyze genetic diversity and shifts in allelic composition across complete organellar genomes. We investigate (1) the degree of stability, response and resilience of *S. marinoi* to natural environmental changes in the Baltic Sea over the last ca. 8000 years, and (2) identify changes in the genetic composition of populations in recent centuries of heightened anthropogenic activities.

2 | Results

We analyzed sediment samples of two cores located in the Baltic Sea, the Eastern Gotland Basin (EGB) and the Gulf of Finland (GOF) (Figure 1A), covering a time span up to approximately the Ancylus Lake stage (extrapolated age: 8148 years cal BP) (Figure 1B). We investigated the population structure of *S. marinoi* over this period at the two locations by focusing on Single Nucleotide Polymorphisms (SNPs) on the organelle genomes (Figure 1C). This was achieved by target enrichment of the chloroplast and the mitochondrion.

This study provides an analysis of the genetic dynamics of *S. marinoi* populations in the EGB and GOF over millennia, revealing insights into the effects of both natural environmental changes and anthropogenic activities. The use of RNA baits for hybridization enrichment resulted in a higher degree of resolution, enabling the identification of a greater number of SNPs in both mitochondrial and chloroplast genomes. The analysis revealed that climate events exert an influence on genetic variations, with specific climate events aligning with temporal variations in the population's genetic makeup, but that the genetic composition reverted back to a state that was mostly stable across millennia in between these events. Longer-lasting patterns of genetic change over time were observed at both sites in the past two millennia, coinciding with periods of intensified anthropogenic activities. These findings imply high resilience of *S. marinoi* populations across time and climate events across millennia, along with more recent changes.

2.1 | General Data Assessment

2.1.1 | DNA Versus RNA Baits

In order to study past *S. marinoi* population dynamics in the EGB and GOF, we employed DNA and RNA baits for hybridization enrichment of full chloroplast and mitochondrial genomes. The use of RNA baits resulted in a higher degree of resolution. Following trimming, DNA and RNA baits yielded 34.9 million and 51.8 million sequences, respectively. Of these, 34.8 million (DNA) and 35.3 million (RNA) reads were successfully mapped to reference organelles (Figure 2A and Table S1). In the case of RNA baits, 6.41 million reads were mapped to the mitochondrion, while 28.9 million were mapped to the chloroplast. For DNA baits, the numbers were 6.27 million and 28.6 million, respectively. The RNA baits identified a greater number of SNPs in both the mitochondrial (301 vs. 92) and chloroplast (1716 vs. 403) genomes. Consequently, the analysis focuses on the results obtained from RNA baits. The results of the DNA bait analysis can be found in the Section S2.1.

The average coverage achieved for the experimental samples was generally high, with an average mitochondrial coverage of

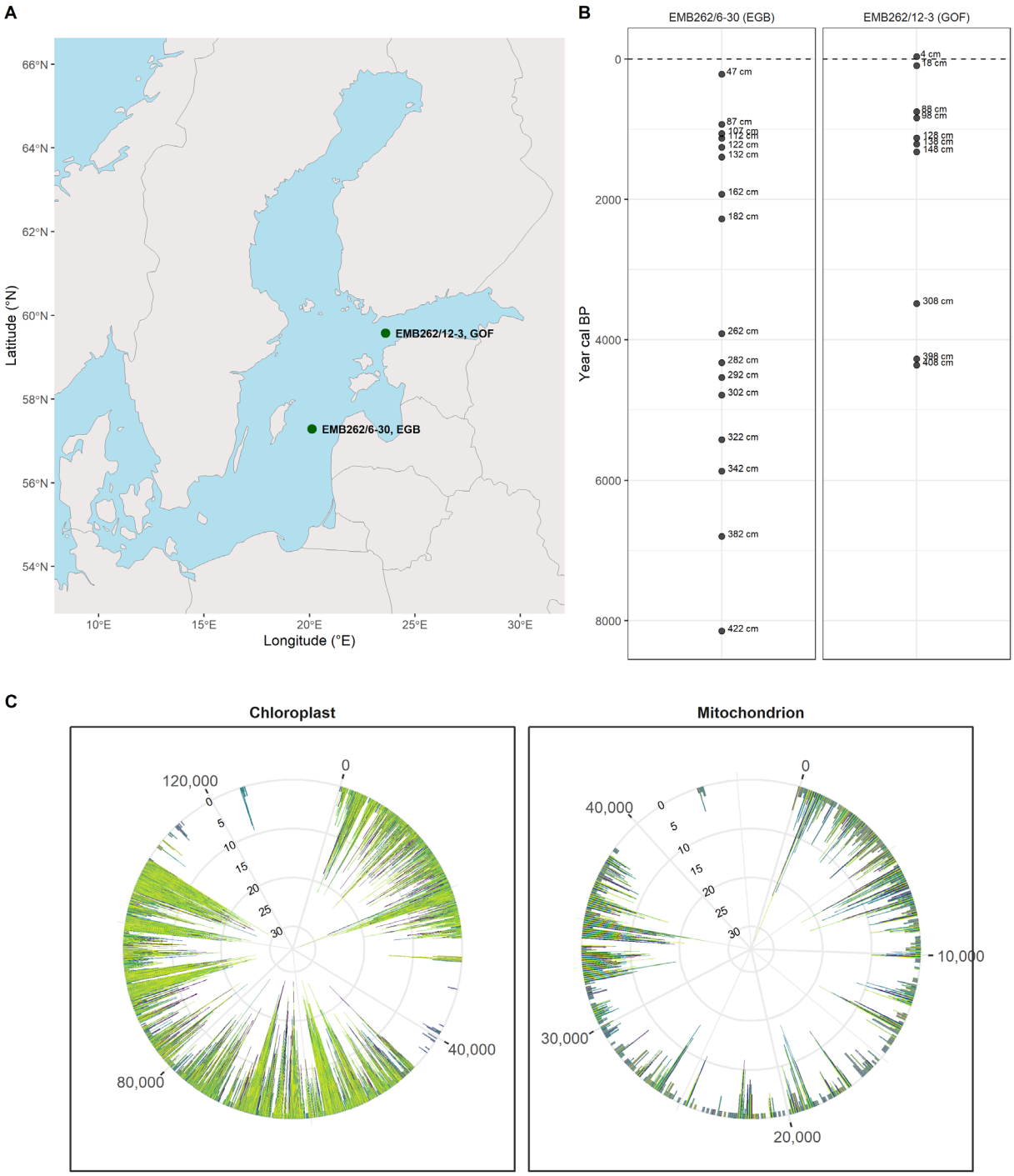

FIGURE 1 | (A) Location of the coring sites and corresponding cores in the central Baltic Sea. Gulf of Finland (GOF; core EMB262/12-3GC) and Eastern Gotland Basin (EGB; core EMB262/6-30GC). Map lines delineate study areas and do not necessarily depict accepted national boundaries. (B) Sample distribution (in cm) in the sediment cores and corresponding ages. (C) Number of SNPs called per 100 base pairs across the genome for each sample. The mitochondrion and chloroplast genomes of *S. marinoi* are shown. The gaps indicate the repeat masked regions.

78.77 and an average chloroplast coverage of 575.5. This coverage demonstrates the efficiency of the hybridization capture approach and ensures the reliability of the genomic data collected. Furthermore, the Extraction Blanks and Library Blanks produced low to non-meaningful coverage (see Table S2). All information about the samples, corresponding age, location, and other metadata is available in Table S3.

