Research Square

Preprints are preliminary reports that have not undergone peer review.
They should not be considered conclusive, used to inform clinical practice,
or referenced by the media as validated information.

Mitochondrial diversity and demographic history of Arctica islandica (Bivalvia: Venerida) in the German waters of the Baltic Sea

Louisa Alina Schulz

louisa.schulz@iow.de

Leibniz Institute for Baltic Sea Research Warnemünde

Katharina Kniesz

Leibniz Institute for Baltic Sea Research Warnemünde

Heiko Stuckas

Senckenberg Natural History Collections Dresden

Fabian Wolf

Leibniz Institute for Baltic Sea Research Warnemünde

Michael Lothar Zettler

Leibniz Institute for Baltic Sea Research Warnemünde

Article

Keywords: Arctica islandica, Baltic Sea, mitochondrial DNA, demographic history, genetic diversity, phylogeography

Posted Date: September 11th, 2026

DOI: https://doi.org/10.21203/rs.3.rs-10442059/v1

License: This work is licensed under a Creative Commons Attribution 4.0 International License.
Read Full License

Additional Declarations: No competing interests reported.

Version of Record: A version of this preprint was published at Scientific Reports on October 20th, 2026. See the published version at https://doi.org/10.1038/s41598-026-76449-1.

Abstract

The semi-enclosed Baltic Sea is a comparatively young brackish ecosystem characterised by strong environmental gradients that can shape genetic diversity and demographic history in marine species. The amphi-Atlantic bivalve *Arctica islandica* (Linnaeus 1767) inhabits the southwestern Baltic Sea, where populations experience environmental conditions distinct from fully marine habitats. We analysed mitochondrial cytochrome c oxidase subunit I (COI) and cytochrome b (CytB) sequences to assess mitochondrial diversity and infer historical demographic patterns of *A. islandica* in the German waters of the Baltic Sea.

Mitochondrial diversity was high, with widespread haplotype sharing among sampling regions and no evidence of regional structuring. Analyses of molecular variance and pairwise differentiation showed that most variation occurred within rather than among regions. Demographic analyses supported a history of population expansion, while comparison with previously published CytB haplotypes indicated that Baltic Sea specimens belong to widespread mitochondrial lineages distributed across the species' range.

Overall, the mitochondrial data indicate that *A. islandica* populations in the German waters of the Baltic Sea retain substantial shared mitochondrial diversity despite inhabiting environmentally distinct brackish habitats. These patterns are consistent with postglacial colonisation and a shared demographic history and provide a baseline for future genome-wide studies of population connectivity and adaptive variation.

Introduction

Genetic diversity provides fundamental insights into the evolutionary history and demographic processes shaping population structure and is therefore central to understanding patterns of intraspecific genetic variation [1]. Populations at the margins of species distributions often experience distinct environmental conditions, reduced connectivity, and demographic constraints that can influence patterns of genetic diversity [2, 3]. These characteristics make marginal populations particularly informative for investigating how contemporary environmental conditions and historical processes influence genetic variation.

The Baltic Sea represents a unique environment for studying these processes. The young postglacial basin formed following the retreat of the Fennoscandian Ice Sheet, with modern brackish conditions becoming established during the Littorina Sea stage approximately 8,000–7,000 years BP [4, 5]. Many marine species colonised the Baltic Sea during or shortly after the Littorina transgression [6]. Today, sporadic saline inflows through the Danish Straits, freshwater discharge, and complex basin morphology create pronounced gradients in salinity, temperature, and oxygen availability [7–10]. These environmental gradients, together with the semi-enclosed nature of the basin, have the potential to influence population demographic history, connectivity, and patterns of genetic diversity [1, 3]. Accordingly, several marine species exhibit differences in genetic patterns between Baltic Sea populations and populations from adjacent North Atlantic regions [11–14].

The amphi-Atlantic bivalve *Arctica islandica* (Linnaeus 1767) provides an opportunity to investigate genetic diversity and historical demographic processes in a long-lived marine species inhabiting contrasting environments. The species is distributed throughout the North Atlantic, from waters south of Spitsbergen to the continental shelf of the eastern United States [15]. In cold, fully marine habitats, individuals can attain lifespans of several centuries [16]. Across its distribution range, *A. islandica* exhibits variation in shell morphology, growth rates, recruitment success, and population dynamics [17–21]. Previous molecular studies have generally identified weak mitochondrial population structure and extensive sharing of dominant haplotypes across the North Atlantic [15, 20]. However, regional differences in mitochondrial diversity indicate that historical climatic fluctuations, geographic isolation, and hydrographic conditions have contributed to shaping present-day genetic patterns [15].