2.2 | Ancient DNA—Damage Pattern

We analyzed damage patterns in ancient DNA (aDNA) samples, focusing on C-to-T substitutions. These substitutions are key aDNA authentication markers due to their pervasiveness in aDNA and their function in indicating cytosine deamination, a prevalent form of DNA damage. No significant correlation

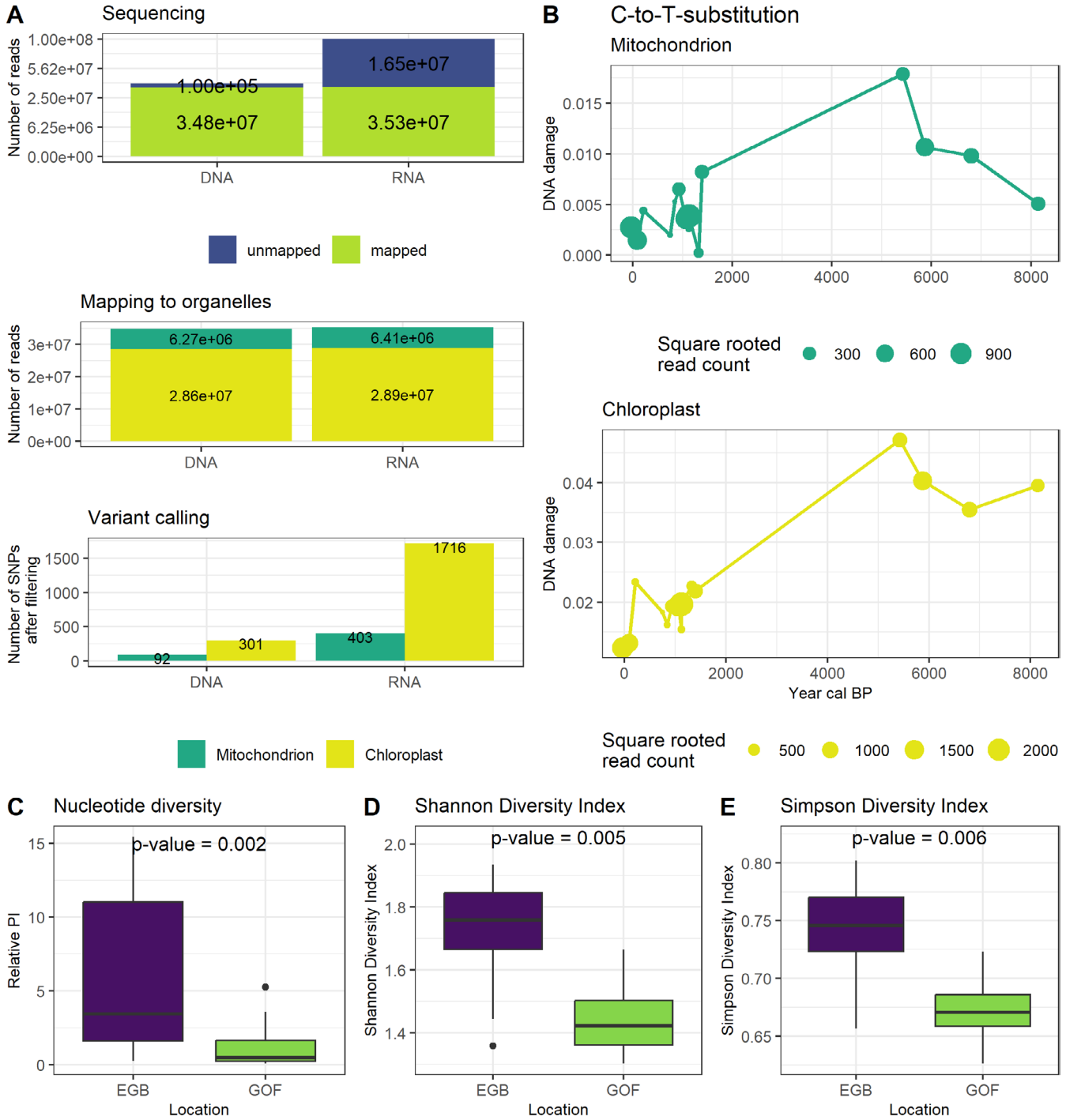

FIGURE 2 | Data assessment: (A) sequencing yield and single nucleotide polymorphisms (SNPs): post-trimming sequencing yield for DNA and RNA baits, and the number of SNPs detected in mitochondrial and chloroplast genomes for each bait set. (B) C-to-T substitution: analysis of C-to-T substitutions over time for each organelle from all data (GOF and EGB). (C–E) Comparative analysis of normalized nucleotide diversity and diversity indices. (C) Relative nucleotide diversity (PI), (D) Shannon, and (E) Simpson between Eastern Gotland Basin (EGB) and Gulf of Finland (GOF). Each bar graph shows data for both sites with significant *p*-values.

($R = 0.18$, $p = 0.315$) was found between mapping coverage and substitution frequency, suggesting that the damage pattern does not affect the mapping coverage. The degree of damage was found to significantly increase with the age of the samples ($R = 0.65$, $p = 0.0003$, Figure 2B). A greater number of sequences were mapped to the chloroplast due to its larger genome size. This allows a greater number of reads to be used to detect damage patterns, increasing the overall value of the data.

2.3 | Genetic Diversity and Spatial Differentiation

A comparison of the genetic differences between *S. marinoi* retrieved from the EGB and the GOF respectively revealed that while the two locations exhibited some differences, they also shared a considerable degree of similarity. This was evidenced by the FST value, a measure used in population genetics to quantify the genetic differentiation between populations, which ranged

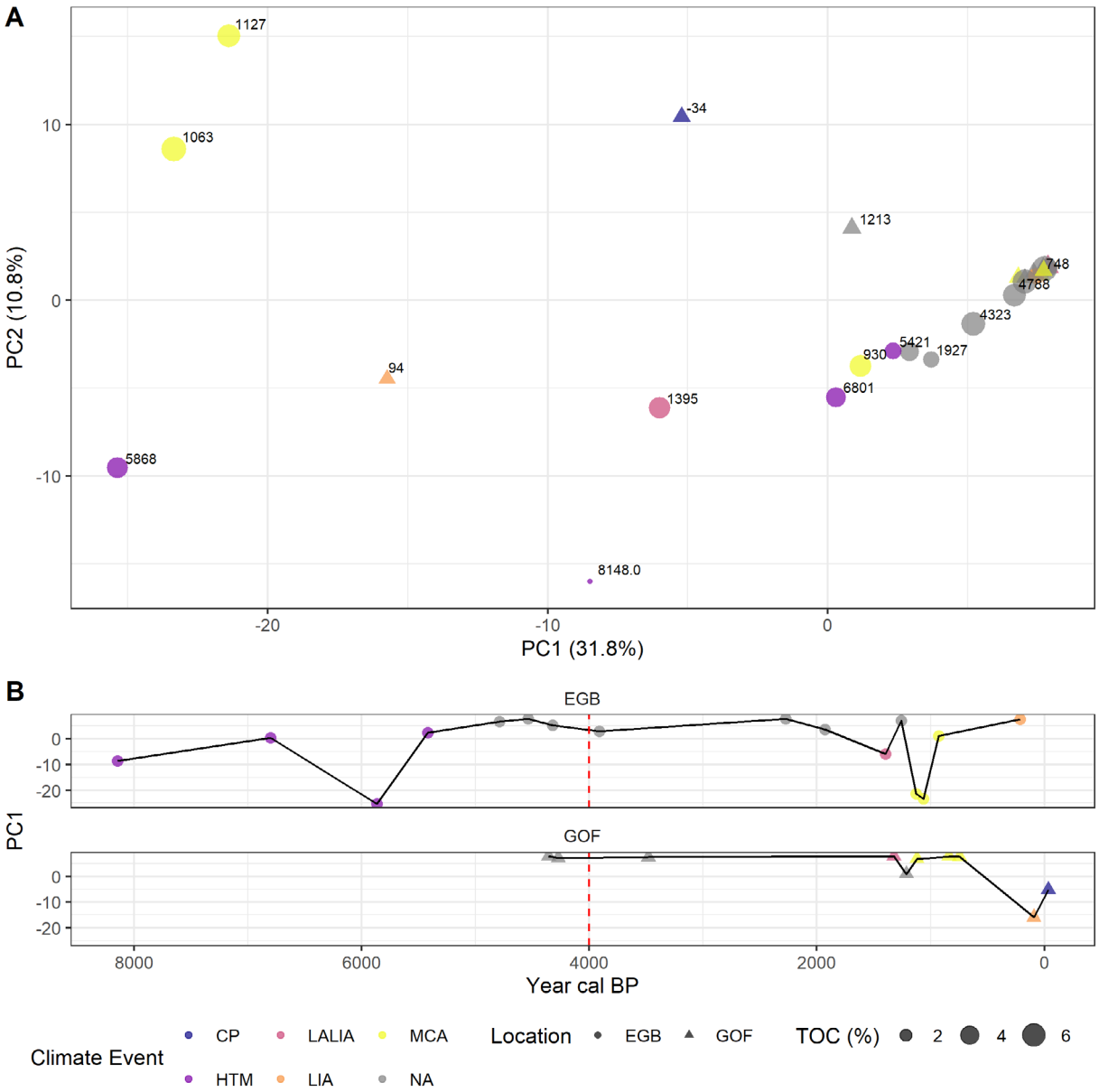

FIGURE 3 | Principal component analyses of the allelic composition of *S. marinoi* organelles, demonstrating the genetic diversity and population structure. (A) PC1 and PC2 are categorized by climate events, total organic carbon (TOC) and the age of each sample is given for both sites. (B) PC1 versus time for both sites. The red dashed line marks the transition from the Littorina Sea to the Modern Baltic Sea. Climate events include the Holocene Thermal Maximum (HTM), Late Antique Little Ice Age (LALIA), Medieval Climate Anomaly (MCA), Little Ice Age (LIA), Contemporary Period (CP) and (NA) no event.

between 0.05 and 0.1 (see Supporting Information, Figure S6). Notably, the genomic data from EGB shows a higher level of genetic diversity than the one from GOF. This is presented by different measures of distinct variant diversity, with significant differences observed (p: 0.002, 0.005, 0.006, see Figure 2C–E).