Although *A. islandica* has been extensively investigated in fully marine regions of the North Atlantic, comparatively little is known about populations inhabiting the environmentally marginal Baltic Sea. In the German waters of the Baltic Sea, *A. islandica* represents an important component of benthic biomass in the central Kiel Bay and the Bay of Mecklenburg and reaches its easternmost distribution limit in the Arkona Basin [17,22;23]. Baltic Sea populations experience physiological stress, reduced reproductive success, and substantially shorter lifespans (40–50 years) compared with conspecifics from fully marine habitats [24–28]. Despite these constraints, the species contributes substantially to benthic ecosystem functioning through biomass production, bioturbation, and filtration [17, 29–31]. *Arctica islandica* is currently classified as Vulnerable in Germany (Red List Category 3;[32]), and its characteristic biotope is considered critically endangered according to the HELCOM Red List classification (AB.H3L3; [33]).

Whether Baltic Sea populations exhibit regional differences in mitochondrial diversity or retain patterns consistent with shared postglacial colonisation remains unresolved. Given the environmental gradients and hydrographic complexity of the southwestern Baltic Sea, we investigated patterns of mitochondrial diversity and signatures of historical demographic processes in *A. islandica*. To address these questions, we analysed mitochondrial cytochrome c oxidase subunit I (COI) and cytochrome b (CytB) sequences to (1) characterise mitochondrial genetic diversity within Baltic Sea populations, (2) assess patterns of mitochondrial variation among regions, and (3) evaluate whether Baltic Sea populations show signatures consistent with historical demographic expansion. This study provides new baseline information on mitochondrial diversity and historical demographic patterns of an ecologically important and vulnerable marine bivalve inhabiting the environmentally distinct Baltic Sea.

Materials and Methods

Sampling

Arctica islandica specimens analysed in this study originated from multiple sampling campaigns conducted in the German waters of the Baltic Sea, including Kiel Bay, the Bay of Mecklenburg, and the Arkona Basing (Table 1; Fig. 1). Most individuals were collected during research expeditions organised

by the Leibniz Institute for Baltic Sea Research Warnemünde (IOW; LEGRA2023, MGFSalinity2023, LEGRA2024, and Arkobi2024). Additional specimens were obtained through collaborations with the Thünen Institute of Baltic Sea Fisheries (cruises Solea832 and Solea833), the GEOMAR Helmholtz Centre for Ocean Research Kiel (Littorina cruise, 7 Mar 2024), and the University of Rostock, which provided three specimens collected within the coastal waters of the Bay of Mecklenburg (Nienhagen).

Table 1
Sampling details of *Arctica islandica* specimens collected in the German waters of the Baltic Sea, including cruise details, research vessels, duration, and responsible institutes.

Cruise ID	Research vessel	Sampling period	Responsible institute
LEGRA2023	*Elisabeth Mann Borgese*	1–9 Jun 2023	IOW
MGFSalinity2023	*Elisabeth Mann Borgese*	16 Jun – 3 Jul 2023	IOW
Solea832	*Solea*	5–9 Feb 2024	Thünen Institute of Baltic Sea Fisheries
Solea833	*Solea*	21 Feb – 16 Mar 2024	Thünen Institute of Baltic Sea Fisheries
Littorina070324	*Littorina*	7 Mar 2024	GEOMAR
LEGRA2024	*Elisabeth Mann Borgese*	21 Jun – 2 Jul 2024	IOW
Arkobi2024	*Fortuna Kingfisher*	2–12 Sep 2024	IOW

Adult individuals were sampled using a van Veen grab (0.1 m^2 sampling area; 10–15 cm penetration depth), a dredge (“Kieler Kinderwagen”; 100 x 40 x 45 cm rectangular opening; 5 mm mesh size), or a beam trawl. Following collection, specimens were stored frozen at -20°C. Samples collected during the IOW expeditions in 2023 were initially preserved in a 4% buffered formaldehyde-seawater solution and subsequently transferred to 70% ethanol after sorting.

DNA extraction, amplification, and sequence processing

In total, 207 adult specimens from the German waters of the Baltic Sea were included in the molecular analyses. Prior to dissection, all specimens were photographed and measured (described by Turra et al. [34]). Collection locality, collection dates, geographic coordinates, and voucher information are listed in Supplementary Data S1. Digital voucher photographs, specimen metadata, and sequence trace files were deposited in the Barcode of Life Data System (BOLD; project code ARKOB). Tissue samples from the anterior and/or posterior adductor muscles were used for DNA extraction. Genomic DNA was extracted using 30–50 µL of InstaGene Matrix (Bio-Rad) following incubation at 56°C for 20 min and 99°C for 10 min in a thermal cycler.

Fragments of the mitochondrial cytochrome c oxidase subunit I (COI) gene were amplified using primers AIS-COIF (5'-TTGAGCAGGATTAATAGGAACT-3') and AIS-COIR (5'AAATGAACAAATAACACAGGATCT-3') [35]. The cytochrome b (CytB) fragments were amplified using primers CytB-397F (5'-YWYTRCCTTggRggRCARATATC-3') and CytB-811R (5'- gCRWAYARAAARTAYCAYTCWgg-3') [15]. All primers were modified with M13 universal tails (M13F- pUC: GTTTTCCCAGTCACGAC; M13R- pUC: CAGGAAACAGCTATGAC) to facilitate Sanger sequencing.