2.4 | Effects of Environmental Change

Our study on *S. marinoi* organelles at two locations in the Baltic Sea reveals that across several millennia the genetic composition of the population remained stable, punctuated by differences in specific periods, putatively coinciding with environmental changes. A Principal Component Analysis (PCA), conducted to investigate differences in allelic composition between sediment layers, showed that the majority of samples are situated within a primary cluster, but a number of smaller clusters are found that correspond with periods marked by specific environmental events (Figure 3A). Together, PC1 and PC2 describe 42.6% of the data variance.

The retrieved specific clusters (Figure 3A) correspond to specific climate periods, including the HTM, LALIA, MCA, LIA and CP. We verified that existing variation in allelic composition is not a result of the C-to-T-substitution rate by performing a PERMANOVA, which showed that the C-to-T-substitution rate accounted for approximately 6.7% of the variation in the PCA space ($R^2 = 0.067$, $p = 0.19$), though this was not statistically significant (see Figure S5). Additionally, we performed a PERMANOVA to assess the impact of Total Organic Carbon

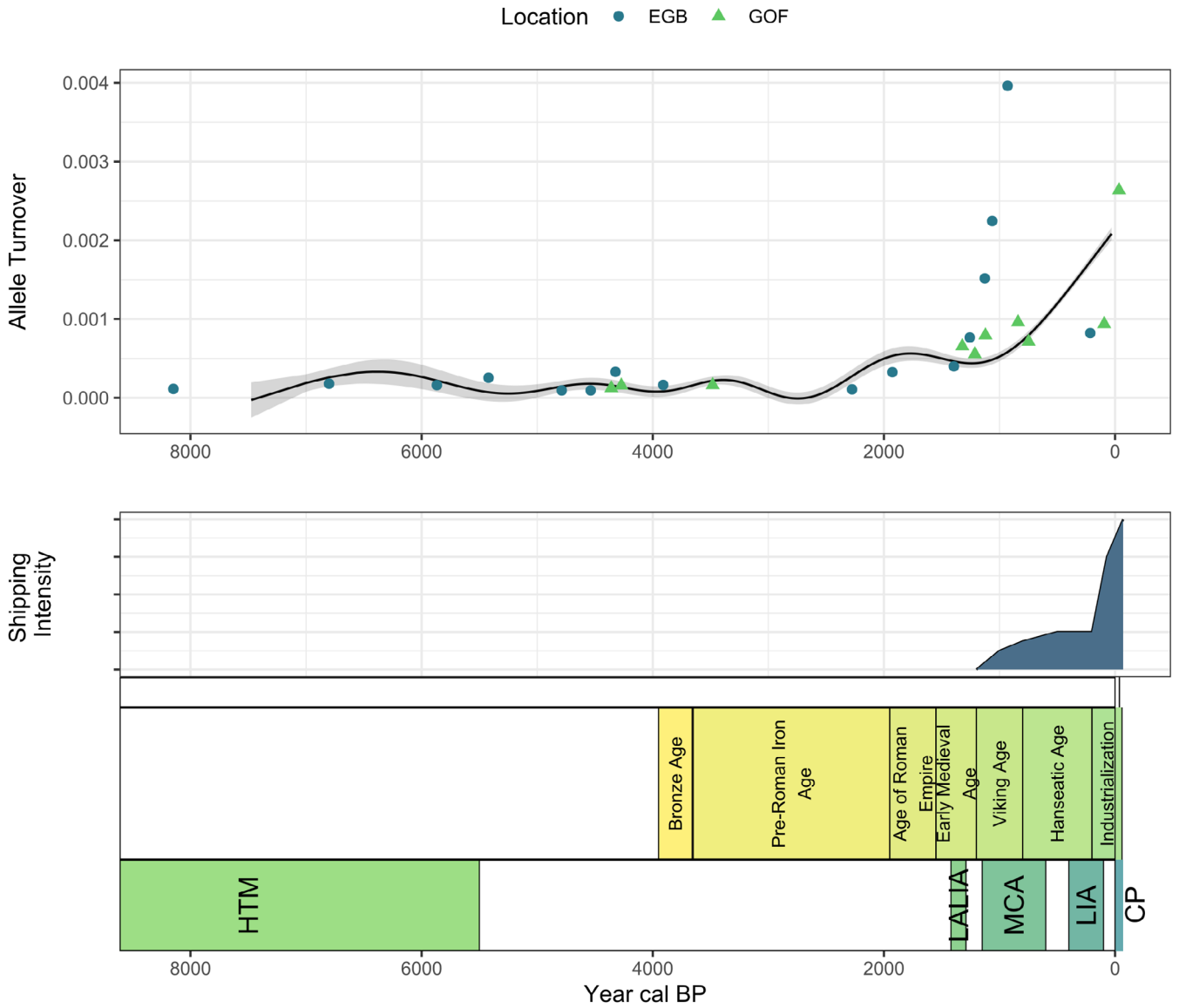

FIGURE 4 | Temporal analysis of allele turnover in *S. marinoi*. This figure presents the Generalized Additive Model (GAM) fitted to the allele turnover over time (year cal BP). The data includes both Eastern Gotland Basin (EGB) and Gulf of Finland (GOF) sites. Key environmental events, such as the HTM, LALIA, MCA, LIA, and CP, are noted. Additionally, anthropogenic periods and associated shipping activity estimated from literature sources are shown.

(TOC) on the variation in the PCA space, which showed that TOC accounted for approximately 4.5% of the variation ($R^2 = 0.045$, $p = 0.328$), also not statistically significant.

In the EGB, the period under consideration extends to the Ancylus Lake (extrapolated age: 8148 years cal BP), and responses are observed during the HTM, LALIA, MCA, and LIA periods. The GOF record, which covers the last ca. 4300 years, displays changes during the LIA and CP periods. During periods without profound climate events, we observe a consistency in allelic composition, which points to resilience of the algal populations over time. However, within warm periods (e.g., HTM and MCA), there is a notable degree of variability, particularly for EGB. This pattern of long-term stability and resilience, interrupted by distinct variation, is visualized in Figure 3B, depicting changes along PC1 in both cores. This shows temporal variations that align with specific climate events, suggesting that the population's genetic makeup is undergoing changes in response to these events. Additionally, nucleotide diversity increased significantly during the transition from the Littorina Sea to the Modern Baltic Sea, around 4000 years cal BP, and then successively decreased again (Supporting Information, Figure S7).

Allele turnover, a measure of the rate at which new alleles replace old ones, provides insights into genetic variation over time. Figure 4 displays patterns of genetic change over time. A Generalized Additive Model (GAM) was used to analyze allele turnover as a function of time.

At EGB, an increase in allele turnover is observed around 1500–1000 years cal BP, indicating a potential for heightened genetic change from the MCA onwards. At GOF, turnover remains consistent until around 94 to −34 years cal BP. While

industrialization and anthropogenic impacts may be associated with recent genetic shifts, establishing a causal link between these changes and earlier historical periods requires caution.