PCR amplifications were performed in 12.5 µL reaction volumes containing AccuStart II PCR ToughMix (Quantabio), nuclease-free water, primers, GelTrack loading dye, and 1 µL DNA template. Thermal cycling conditions were an initial denaturation at 94°C for 3 min, followed by 40 cycles of 94°C for 30 s, 48°C for 45 s, and 72°C for 45 s, with a final extension at 72°C for 5 min. Amplification success was verified by 1.2% agarose gel electrophoresis. PCR products were purified using ExoSAP-IT™ (Applied Biosystems) and sequenced bidirectionally by LGC Genomics (Berlin, Germany) and Macrogen Europe Inc. (Amsterdam, Netherlands). Consensus sequences generated in this study have been deposited in GenBank under accession numbers PZ807415–PZ807575 (CytB) and PZ807578–PZ807751 (COI). Corresponding specimen records, voucher photographs, metadata, and raw sequence trace files are available through the Barcode of Life Data Systems (BOLD) under dataset DS-ARKO03 (dx.doi.org/10.5883/DS-ARKO03).

Raw chromatograms were assembled and edited in Geneious Prime v2024.0.7 [36]. Forward and reverse reads were merged into consensus sequences, ambiguous base calls were inspected manually, and sequences were aligned using MUSCLE implemented in Geneious. Individuals for which both COI and CytB sequences were available were included in concatenated analyses.

An ambiguous nucleotide position was detected at site 59 of the COI alignment. In several individuals, chromatogram inspection did not permit unambiguous discrimination between adenine (A) or cytosine (C), resulting in assignment of the IUPAC ambiguity code "M" by Geneious. The ambiguity occurred consistently across sequencing runs and sampling regions despite otherwise high-quality chromatograms.

To evaluate potential effects on downstream analyses, two alternative treatments of position 59 were compared. In the first approach, the site was treated as missing data and excluded from diversity estimates, whereas in the second approach the ambiguity code "M" was retained. Although retaining the ambiguous position slightly increased diversity estimates, the overall interpretation of diversity patterns remained unchanged. Consequently, the more conservative missing-data approach was adopted for the final analyses.

Sequence data processing and genetic analyses

Aligned sequences were imported into R and processed as DNAbin objects (*ape* package, [37]). Gap-neutral pairwise distances between sequences were calculated by excluding all positions containing

gaps (“-“) or missing bases (“?”) in either sequence. Columns consisting entirely of gaps were removed prior to identifying polymorphic sites. Haplotypes were defined as unique sequence variants based on pairwise gap-neutral distances.

Representative sequences for each haplotype were exported to PopART 1.7 [38] to construct minimum spanning haplotype networks (MSTs). During network generation, alignment positions containing more than 5% missing data were excluded automatically. Circle size reflected haplotype frequency, pie-chart segments indicated regional composition, and hash marks on branches represented the number of nucleotide differences (mutational steps) between neighbouring haplotypes.

For each sampling region, standard genetic diversity indices were calculated, including the number of haplotypes (K), polymorphic sites (S), haplotype diversity (Hd), and nucleotide diversity (π). Nucleotide diversity was calculated as the total number of pairwise nucleotide differences divided by the total number of comparable nucleotide positions across all pairwise sequence comparisons, thereby accounting for missing data and alignment gaps.

Demographic history and genetic population structure were analysed in Arlequin v3.5.2.2 [39] using concatenated COI and CytB datasets as well as individual-marker datasets. Only alignment positions with ≤ 10% missing data were retained for downstream analyses.

Mismatch distribution analyses were performed under sudden and spatial expansion models to evaluate alternative demographic scenarios. Parameters estimated under the sudden expansion model included time since expansion (τ), ancestral population size (θ_0), and post-expansion population size (θ_1), whereas the spatial expansion model additionally incorporated a migration parameter (M). Model fit was assessed using the sum of squared deviations (SSD) and Harpending’s raggedness index (r), with significance evaluated using 1,000 parametric bootstrap replicates.

Neutrality tests included Tajima’s D [40] and Fu’s F_S[41], with significance evaluated using 1,000 coalescent simulations.

Population genetic structure among sampling regions was assessed based on pairwise fixation indices (F_{ST}), analyses of molecular variance (AMOVA), and average pairwise sequence divergence estimates (πXY). Statistical significance of pairwise F_{ST} values and AMOVA variance components was evaluated using 10,000 permutations. Distances were calculated as pairwise nucleotide differences without gamma correction, and insertions/deletions were excluded from analyses.