3 | Discussion

The millennial-long stability, spanning from the Ancylus Lake stage (approximately 8148 years cal BP) to 1500–1000 years cal BP in the Eastern Gotland Basin (EGB), and from around 4300 to 94–34 years cal BP in the Gulf of Finland (GOF), aligns with findings from other phytoplankton studies, although those typically cover much shorter timescales, ranging from seasonal to decadal periods (Godhe and Rynearson 2017; Rynearson and Armbrust 2005). The findings of these studies indicate that long-term genetic stability is maintained in marine phytoplankton populations due to their substantial population size and high dispersal capacity, even in the face of significant environmental changes (Pinseel et al. 2025; Rengefors et al. 2017). These factors contribute to a buffering effect against genetic drift and local extinctions, allowing populations to maintain genetic diversity over long periods of time. The ability of *S. marinoi* to cope with changing environmental conditions through reversible shifts, evidenced by the re-emergence of earlier allelic compositions as shown here for the Baltic Sea further supports this stability. This resilience is a common trait among phytoplankton, allowing them to respond to environmental changes without losing overall genetic diversity (Laso-Jadart et al. 2023). The observed stability is expected given the ecological and evolutionary characteristics of phytoplankton populations. Large population sizes, high reproductive rates, and the potential for gene flow between populations contribute to the maintenance of genetic diversity and stability over long periods of time (Brand 1980). Other findings, such as studies of diatoms and other phytoplankton species have reported patterns of genetic stability and adaptability of phytoplankton to environmental change (Salmaso and Tolotti 2021). These findings imply that the observed stability in *S. marinoi* populations is not only expected, but also indicative of the broader ecological and evolutionary dynamics of marine phytoplankton. Our data demonstrates that this stability can be upheld across several millennia.

However, this stability is not without punctuated interruptions. Our results show that climatic events have an influence on the allelic composition of *S. marinoi* populations. For example, shifts in the genetic composition of the EGB population were observed during the HTM, LALIA, and MCA. Similarly, the GOF population showed changes during the Little Ice Age and the Modern Warm Period. These shifts highlight the ability of *S. marinoi* to cope with different climatic events. The discrepancy between EGB and GOF may be due to the slightly higher genetic diversity in the EGB (Figure 2C–E), which may facilitate adaptation. The differences between the two sites can also be attributed to their distinct geographical characteristics. The EGB, located in the Baltic Proper, may experience an influx of migrants from other populations, increasing genetic diversity and resilience. In contrast, the genetic composition of the GOF population could be influenced by its unique environment, characterized by freshwater influx and lower salinity levels (Myrberg and Soomere 2013), as well as more extensive ice cover in the northern regions of the Baltic Sea (Leppäranta 2023). In particular, samples from the LIA and CP show more pronounced responses in the GOF. The allelic composition remains relatively constant in the absence of climatic events, indicating a stable genetic structure under stable conditions and once a shift has manifested.

After this long period of punctuated genetic stability, recent centuries reveal a novel pattern of rapid allelic turnover, and this coincides with increased human activity. This rapid turnover is particularly evident in the GOF during periods such as the pre-Roman Iron Age, the Viking Age, the Hanseatic Age, and the Industrial Revolution. These results highlight the possible impact of human activities on the genetic dynamics of *S. marinoi* populations. This increased activity is manifested by increased shipping activity in the Baltic Sea (Salimi et al. 2021; Wang et al. 2020). Ballast water exchange (Andrés et al. 2023) in the last two centuries could have been a specific agent of increased changes in haplotype composition, causing rapid translocation of populations. This rapid allelic turnover contrasts with the more gradual and reversible shifts observed in response to natural climatic events, highlighting the influence of anthropogenic factors on the genetic composition of these populations. Due to its coastal position, the GOF is more exposed to these changes, and perhaps the phytoplankton is also more directly affected.

The rapid allelic turnover observed in recent centuries, particularly in response to human activities, underscores the influence that anthropogenic factors may have on the genetic dynamics of populations. Our study on the population dynamics of *S. marinoi* populations provides valuable insights into the long-term resilience and adaptability of marine phytoplankton. The observed genetic stability over several millennia, punctuated by reversible shifts in response to climatic events, underscores the inherent resilience of these populations. However, the recent rapid allelic turnover highlights the potential impact of human activities on population dynamics and structure, and thus presents an opportunity for further investigation.

At the same time it is important to acknowledge the limitations of our study. The limited number of samples included may affect the overall strength and generalizability of our findings. In addition, the lack of precise tests limits our ability to draw definitive conclusions about long-term genetic trends and the full extent of human impact. To date, we also lack a sufficient understanding of the distribution and taphonomy of ancient eDNA, but in sediments, DNA of small organisms, such as phytoplankton, has been shown to give a representative signal of a water body (Wang et al. 2023). Despite site-specific differences, such as higher diversity in the EGB or variation in recent layers due to the different time spans covered, both cores show congruent long-term patterns: extended periods of genetic stability followed by increased allele turnover in recent centuries. Similar work by Lammers et al. (2021) also demonstrated that full organelle genomes can be retrieved from sedaDNA using shotgun metagenomics, though their study did not address temporal change. Together, these findings highlight both the potential of sedaDNA for organellar reconstructions and the need for larger sample series to investigate population-level dynamics. Future

studies with larger sample sizes and for example, more locations are needed to further explore the complex interactions between environmental change and genetic responses.

The results of our study provide a base for future research on the effect of current global change on the genetic composition of natural populations across millennia. By understanding the genetic stability and adaptability of *S. marinoi* populations, we can better understand ecological and evolutionary dynamics of marine phytoplankton. This knowledge is crucial for predicting how these populations may respond to current and future environmental changes, including climate change and direct anthropogenic pressures, and thus offer a valuable foundation for future conservation efforts. Our study provides novel insights into the genetic resilience and adaptability of *S. marinoi* populations. It demonstrates that these populations maintain stability over millennia and respond dynamically to both natural climate fluctuations and human-induced changes. While our data do not allow precise predictions about future adaptation patterns, the increased allele turnover observed in recent centuries suggests ongoing population responses to intensified human impact, visible in the genomic makeup. Given its historic stability and high dispersal, *S. marinoi* may continue to adapt while maintaining its generalist nature. As our focus was on population-level genomic structure, we did not assess the functional effect of specific allelic changes, which will be an important direction for future work. In sum, it highlights the importance of considering both natural and anthropogenic drivers and their relative impacts when assessing and predicting genetic resilience of marine ecosystems.

4 | Material and Methods

4.1 | Study Area

The Baltic Sea is a relatively young and shallow brackish water system currently facing a significant risk of increasing hypoxia, a condition characterized by low oxygen levels and bottom water anoxia. This phenomenon is primarily attributable to the reduction in dissolved oxygen and nutrient discharge resulting from warmer water temperatures, which in turn promote the formation of algal blooms (Carstensen et al. 2014). These blooms decompose and consume oxygen, leading to the development of hypoxia. In recent history, the Baltic Sea has experienced a notable increase in eutrophication, a process driven by the excessive input of nutrients such as nitrogen and phosphorus from agricultural runoff, wastewater discharge, and industrial activities (Reusch et al. 2018). The enrichment of nutrients has resulted in the proliferation of phytoplankton and algal blooms, which, upon decomposition, have further depleted oxygen levels in the water. The Baltic's unique position as a land-enclosed sea with high human and industrial activity, coupled with its low biodiversity, makes it particularly vulnerable to these changes.

The Baltic Sea's history is well known. It has undergone substantial environmental changes in the past. After the end of the last glaciation approximately 10,000 years ago, it went through several fresh- and saltwater stages, starting as a large meltwater lake, then transitioning into various states of salinity due to glacial retreat and isostatic land rebound (Snoeijs-Leijonmalm and Andrén 2017). These stages included the Baltic Ice Lake, the Yoldia Sea, the Ancylus Lake, and the Littorina Sea (Andrén et al. 2011). The Baltic Sea's temperature and salinity have fluctuated over time, with notable increases during the HTM and MCA, and a recent increase since 1850 (Kabel et al. 2012; Seppä et al. 2009; Snoeijs-Leijonmalm and Andrén 2017).

Within the Baltic Sea, this study covers a time series of two distinct locations: the Eastern Gotland Basin, located in the Baltic Proper with a profound water depth maximum of 249 m, and the comparatively shallower Gulf of Finland, reaching a depth of 81 m. At both locations, we collected sediment cores to inform on the effects of environmental changes on the population genetic composition of *S. marinoi*.