Range-wide CytB haplotype network analysis

To place the *A. islandica* population from the German waters of the Baltic Sea into a broader phylogeographic context, a range-wide CytB dataset was compiled from previously published sequences and analysed together with sequences generated in the present study. The reference dataset included 11 CytB haplotypes (396 bp) representing 83 specimens from across the species’ distribution range

reported by Dahlgren et al. [15] (Table 2). In addition, three CytB sequences (398 bp) obtained from complete mitochondrial genome sequences published by Glöckner et al. [42] were included (GenBank accession numbers KC197241, KF363951, KF363952), representing Iceland and the Baltic Sea. Furthermore, 315 CytB sequences were obtained from Supplementary Data 4 of Dégletagne et al. [43], covering Norway (n = 33), Iceland (n = 60), the Baltic Sea (n = 77), Helgoland (n = 47), the U.S. east coast (n = 58), the Kattegat (n = 17), and the White Sea (n = 23).

Table 2
Published mitochondrial CytB haplotypes of *Arctica islandica* reported by Dahlgren et al. [15], including GenBank accession numbers, geographic origin, and the number of individuals per haplotype and location.

Haplotype	GeneBank ID	Location	Frequency [n]
P	AF202095	North Sea, Sweden	1
		Northeastern Atlantic, Iceland	2
		Northwestern Atlantic, Canada	12
		Northeastern Atlantic, U.S.	26
Q	AF202096	Northeastern Atlantic, Iceland	4
		Northwestern Atlantic, Canada	6
		Northeastern Atlantic, U.S.	10
R	AF202097	Northeastern Atlantic, Iceland	1
		Northeastern Atlantic, U.S.	4
S	AF202100	North Sea, Sweden	4
		North Sea, Norway	4
		Northeastern Atlantic, Faroe Islands	2
T	AF202098	Northeastern Atlantic, Faroe Islands	1
U	AF202099	Northeastern Atlantic, Faroe Islands	1
V	AF202102	Northeastern Atlantic, Iceland	1
W	AF202103	Northeastern Atlantic, Iceland	1
X	AF202101	Northwestern Atlantic, Canada	1
Y	AF202105	North Sea, Norway	1
Z	AF202104	North Sea, Sweden	1

Results

Genetic diversity and demographic history based on concatenated COI-CytB sequences

Of the 231 *Arctica islandica* specimens processed for COI sequencing, 174 yielded high-quality sequences of up to 614 bp, whereas 57 sequences were excluded due to insufficient sequence quality or length. For CytB, 161 high-quality sequences of up to 398 bp were obtained from 207 analysed specimens, while 46 sequences were excluded for the same reasons.

Concatenated mitochondrial COI-CytB sequences of up to 1,012 bp were obtained for 128 specimens for which both markers were available. They represented sampling sites across the German waters of the Baltic Sea, with the majority originating from Kiel Bay (n = 81). The haplotype network revealed widespread sharing of dominant haplotypes among sampling regions and short mutational distances between neighbouring haplotypes (Fig. 2). No evidence of geographic structuring of haplotypes was observed. Patterns inferred from the individual COI and CytB datasets were consistent with those observed in the concatenated dataset (Fig. S1).

Across regions, concatenated mitochondrial sequences exhibited relatively high haplotype diversity (Hd = 0.82–0.84; Table 3) and moderate nucleotide diversity (π = 0.69 and 0.74%). The number of haplotypes (K = 7–21) and polymorphic sites (S = 18–32) per region varied and likely partly reflected differences in sample size (n = 17–81). Kiel Bay showed the highest haplotype richness and number of polymorphic sites, whereas the Bay of Mecklenburg and Arkona Basin exhibited fewer haplotypes and polymorphic sites but similar levels of haplotype and nucleotide diversity (Table 3). Overall, haplotype distribution was relatively even, and sequence divergence was moderate across the concatenated mtCOI-CytB fragment.

Table 3
Mitochondrial diversity indices based on concatenated COI-CytB sequences of *Arctica islandica* from the German waters of the Baltic Sea. Abbreviations: KB, Kiel Bay; MB, Bay of Mecklenburg; AB, Arkona Basin; n, number of specimens; K, number of haplotypes; S, number of polymorphic sites; Hd, haplotype diversity; π, length-normalised nucleotide diversity.

Region	n	K	S	Hd	π (norm.) [%]
KB	81	21	32	0.83	0.69
MB	30	10	23	0.82	0.74
AB	17	7	18	0.84	0.74

Mismatch distribution analyses supported a scenario of recent demographic expansion in all regions (Table 4). Under the sudden expansion model, expansion time estimates were similar among regions (τ = 14.00–15.05), with θ_0 values close to zero and higher post-expansion population size estimates (θ_1 =

9.12–12.18). Model fit was generally good, although SSD was significant in the Bay of Mecklenburg, indicating a deviation from the expected mismatch distribution under a strict sudden expansion model.

The spatial expansion model yielded consistent estimates across regions, with comparable expansion times (τ = 10.77–12.87) and moderate migration rates (M = 1.32–1.60). Effective population size estimates were similar among regions (θ = 2.09–2.95). Under this model, SSD and Harpending's raggedness indices were non-significant in all regions, supporting a spatially structured expansion scenario.

Neutrality tests further supported historical demographic expansion. Fu's F_s values were strongly negative and significant in all regions (Table 4), indicating an excess of rare haplotypes consistent with population growth. Tajima's D values were non-significant throughout (D = 0.23 to 1.45), consistent with neutral expectations and historical demographic expansion rather than strong selective effects.

Table 4
Demographic expansion and neutrality test results for *Arctica islandica* from the German waters of the Baltic Sea based on concatenated mitochondrial COI-CytB sequences. Significance levels for the sum of squared deviations (SSD), Harpending's raggedness index (r), and Fu's F_S is indicated by asterisks: * $p \leq 0.05$, ** $p \leq 0.01$. Abbreviations: τ, time since expansion; θ_0 / θ_1, population size before/after expansion; M, migration parameter.

	Kiel Bay	**Bay of Mecklenburg**	**Arkona Basin**
Sudden expansion model			
τ	14.00	15.05	14.76
θ_0	0.00	0.00	0.00
θ_1	9.12	9.79	12.18
SSD	0.04	0.09**	0.05
r	0.04	0.07	0.05
Spatial expansion model			
τ	10.77	12.87	11.88
θ	2.95	2.09	2.82
M	1.32	1.37	1.60
SSD	0.02	0.05	0.03
r	0.04	0.07	0.05
Neutrality tests			
Tajima's D	0.23	0.93	1.45
Fu's Fs	–25.01**	–25.01**	-11.62**

A total of 986 nucleotide positions met the quality criteria (≤ 10% missing data per position) and were retained for analyses of genetic differentiation. AMOVA revealed that the vast majority of genetic variation was partitioned within rather than among regions, resulting in a slightly negative and non-significant fixation index (F_{ST} = -0.025, p = 0.98). Pairwise F_{ST} values and average pairwise nucleotide differences (πXY) were likewise low and non-significant, indicating an absence of detectable mitochondrial genetic structure among regions.

Range-wide context of Baltic Sea CytB haplotypes

The combined CytB haplotype network, incorporating previously published sequences and those generated in the present study, showed that the most common haplotypes were shared among

populations throughout the distribution range of *A. islandica* (Fig. 3). These dominant haplotypes were separated by only a few mutational steps, indicating low overall sequence divergence. Specimens from the German waters of the Baltic Sea were predominantly associated with these widespread haplotypes and did not form a distinct cluster within the network.

Several low-frequency haplotypes exhibited greater mutational divergence from the main haplotype group. These divergent haplotypes corresponded to lineages previously identified as rare male-transmitted mitochondrial (M-type) genomes [43]. In the combined dataset, M-type-associated haplotypes were detected exclusively in North Atlantic populations and were absent from samples from the White Sea, North Sea, and Baltic Sea. When these divergent M-type lineages were excluded, the network displayed a shallow star-like topology centred on a small number of common haplotypes shared among multiple geographic regions.

Discussion

The present study provides the first comprehensive assessment of mitochondrial genetic diversity of *Arctica islandica* in the German waters of the Baltic Sea based on COI and CytB sequences. Across the investigated regions, mitochondrial diversity was high, dominant haplotypes were shared, and no evidence of regional mitochondrial structuring in mitochondrial diversity was detected. Similar patterns were observed across individual COI and CytB datasets (Supplementary Information) as well as the concatenated COI-CytB dataset, indicating that the observed mitochondrial patterns were robust across markers. Analyses of molecular variance showed that most mitochondrial variation occurred within rather than among regions, while pairwise differentiation estimates remained low and non-significant, suggesting limited mitochondrial differentiation among Baltic Sea regions at the spatial scale examined.

Demographic analyses revealed a shared demographic signal among sampling regions. Negative and significant Fu's F_S values for both mitochondrial markers, together with mismatch distributions supporting expansion models, indicated an excess of rare haplotypes consistent with historical population growth. Similar expansion patterns were observed in the concatenated dataset, suggesting comparable demographic trajectories among populations. Although neutrality-based statistics may be influenced by processes such as selection or population structure, the concordance among neutrality tests, mismatch distributions, and haplotype patterns supports a scenario of recent demographic expansion following postglacial colonisation of the Baltic Sea.

Comparison with North Atlantic mitochondrial diversity

Previous studies of *A. islandica* have reported weak mitochondrial differentiation across large geographic distances within the species' North Atlantic distribution. Dahlgren et al. [15] identified only eleven CytB haplotypes despite sampling populations separated by thousands of kilometres, with dominant haplotypes occurring across geographically distant regions (Table 2). Similarly, Begum et al. [20] reported extensive sharing of mitochondrial haplotypes and weak geographic structuring among

North Atlantic populations. Together, these findings indicate that mitochondrial lineages in *A. islandica* generally exhibit shallow divergence despite substantial environmental and geographic variation throughout the species' distribution range.

The range-wide CytB haplotype network generated in the present study further supports this pattern (Fig. 3). Baltic Sea specimens were predominantly associated with common haplotypes occurring across multiple regions, and no clearly distinct Baltic Sea mitochondrial lineage was detected. Instead, Baltic Sea haplotypes were embedded within the broader pattern of North Atlantic mitochondrial diversity. This suggests that colonisation of the Baltic Sea has not resulted in substantial mitochondrial divergence, likely reflecting the relatively recent formation of the modern brackish basin and the limited time available for lineage differentiation.