4.2 | Sampling

Two sediment cores were taken (Figure 1A) in April 2021, during expedition EMB262. (1) Eastern Gotland Basin (EGB, 57°17.004′N, 020°07.244′E, 241 m water depth, core EMB262/6-30GC); (2) Gulf of Finland (GOF, 59°34.443′N, 023°36.461′E, 81 m water depth, core EMB262/12-3GC). The cores (Figure 1B, ca. 500 cm) were taken using a gravity corer (GC). The sampling for the EGB began at a depth of 32 cm. The cores were sampled on board the research vessel using sterile syringes according to Epp et al. (2019) and immediately frozen for storage.

Core dating was performed as described in Schmidt et al. (2024). This was done by correlating organic carbon records from post-Littorina transgression sediments in the Baltic Sea. The chronology of the cores is determined by the relative S content and the Br/K ratio. These geochemical indicators were applied to the EGB core, where the Br/K ratio reflects changes in the bulk organic carbon content of the sediments. The data are visually matched with X-ray fluorescence (XRF) and organic carbon data from dated sediment cores from the same or nearby locations for different historical periods. For the sediment core from the Gulf of Finland, an independent Bayesian age model was constructed based on radiocarbon dates of bulk organic matter in the sediments. This allows the sediments to be accurately dated to around 4250 years cal BP. In this study, the same core samples were used as in Schmidt et al. (2024).

4.3 | Laboratory Work

4.3.1 | DNA Extraction

The PowerSoil Pro Kit from Qiagen (Hilden, Germany) was used to extract DNA from both sediment cores ($n = 26$, see Table S1) covering various depths (ages). For the extraction, 0.5 g of sediment was used per sample, resulting in 26 samples and 2 extraction blanks. The extraction process was carried out according to the manufacturer's protocol with some modifications, including an overnight incubation at 56°C with the addition of 20 μL proteinase K (20 mg/mL) to enhance sample lysis. The washing steps were performed using a Qiagen Vacuum Pump (Hilden, Germany). Subsequently, samples were centrifuged for 3 min. After centrifugation, the elution process was performed in two steps. Each part involved adding 75 μL of elution buffer to

the sample, allowing it to incubate for 5 min, and then collecting the eluate. Both eluates were collected in the same tube.

4.3.2 | Library Preparation

A single-stranded library approach according to Gansauge et al. (2020) was performed to maximize the retrieval of genetic information from these degraded sedaDNA samples. This method, optimized for fragmented DNA, has been shown to significantly increase the sequence yield and preserve unique molecules, thereby providing a more comprehensive genomic analysis. The library preparation was conducted with 40 ng input DNA. All 26 samples and 2 extraction blanks were processed in the library preparation. Additionally, 2 library blanks were created.

After the indexing PCR, each library was cleaned using the MinElute PCR purification Kit (50,250; Qiagen) resulting in a final amount of 20 μL per sample (For more detailed info, see Section S1.1). The samples were then analyzed on a 2100 Bioanalyzer (Agilent Technologies, Santa Clara, CA, USA) using the Agilent Bioanalyzer High Sensitivity DNA Analysis Kit (Agilent Technologies, Santa Clara, CA, USA). Due to adapters still being present in the samples, we performed an additional purification using the HighPrep bead cleanup (MagBio Genomics Inc., Gaithersburg, MD, USA). 1.6× of HighPrep PCR reagent was used. The DNA concentration was measured using ds-DNA HS Assay Kit and the Qubit 4 fluorometer (Invitrogen Thermo Fisher, Waltham, MA, USA). The libraries were combined into pools of four, each with the same DNA amount. The extraction and library blanks were incorporated in the same volume as the sample with the lowest concentration. The libraries were then further used for hybridization enrichment of chloroplast and mitochondrial genomes.

4.3.3 | Hybridization Enrichment

In this study, a hybridization enrichment approach was employed. Hybridization enrichment allows for targeted isolation of specific sequences, improving sequencing efficiency by reducing the presence of non-target DNA. Thus, it provides a better representation of the studied species, enabling a more detailed and precise analysis of its genetic composition.

4.3.3.1 | Bait Design. The design of the bait set was carried out for two target reference organelle genomes: the mitochondrion and the chloroplast (GenBank PRJNA493755). Together, these genomes consist of 170,788 nucleotides (nt), with 127,202 nt from the chloroplast and 43,586 nt from the mitochondrion, and an average GC content of 30.9%. To improve the accuracy of the baits, the contigs were softmasked for simple and low-complexity repeats.

Subsequently, baits were designed with a length of 80 nt and a tiling coverage of 4×. This means that, on average, each nucleotide in the target sequence is covered by four different baits, thereby ensuring redundancy and enhancing the probability of successful hybridization. This process led to the generation of 10,000 probes. The baits were then filtered based on softmasking for simple and low-complexity repeats. Only those with 35% or less softmasking were retained. A total of 7985 baits passed this filtering step.

4.3.3.2 | Enrichment. This bait design was then used for two different bait sets: (1) RNA baits (BioCat, Heidelberg, Germany); (2) DNA baits (Integrated DNA Technologies, IDT). The libraries were enriched with both RNA and DNA baits, resulting in two sets of libraries: (1) RNA baits enriched; (2) DNA baits enriched. General steps are explained in the following. More detailed information on the used protocols can be found in the Supporting Information (Section S1.2).

The enrichment with RNA baits was conducted according to the myBaits v.5.02 manual. A two-round enrichment strategy was performed. The hybridization mix was prepared and transferred to a rotation oven once the 24-h incubation at a hybridization temperature of 63°C started. In the following bead cleanup, the libraries were resuspended and amplified. Each 27.4-μL PCR reaction included the following nine components: (1) 3.45 μL of DEPC treated H_2O; (2) 2.5 μL 10X HiFi PCR Buffer (Invitrogen Thermo Fisher, Waltham, MA, USA); (3) 0.25 mM dNTPs (25 mM); (4) 1 μL BSA (20 mg/mL); (5) 1 μL $MgSO_4$ (50 mM); (6) 0.2 μL Platinum Taq DNA-Polymerase High Fidelity (5 U/μL) (Invitrogen Thermo Fisher, Waltham, MA, USA); (7) 2 μL IS5_bridge_P5 (10 μM); (8) 2 μL IS5_bridge_P5 (10 μM); (9) 15 μL library pool. The amplification was run using the following settings: 1 min initiation at 94°C, 14 cycles of 15 s denaturation at 94°C, 20 s annealing at 60°C, and 1 min extension at 68°C, followed by 2 min of final elongation at 68°C, and afterward the sample was stored at a temperature of −20°C. Afterwards, the samples were purified with beads and eluted in 10 μL. The second round of enrichment was performed in a similar way. The PCR was conducted in 8 cycles, and the pools were eluted in 17 μL after the bead purification (see more detailed in Section S1.2.2).

Enrichment with DNA baits was also performed in two rounds following the IDT (Integrated DNA Technologies, Löwen, Belgium) xGen hybridization capture of DNA libraries protocol (option: AMPure XP Bead DNA concentration protocol), with the following modification. The hybridization temperature was set to 63°C. Once this temperature was reached on the thermal cycler, the tubes were moved to a rotation oven and incubated for 16 h (see more detailed in Section S1.2.1).

All resulting pools were quantified using Qubit ds-DNA HS Assay Kit and Agilent Bioanalyzer HS Kit. Afterwards, the pools enriched with RNA baits were collectively combined into a single pool, while those enriched with DNA baits were combined into another separate pool, each in equal DNA amounts. This resulted in two distinct library pools. Both of these pools were sent for Illumina sequencing (paired-end, 2 × 150 bp, MiSeq-v3) at Fasteris SA (Geneva, Switzerland).

4.4 | Bioinformatics

The sequences were trimmed, mapped against references, and converted to finally calculate mapping coverage and for variant calling. First, sequence file names were modified to fit the sample identifier using python v3.10.13. Then raw sequence reads

were processed using Autotrim v0.6.1, a tool that automates the quality control and trimming of high-throughput sequence data (Waldvogel et al. 2018). Autotrim employs Trimmomatic v0.39 (Bolger et al. 2014) to trim sequences based on quality and remove adapters, FastQC v0.12.1 (Andrews 2021) to assess the quality of the raw sequence data, and MultiQC v1.14 (Ewels et al. 2016) to aggregate the results into a single report. Following the initial processing, the trimmed reads were mapped to the reference chloroplast and mitochondrial genomes (GenBank: PRJNA493755) using BWA-MEM v0.7.17 (Li and Durbin 2009). BWA is a software package for mapping low-divergent sequences against a reference genome, which is particularly useful for precisely aligning sequencing reads.