The persistence of shared mitochondrial lineages across geographically separated populations may reflect the combined effects of species-specific life-history traits and demographic history. *Arctica islandica* is characterised by longevity, delayed maturity, and a relatively long planktonic larval phase [44], which may contribute to the persistence of shared genetic variation over extended time periods. Together with the recent postglacial history of the Baltic Sea, these characteristics provide a plausible explanation for limited mitochondrial divergence among populations.

Mitochondrial inheritance patterns and implications for interpretation

Interpretation of mitochondrial diversity in bivalves requires consideration of doubly uniparental inheritance (DUI), an unusual inheritance system in which distinct female-associated (F-type) and male-associated (M-type) mitochondrial genomes coexist within species [45, 46]. Previous studies have identified divergent M-type mitochondrial lineages in some North Atlantic populations of *A. islandica* [15, 42], raising the possibility that mitochondrial diversity patterns may be influenced by the representation of these lineages.

To evaluate this possibility, CytB sequences generated in the present study were analysed jointly with previously published datasets spanning the species' distribution range [15, 42, 43]. Divergent M-type-associated haplotypes were detected only among North Atlantic samples and were absent from the Baltic Sea, North Sea, and White Sea. Excluding these divergent lineages resulted in a shallow star-like network cantered around few dominant haplotypes shared among geographic regions.

These findings indicate that the mitochondrial diversity analysed in the German waters of the Baltic Sea predominantly represents the widespread mitochondrial lineage occurring across the species' distribution range. Consequently, the patterns of mitochondrial diversity and demographic history reported here are unlikely to be strongly influenced by divergent M-type-associated lineages.

Environmental context and potential drivers of weak mitochondrial differentiation

Marine population structure is likely shaped by interactions between species-specific life-history traits, dispersal potential, and the physical characteristics of the marine environment [47, 48]. Although adult *A. islandica* are largely sessile, dispersal occurs during the planktonic larval stage. The comparatively long planktonic larval duration of 32–55 days [44] may facilitate passive transport over considerable distances by ocean currents [49] and has previously been proposed as one explanation for the extensive sharing of mitochondrial haplotypes among North Atlantic populations [15, 20].

The southwestern Baltic Sea provides a particularly suitable natural system for investigating how environmental heterogeneity interacts with historical and biological processes shaping genetic diversity. Pronounced gradients in salinity, temperature, oxygen availability, and habitat suitability arise from episodic North Sea inflows, freshwater input, and complex basin morphology [8–10]. Within the German waters of the Baltic Sea, *A. islandica* inhabits deeper, comparatively saline habitats in the central Kiel Bay and the Bay of Mecklenburg, while reaching its easternmost distribution limit in the Arkona Basin [17, 22, 23, 29].

Hydrographic structures within this region could potentially reduce connectivity among local populations. Kiel Bay and the Bay of Mecklenburg are connected through the Fehmarn Belt, whereas exchange with the Arkona Basin is constrained by the shallow Darss Sill [8, 10, 50]. Furthermore, reduced salinity and increased environmental variability on the shallow Rugia–Falster plate limit the occurrence of suitable habitat for *A. islandica*, contributing to the fragmented distribution of populations within the southwestern Baltic Sea [23]. Comparable hydrographic and ecological discontinuities have been associated with genetic differentiation in several marine species in the Baltic Sea [3, 12, 14].

The absence of mitochondrial differentiation despite environmental heterogeneity is consistent with a scenario in which the combined effects of recent postglacial colonisation, larval dispersal, and intermittent hydrographic connectivity have contributed to maintaining shared mitochondrial variation. Episodic Major Baltic Inflows may periodically facilitate exchange among basins [10, 50], while the relatively long planktonic larval phase likely enables long-distance dispersal during favourable hydrographic conditions.

The recent geological history of the Baltic Sea provides additional context for these observations. Marine species colonised the basin following the establishment of brackish conditions during the Littorina transgression approximately 8,000–7,000 years BP [4, 5]. For a long-lived species such as *A. islandica*, this relatively short evolutionary timeframe may have limited the accumulation of substantial mitochondrial divergence, particularly if intermittent connectivity among populations has persisted. The observed mitochondrial homogeneity is therefore consistent with the combined effects of postglacial colonisation, ongoing larval-mediated connectivity, and the retention of widespread ancestral mitochondrial lineages.

Conservation implications

The absence of detectable mitochondrial differentiation among the investigated regions suggests that *A. islandica* populations in the German waters of the Baltic Sea share a common mitochondrial background at the spatial scale examined. Consequently, conservation and monitoring efforts may benefit from a coordinated regional framework rather than approaches based on geographically separated mitochondrial lineages. However, this interpretation should be regarded as provisional because mitochondrial diversity reflects only one component of population history and does not directly resolve adaptive differentiation or fine-scale population structure.