The mapped reads were then converted to bam format using Samtools v1.15 (Danecek et al. 2021), a suite of programs for interacting with high-throughput sequencing data. In addition, the per-sample mapping coverage was calculated. After careful consideration, we decided against deduplicating our sequence data, as deduplication resulted in a significant loss of data. This is probably due to the nature of our short and fragmented sequences. In addition, each variation, even those present in duplicates, may hold biologically significant information. Therefore, removing duplicates may have eliminated critical genetic diversity, compromising the integrity of our analysis.

VCFtools v0.1.16 (Danecek et al. 2011) and BCFtools v1.19 (Danecek et al. 2021) were used for calling and filtering variants from the alignment. Variant calling is the process of identifying differences, such as single-nucleotide polymorphisms (SNPs) and insertions/deletions (indels), between the sequenced sample and the reference genome. Variants were filtered to include only those with a quality score (Q) of 30 or higher. The identified variants were then phased into haplotypes using Beagle v5.4 (Browning et al. 2021). Haplotyping, or phasing, is the process of determining the distribution of alleles of multiple variants along each chromosome. In this context, it can be said that it accounts for unique combinations of alleles at variant sites (distinct variations) across the chloroplast and mitochondrial genome.

The pattern of ancient DNA damage was assessed using mapDamage2 v2.2.2 (Jónsson et al. 2013). This tool quantifies patterns of DNA damage in ancient samples, which can provide insights into the preservation and authenticity of ancient DNA.

4.5 | Analyses

The bioinformatic output was converted into a table format and for further analyses with R v4.3.1: The mapping coverage (i.e., the number of reads mapped against reference genome), allele frequencies, distinct variants, nucleotide diversity, and C-to-T substitution rate were combined with the sample metadata (Table S3) using the R package "tidyverse" (Wickham et al. 2019). The data was visualized using the packages "tidyverse," "ggpubr" v0.6.0 (Kassambara 2023), and "tidypaleo" v0.1.3 (Dunnington et al. 2022).

In order to facilitate a comparison of the genetic diversity between GOF and EGB, nucleotide diversity (resulting from Samtools) and distinct variants (resulting from Beagle) were normalized based on the mapping coverage for mitochondria and plastid. Second, Pearson's correlation was employed to verify the consistency of nucleotide diversity between the mitochondrion and chloroplast. For comparison, the dataset was subset to the overlapping time period of both locations. Subsequently, a t-test was applied to compare and test the significance of the nucleotide diversity (mitochondrial and chloroplast data combined) between the two sites. In addition, each distinct genetic variant was assigned a unique identifier for easy reference. These identifiers were utilized to calculate two diversity indices: the Shannon index and the Simpson index. These indices were compared between the EGB and GOF sites using a t-test.

To further identify spatial differences between GOF and EGB, we analyzed allele frequencies (resulting from VCFtools and BCFtools) and calculated the Fixation Index (FST) using corresponding samples from both locations. The FST is a measure of population differentiation attributable to genetic structure. The FST value ranges from 0 to 1, with 0 indicating complete interbreeding (i.e., the two populations are freely intermixing) and 1 indicating that all genetic variation is explained by the population structure (i.e., the two populations do not share any genetic diversity). We implemented a custom R function to calculate the FST over time. This process involved sorting the data by age, subsetting samples within a specified time window, and computing FST based on allele frequency variance. The allelic composition, derived from parsing VCFtools output, was analyzed using Principal Component Analysis (PCA) to examine the genetic structur. We also performed Pearson's correlation and PERMANOVA to assess the impact of C-to-T substitution rates and Total Organic Carbon (TOC) on the variation in the PCA space, specifically the first two principal components (PCs). These analyses helped determine the extent to which these factors influenced genetic composition. For PCA and PERMANOVA, we also used the functions provided by the package "vegan" v2.6.4 (Oksanen et al. 2020).

The C-to-T substitutions at the first position from the mapDamage2 output were examined to authenticate the ancient DNA (aDNA) and analyze the damage patterns. A Pearson's correlation test was conducted to assess the influence of mapping coverage on these substitutions. This was done to evaluate if coverage has an impact on the observed damage. The Baltic Sea Mn/Ti ratio data were also integrated into the analysis.

To assess the genetic diversity and adaptability of the population, we calculated the rate of allele turnover. This measure, derived from the ratio of significant allele changes (greater than 1%) to total generations, reflects the estimated rate of genetic change over time based on the present data. Given the low FST values, we inferred that the two sites, EGB and GOF, belong to a single population. The calculation covered all of the data, from the oldest sample from EGB to the youngest sample from GOF, providing insight into the evolving genetic makeup of the population.

To identify phases of change in the allele turnover across the entire dataset, a generalized additive model (GAM) was fitted using the "gam" function from the "mgcv" package (Wood 2011). This model was applied to the complete dataset, including periods where we did not have direct samples, as the allele turnover was estimated based on the available data. We calculated the mean

allele turnover for the present data points, which were then included in the GAM plot. Allele turnover was used as a response variable to fit a GAM model as a function of "age".

Corresponding metadata to this analysis can be found in Supporting Information (Table S3). Data on shipping activity in the Baltic Sea were obtained from three main sources: Kontny (2023), Mägi (2018), and Rytkönen et al. (2002). Kontny's work provided insights into maritime contacts during the Roman and Migration Periods (1st–7th centuries AD), while Mägi's research focused on the role of the Eastern Baltic in Viking Age communication across the Baltic Sea. Rytkönen et al.'s research on the statistical analysis of Baltic Sea shipping revealed a significant increase in maritime traffic during the late 20th and early 21st centuries. These sources were used to establish a timeline of shipping intensity from 1200 years cal BP to the present.

Author Contributions

Alexandra Schmidt: conceptualization, data curation, formal analysis, investigation, methodology, software, visualization, writing – original draft, writing – review and editing. **Sarah Bolius:** investigation, writing – review and editing. **Anna Chagas:** formal analysis, writing – review and editing. **Juliane Romahn:** data curation, writing – review and editing. **Jérôme Kaiser:** data curation, writing – review and editing. **Helge W. Arz:** data curation, writing – review and editing. **Miklós Bálint:** funding acquisition, writing – review and editing. **Anke Kremp:** data curation, funding acquisition, methodology, writing – review and editing. **Laura S. Epp:** conceptualization, data curation, methodology, project administration, supervision, writing – review and editing.

Acknowledgments

This study was funded by the K314/2020 grant of the Collaborative Excellence Programme of the Leibniz Association. The authors acknowledge support by the High Performance and Cloud Computing Group at the Zentrum für Datenverarbeitung of the University of Tübingen, the state of Baden-Württemberg through bwHPC, and the German Research Foundation (DFG) through grant no INST 37/935-1 FUGG. A.S. acknowledges funding from the International Max Planck Research School for Quantitative Behaviour, Ecology and Evolution. M.B. is supported by the Hessian Ministry of Higher Education, Research and the Arts through the LOEWE Centre for Translational Biodiversity Genomics. For help with preparing reagents for library preparation and enrichment experiments, we thank Clara Linde Schlimbach and Anna Weis. For setting up the ancient DNA clean laboratory in Frankfurt where all DNA extractions were done by A.S. and J.R., we thank Leonie Schardt. Open Access funding enabled and organized by Projekt DEAL.

Disclosure

In the preparation of this manuscript, we employed artificial intelligence (AI) tools to enhance the quality of our work and to optimize our research process. R Script Optimization: we utilized an AI-based code optimization to refine our R scripts. The tool provided suggestions for code enhancement, identified potential bugs, and recommended more efficient coding practices. This not only improved the performance of our scripts but also ensured the reproducibility and reliability of our results. We believe that the use of AI in our research process has improved the quality of our work. However, we stress that the final decisions on manuscript content and the interpretation of the results were made by the authors.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in figshare at https://doi.org/10.6084/m9.figshare.29882291.v1 and https://doi.org/10.6084/m9.figshare.29882285.v1. Sequence data are available in the European Nucleotide Archive (ENA) under accession number PRJEB91557.