The relatively high mitochondrial diversity observed across the study area indicates that *A. islandica* has retained substantial mitochondrial variation despite inhabiting a brackish environment characterised by pronounced environmental gradients and potential barriers to dispersal. Nevertheless, mitochondrial homogeneity should not be interpreted as evidence for unrestricted resilience. In the Baltic Sea, populations experience environmental conditions distinct from fully marine habitats and are exposed to multiple stressors, including eutrophication, habitat degradation, oxygen depletion, and climate-driven changes in salinity and temperature regimes [9, 51–53].

Given the longevity of *A. islandica*, demographic responses to environmental deterioration may become apparent only after considerable time lags, potentially obscuring ongoing declines in recruitment success or abundance [54]. The southern North Sea provides a cautionary example, where declines in abundance and limited juvenile recruitment have been associated with both environmental variability and bottom trawling [55, 56]. Environmentally marginal habitats such as the Arkona Basin may be particularly sensitive to future environmental change because hydrographic isolation, reduced salinity, and recurrent oxygen depletion may constrain population persistence [2, 3].

Maintaining viable population size, habitat quality, and hydrographic conditions favouring connectivity should therefore remain priorities for the conservation of *A. islandica* in the German waters of the Baltic Sea. Sustaining sufficiently large populations is essential for preserving genetic diversity and the long-term evolutionary potential of the species, particularly in environmentally marginal habitats that may become increasingly vulnerable under future environmental change [1]. Continued ecological monitoring, complemented by future genomic studies, will be important for detecting changes in population status, genetic diversity, and adaptive potential.

Limitations of mitochondrial markers and future directions

Concatenating COI and CytB sequences increased the number of informative mitochondrial sites and provided a more comprehensive assessment of mitochondrial diversity and demographic history than either marker alone [57]. Nevertheless, mitochondrial data represent a single, maternally inherited genetic compartment and therefore provide only a partial view of population history. Consequently, recent population divergence, weak restrictions to gene flow, or adaptive differentiation may remain undetected if these processes are primarily reflected in the nuclear genome.
COI and CytB have been widely used to investigate genetic diversity and population structure in marine species, including *A. islandica* [14,15,20,47,57,58]. However, their ability to resolve fine-scale

differentiation depends on the magnitude and duration of population isolation, the persistence of gene flow, and the evolutionary timescale over which divergence has accumulated [59,60]. This limitation is particularly relevant in the Baltic Sea, where the comparatively recent postglacial history of the basin may have constrained mitochondrial divergence in a long-lived species such as *A. islandica*, particularly if larval-mediated connectivity among regions has persisted. Accordingly, the observed mitochondrial homogeneity does not exclude fine-scale population structure or local adaptation that may be detectable using nuclear genomic data.

Future studies should complement mitochondrial analyses with high-resolution nuclear genomic approaches, including genome-wide single nucleotide polymorphisms (SNP) datasets or reduced-representation sequencing methods such as RAD-seq. Integrating genomic, ecological, and demographic data will provide a more comprehensive understanding of population connectivity, evolutionary history, and adaptive potential in *A. islandica* inhabiting the environmentally marginal Baltic Sea.

Conclusions

Mitochondrial analyses revealed extensive haplotype sharing among *Arctica islandica* populations in the German waters of the Baltic Sea, together with high mitochondrial diversity and demographic patterns consistent with historical expansion. These findings indicate a shared mitochondrial history, likely shaped by postglacial colonisation, the persistence of widespread mitochondrial lineages, and species-specific life-history traits.

Despite pronounced environmental gradients and hydrographic complexity within the southwestern Baltic Sea, no evidence of regional mitochondrial differentiation was detected at the spatial scale examined. However, mitochondrial homogeneity should not be interpreted as evidence against fine-scale population structure or local adaptation. Future studies integrating high-resolution nuclear genomic, ecological, and demographic data will be essential for resolving contemporary population connectivity, assessing adaptive variation, and supporting the long-term conservation of the environmentally marginal and vulnerable Baltic Sea *A. islandica* population.

Declarations

Acknowledgements

This research was conducted as part of LAS's dissertation within the *ArKoBi* project (grant number 3523NK3500) at the Leibniz Institute for Baltic Sea Research Warnemünde (IOW), funded by the Federal Agency for Nature Conservation (BfN) under the Natural Climate Protection Action Program (ANK). We sincerely thank all colleagues and collaborating institutions involved in field sampling and laboratory work for their contributions to this study.

Specimen collection was supported by several research initiatives, including the LEGRA project (grant number 3519532202, funded by BfN; Dr. Katharina Romoth, IOW) and the MGF-Ostsee II project (grant

number 03F0937A, funded by the German Federal Ministry of Research, Technology and Space (former Federal Ministry of Education and Research); Dr. Mayya Gogina, IOW), as well as sampling activities conducted within Thünen Institute of Baltic Sea Fisheries cruises SOLEA-832 (Dr. Constanze Hammerl) and SOLEA-833 (Dr. Andrés Velasco), and GEOMAR Helmholtz Centre for Ocean Research Kiel (Renate Schütt). Additional contributions were provided by PD Dr. Stefan Forster (University of Rostock).