References

Andrén, T., S. Björck, E. Andrén, D. Conley, L. Zillén, and J. Anjar. 2011. "The Development of the Baltic Sea Basin During the Last 130 Ka." In *The Baltic Sea Basin*, edited by J. Harff, S. Björck, and P. Hoth, 75–97. Springer. https://doi.org/10.1007/978-3-642-17220-5_4.

Andrés, J., P. Czechowski, E. Grey, et al. 2023. "Environment and Shipping Drive Environmental DNA Beta-Diversity Among Commercial Ports." *Molecular Ecology* 32, no. 23: 6696–6709. https://doi.org/10.1111/mec.16888.

Andrews, S. 2021. "FastQC: A Quality Control Analysis Tool for High Throughput Sequencing Data [Java]." https://github.com/s-andrews/FastQC.

Barbier, E. B., ed. 2010. "The Contemporary Era (From 1950 to the Present)." In *Scarcity and Frontiers: How Economies Have Developed Through Natural Resource Exploitation*, 552–662. Cambridge University Press. https://doi.org/10.1017/CBO9780511781131.010.

Benoiston, A.-S., F. M. Ibarbalz, L. Bittner, et al. 2017. "The Evolution of Diatoms and Their Biogeochemical Functions." *Philosophical Transactions of the Royal Society, B: Biological Sciences* 372, no. 1728: 20160397. https://doi.org/10.1098/rstb.2016.0397.

Björck, S. 2008. "The Late Quaternary Development of the Baltic Sea Basin." In *Assessment of Climate Change for the Baltic Sea Basin*, 398–407. Springer. https://portal.research.lu.se/en/publications/the-late-quaternary-development-of-the-baltic-sea-basin.

Bolger, A. M., M. Lohse, and B. Usadel. 2014. "Trimmomatic: A Flexible Trimmer for Illumina Sequence Data." *Bioinformatics* 30, no. 15: 2114–2120. https://doi.org/10.1093/bioinformatics/btu170.

Boyd, P. W., and D. A. Hutchins. 2012. "Understanding the Responses of Ocean Biota to a Complex Matrix of Cumulative Anthropogenic Change." *Marine Ecology Progress Series* 470: 125–135. https://doi.org/10.3354/meps10121.

Brand, L. E. 1980. "Review of Genetic Variation in Marine Phytoplankton Species and the Ecological Implications." *Biological Oceanography* 6, no. 5-6: 397–409. https://doi.org/10.1080/01965581.1988.1074954.

Briddon, C. L., M. Nicoară, A. Hegedűs, M. K. Thomas, and B. Drugă. 2025. "Quantifying Evolutionary Changes to Temperature-CO_2 Growth Response Surfaces in *Skeletonema marinoi* After Adaptation to Extreme Conditions." *ISME Communications* 5, no. 1: ycaf069. https://doi.org/10.1093/ismeco/ycaf069.

Browning, B. L., X. Tian, Y. Zhou, and S. R. Browning. 2021. "Fast Two-Stage Phasing of Large-Scale Sequence Data." *American Journal of Human Genetics* 108, no. 10: 1880–1890. https://doi.org/10.1016/j.ajhg.2021.08.005.

Carstensen, J., D. J. Conley, E. Bonsdorff, et al. 2014. "Hypoxia in the Baltic Sea: Biogeochemical Cycles, Benthic Fauna, and Management." *Ambio* 43, no. 1: 26–36. https://doi.org/10.1007/s13280-013-0474-7.

Danecek, P., A. Auton, G. Abecasis, et al. 2011. "The Variant Call Format and VCFtools." *Bioinformatics* 27, no. 15: 2156–2158. https://doi.org/10.1093/bioinformatics/btr330.

Danecek, P., J. K. Bonfield, J. Liddle, et al. 2021. "Twelve Years of SAMtools and BCFtools." *GigaScience* 10, no. 2: giab008. https://doi.org/10.1093/gigascience/giab008.

Dunnington, D. W., N. Libera, J. Kurek, I. S. Spooner, and G. A. Gagnon. 2022. "Tidypaleo: Visualizing Paleoenvironmental Archives Using

ggplot2." *Journal of Statistical Software* 101, no. 7: 1–21. https://doi.org/10.18637/jss.v101.i07.

Ellegaard, M., M. R. J. Clokie, T. Czypionka, et al. 2020. "Dead or Alive: Sediment DNA Archives as Tools for Tracking Aquatic Evolution and Adaptation." *Communications Biology* 3, no. 1: 1–11. https://doi.org/10.1038/s42003-020-0899-z.

Epp, L. S., H. H. Zimmermann, and K. R. Stoof-Leichsenring. 2019. "Sampling and Extraction of Ancient DNA From Sediments." In *Ancient DNA*, edited by B. Shapiro, A. Barlow, P. D. Heintzman, M. Hofreiter, J. L. A. Paijmans, and A. E. R. Soares, vol. 1963, 31–44. Springer. https://doi.org/10.1007/978-1-4939-9176-1_5.

Ewels, P., M. Magnusson, S. Lundin, and M. Käller. 2016. "MultiQC: Summarize Analysis Results for Multiple Tools and Samples in a Single Report." *Bioinformatics* 32, no. 19: 3047–3048. https://doi.org/10.1093/bioinformatics/btw354.

Gansauge, M.-T., A. Aximu-Petri, S. Nagel, and M. Meyer. 2020. "Manual and Automated Preparation of Single-Stranded DNA Libraries for the Sequencing of DNA From Ancient Biological Remains and Other Sources of Highly Degraded DNA." *Nature Protocols* 15, no. 8: 2279–2300. https://doi.org/10.1038/s41596-020-0338-0.

Godhe, A., and T. Rynearson. 2017. "The Role of Intraspecific Variation in the Ecological and Evolutionary Success of Diatoms in Changing Environments." *Philosophical Transactions of the Royal Society, B: Biological Sciences* 372, no. 1728: 20160399. https://doi.org/10.1098/rstb.2016.0399.

Goulletquer, P., P. Gros, G. Boeuf, and J. Weber. 2014. "The Impacts of Human Activities on Marine Biodiversity." In *Biodiversity in the Marine Environment*, edited by P. Goulletquer, P. Gros, G. Boeuf, and J. Weber, 15–20. Springer Netherlands. https://doi.org/10.1007/978-94-017-8566-2_2.

Hattich, G. S. I., S. Jokinen, S. Sildever, et al. 2024. "Temperature Optima of a Natural Diatom Population Increases as Global Warming Proceeds." *Nature Climate Change* 14: 1–8.

Hjerne, O., S. Hajdu, U. Larsson, A. S. Downing, and M. Winder. 2019. "Climate Driven Changes in Timing, Composition and Magnitude of the Baltic Sea Phytoplankton Spring Bloom." *Frontiers in Marine Science* 6: 482. https://doi.org/10.3389/fmars.2019.00482.

Hochfeld, I., B. A. Ward, A. Kremp, et al. 2025. "Ideas and Perspectives: How Sediment Archives Can Improve Model Projections of Marine Ecosystem Change." *Biogeosciences* 22, no. 10: 2363–2380. https://doi.org/10.5194/bg-22-2363-2025.

Johansson, O. N., M. Töpel, M. I. M. Pinder, et al. 2019. "Skeletonema Marinoi as a New Genetic Model for Marine Chain-Forming Diatoms." *Scientific Reports* 9, no. 1: 5391. https://doi.org/10.1038/s41598-019-41085-5.

Jónsson, H., A. Ginolhac, M. Schubert, P. L. F. Johnson, and L. Orlando. 2013. "mapDamage2.0: Fast Approximate Bayesian Estimates of Ancient DNA Damage Parameters." *Bioinformatics* 29, no. 13: 1682–1684. https://doi.org/10.1093/bioinformatics/btt193.

Kabel, K., M. Moros, C. Porsche, et al. 2012. "Impact of Climate Change on the Baltic Sea Ecosystem Over the Past 1,000 Years." *Nature Climate Change* 2, no. 12: 871–874.

Kassambara, A. 2023. "ggpubr: "ggplot2" Based Publication Ready Plots (Version 0.6.0) [Computer Software]." https://cran.r-project.org/web/packages/ggpubr/index.html.

Kontny, B. 2023. "Maritime Contacts Across the Baltic Sea During the Roman and Migration Periods (1st-7th Centuries AD) in the Light of Archaeological Sources From the Central-European Perspective." https://www.academia.edu/100019978/Maritime_contacts_across_the_Baltic_Sea_during_the_Roman_and_Migration_Periods_1st_7th_centuries_AD_in_the_light_of_archaeological_sources_from_the_central_European_perspective.

Kremp, A., J. Dutz, and M. L. Zettler. 2024. "Biological Assessment of the Baltic Sea 2021 [Application/pdf]. Meereswissenschaftliche Berichte No. 124 2024—Marine Science Reports No. 124 2024, 5.295 KB."

Lammers, Y., P. D. Heintzman, and I. G. Alsos. 2021. "Environmental Palaeogenomic Reconstruction of an Ice Age Algal Population." *Communications Biology* 4, no. 1: 220. https://doi.org/10.1038/s42003-021-01710-4.

Laso-Jadart, R., M. O'Malley, A. M. Sykulski, C. Ambroise, and M.-A. Madoui. 2023. "Holistic View of the Seascape Dynamics and Environment Impact on Macro-Scale Genetic Connectivity of Marine Plankton Populations." *BMC Ecology and Evolution* 23, no. 1: 46. https://doi.org/10.1186/s12862-023-02160-8.

Leppäranta, M. 2023. "History and Future of Snow and Sea Ice in the Baltic Sea." In *Oxford Research Encyclopedia of Climate Science*. Oxford Research. https://doi.org/10.1093/acrefore/9780190228620.013.891.

Li, H., and R. Durbin. 2009. "Fast and Accurate Short Read Alignment With Burrows–Wheeler Transform." *Bioinformatics* 25, no. 14: 1754–1760. https://doi.org/10.1093/bioinformatics/btp324.

Mägi, M. 2018. *Austrvegr: The Role of the Eastern Baltic in Viking Age Communication Across the Baltic Sea*. Vol. 84. https://www.academia.edu/36647424/M%C3%A4gi_M_2018_In_Austrvegr_The_Role_of_the_Eastern_Baltic_in_Viking_Age_Communication_across_the_Baltic_Sea_The_Northern_World_Volume_84_Brill_Leiden. BRILL.

Myrberg, K., and T. Soomere. 2013. "The Gulf of Finland, Its Hydrography and Circulation Dynamics." In *Preventive Methods for Coastal Protection: Towards the Use of Ocean Dynamics for Pollution Control*, edited by T. Soomere and E. Quak, 181–222. Springer International Publishing. https://doi.org/10.1007/978-3-319-00440-2_6.

Nguyen, N.-L., D. Devendra, N. Szymańska, et al. 2023. "Sedimentary Ancient DNA: A New Paleogenomic Tool for Reconstructing the History of Marine Ecosystems." *Frontiers in Marine Science* 10: 1185435. https://doi.org/10.3389/fmars.2023.1185435.

Ojaveer, H., A. Jaanus, B. R. MacKenzie, et al. 2010. "Status of Biodiversity in the Baltic Sea." *PLoS One* 5, no. 9: 12467. https://doi.org/10.1371/journal.pone.0012467.

Oksanen, J., F. G. Blanchet, M. Friendly, et al. 2020. ""vegan": Community Ecology Package. R Package Version 2.5–6. 2019." *Community Ecology* 8: 732–740.

Panja, P., T. Kar, and D. K. Jana. 2024. "Impacts of Global Warming on Phytoplankton–Zooplankton Dynamics: A Modelling Study." *Environment, Development and Sustainability* 26: 13495–13513. https://doi.org/10.1007/s10668-023-04430-3.

Pinseel, E., E. C. Ruck, T. Nakov, et al. 2025. "Genome-Wide Adaptation to a Complex Environmental Gradient in a Keystone Phytoplankton Species." *Molecular Ecology* 34: e17817. https://doi.org/10.1111/mec.17817.

Rengefors, K., A. Kremp, T. B. H. Reusch, and A. M. Wood. 2017. "Genetic Diversity and Evolution in Eukaryotic Phytoplankton: Revelations From Population Genetic Studies." *Journal of Plankton Research* 39: fbw098. https://doi.org/10.1093/plankt/fbw098.

Reusch, T. B. H., J. Dierking, H. C. Andersson, et al. 2018. "The Baltic Sea as a Time Machine for the Future Coastal Ocean." *Science Advances* 4, no. 5: eaar8195. https://doi.org/10.1126/sciadv.aar8195.

Rynearson, T. A., and E. V. Armbrust. 2005. "Maintenance of Clonal Diversity During a Spring Bloom of the Centric Diatom *Ditylum brightwellii*." *Molecular Ecology* 14, no. 6: 1631–1640. https://doi.org/10.1111/j.1365-294X.2005.02526.x.

Rynearson, T. A., I. W. Bishop, and S. Collins. 2022. "The Population Genetics and Evolutionary Potential of Diatoms." In *The Molecular Life of Diatoms*, edited by A. Falciatore and T. Mock, 29–57. Springer International Publishing. https://doi.org/10.1007/978-3-030-92499-7_2.

Rytkönen, J., L. Siitonen, T. Riipi, J. Sassi, and J. Sukselainen. 2002. *Statistical Analyses of the Baltic Maritime Traffic*. VTT Technical Research Centre of Finland.

Salimi, P. A., J. C. Creed, M. M. Esch, et al. 2021. "A Review of the Diversity and Impact of Invasive Non-Native Species in Tropical Marine Ecosystems." *Marine Biodiversity Records* 14, no. 1: 11. https://doi.org/10.1186/s41200-021-00206-8.

Salmaso, N., and M. Tolotti. 2021. "Phytoplankton and Anthropogenic Changes in Pelagic Environments." *Hydrobiologia* 848, no. 1: 251–284. https://doi.org/10.1007/s10750-020-04323-w.

Schmidt, A., J. Romahn, E. Andrén, et al. 2024. "Decoding the Baltic Sea's Past and Present: A Simple Molecular Index for Ecosystem Assessment." *Ecological Indicators* 166: 112494. https://doi.org/10.1016/j.ecolind.2024.112494.

Seppä, H., A. E. Bjune, R. J. Telford, H. J. B. Birks, and S. Veski. 2009. "Last Nine-Thousand Years of Temperature Variability in Northern Europe." *Climate of the Past* 5, no. 3: 523–535. https://doi.org/10.5194/cp-5-523-2009.

Snoeijs-Leijonmalm, P., and E. Andrén. 2017. "Why Is the Baltic Sea So Special to Live in?" In *Biological Oceanography of the Baltic Sea*, edited by P. Snoeijs-Leijonmalm, H. Schubert, and T. Radziejewska, 23–84. Springer Netherlands. https://doi.org/10.1007/978-94-007-0668-2_2.

Waldvogel, A.-M., A. Wieser, T. Schell, et al. 2018. "The Genomic Footprint of Climate Adaptation in *Chironomus riparius*." *Molecular Ecology* 27, no. 6: 1439–1456. https://doi.org/10.1111/mec.14543.

Wang, Q., F. Cheng, J. Xue, N. Xiao, and H. Wu. 2020. "Bacterial Community Composition and Diversity in the Ballast Water of Container Ships Arriving at Yangshan Port, Shanghai, China." *Marine Pollution Bulletin* 160: 111640. https://doi.org/10.1016/j.marpolbul.2020.111640.

Wang, Y., M. Wessels, M. W. Pedersen, and L. S. Epp. 2023. "Spatial Distribution of Sedimentary DNA Is Taxon-Specific and Linked to Local Occurrence at Intra-Lake Scale." *Communications Earth & Environment* 4, no. 1: 172.

Wickham, H., M. Averick, J. Bryan, et al. 2019. "Welcome to the Tidyverse." *Journal of Open Source Software* 4, no. 43: 1686. https://doi.org/10.21105/joss.01686.

Wood, S. N. 2011. "Fast Stable Restricted Maximum Likelihood and Marginal Likelihood Estimation of Semiparametric Generalized Linear Models." *Journal of the Royal Statistical Society, Series B: Statistical Methodology* 73, no. 1: 3–36. https://doi.org/10.1111/j.1467-9868.2010.00749.x.

Zillén, L., D. J. Conley, T. Andrén, E. Andrén, and S. Björck. 2008. "Past Occurrences of Hypoxia in the Baltic Sea and the Role of Climate Variability, Environmental Change and Human Impact." *Earth-Science Reviews* 91, no. 1: 77–92. https://doi.org/10.1016/j.earscirev.2008.10.001.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** gcb70467-sup-0001-DataS1.docx.