We further thank Klara Kola for her assistance during her fellowship at the Leibniz Institute for Baltic Sea Research Warnemünde (IOW). She contributed to laboratory work for a subset of specimens from Kiel Bay, including DNA extraction, PCR amplification, and generation of raw sequence data, which supported the molecular analyses presented in this study.

Funding

This work was supported by the Federal Agency for Nature Conservation, project *ArKoBi* (grant number 3523NK3500).

Competing interests

The authors have no relevant financial or non-financial interests to disclose.

Author Contributions (CRediT)

Conceptualisation: LAS, KK, HS, FW, MLZ

Data curation: LAS, KK, MLZ

Formal analysis: LAS

Funding acquisition: MLZ

Investigation: LAS, KK

Methodology: LAS, KK, HS

Project administration: MLZ

Resources: MLZ

Supervision: KK, FW, MLZ

Visualisation: LAS

Writing – original draft: LAS

Writing – review and editing: LAS, KK, HS, FW, MLZ

Data availability

Specimen metadata, collection information, voucher photographs, and raw sequence trace files are available through the Barcode of Life Data Systems (BOLD; dataset DS-ARKO03; dx.doi.org/10.5883/DS-ARKO03). Consensus mitochondrial COI and CytB sequences generated in this study have been deposited in GenBank through BOLD under accession numbers PZ807578–PZ807751 (COI) and PZ807415–PZ807575 (CytB). Supplementary Data S1 provides specimen-level information linking sampling records, molecular data, and repository identifiers.

Ethics approval

This study did not require approval by an animal ethics committee, as it involved the collection of wild marine invertebrates (*Arctica islandica*) and did not include experiments on vertebrate animals. Specimen collection was carried out under the appropriate permits and in accordance with national and institutional regulations governing the sampling of marine organisms.

References

1. Wennerström, L., Jansson, E. & Laikre, L. Baltic Sea genetic biodiversity: current knowledge relating to conservation management. *Aquat. Conserv. Mar. Freshw. Ecosyst.* **27**, 1069–1090. https://doi.org/10.1002/aqc.2771 (2017).
2. Lesica, P. & Allendorf, F. W. When are peripheral populations valuable for conservation? *Conserv. Biol.* **9**, 753–760. https://doi.org/10.1046/j.1523-1739.1995.09040753.x (1995).
3. Johannesson, K. & André, C. Life on the margin: genetic isolation and diversity loss in a peripheral marine ecosystem, the Baltic Sea. *Mol. Ecol.* **15**, 2013–2029. https://doi.org/10.1111/j.1365-294X.2006.02919.x (2006).
4. Björck, S. A review of the history of the Baltic Sea, 13.0–8.0 ka BP. *Quat Int.* **27**, 19–40 (1995).
5. Andrén, T. et al. The development of the Baltic Sea Basin during the last 130 ka. in The Baltic Sea Basin (*eds Harff*, *J.*, *Björck*, *S.* & *Hoth, P.)*; 75–97 (Springer, https://doi.org/10.1007/978-3-642-17220-5_4 (2011).
6. Gabrielsen, T. M., Brochmann, C. & Rueness, J. The Baltic Sea as a model system for studying postglacial colonization and ecological differentiation, exemplified by the red alga *Ceramium tenuicorne*. *Mol. Ecol.* **11**, 2083–2095. https://doi.org/10.1046/j.1365-294X.2002.01601.x (2002).
7. Kautsky, L. & Kautsky, N. The Baltic Sea, including Bothnian Sea and Bothnian Bay. in Seas at the Millennium: An Environmental Evaluation (ed Sheppard, C. R.) C.) (Pergamon, (2000).
8. Tauber, F. *Seabed sediments and seabed relief in the German waters of the Baltic Sea: data positions and sheet index, map no. 2930 [Map] 1:550,000* (Federal Maritime and Hydrographic Agency, 2012).
9. Carstensen, J., Andersen, J. H., Gustafsson, B. G. & Conley, D. J. Deoxygenation of the Baltic Sea during the last century. *Proc. Natl Acad. Sci. U.S.A.* 111, 5628–5633 (2014). https://doi.org/10.1073/pnas.1323156111

10. Mohrholz, V., Naumann, M., Nausch, G., Krüger, S. & Gräwe, U. Fresh oxygen for the Baltic Sea—an exceptional saline inflow after a decade of stagnation. *J. Mar. Syst.* **148**, 152–166. https://doi.org/10.1016/j.jmarsys.2015.03.005 (2015).
11. Larsson, J. et al. Regional genetic differentiation in the blue mussel from the Baltic Sea area. *Estuar. Coast Shelf Sci.* **195**, 98–109. https://doi.org/10.1016/j.ecss.2016.06.016 (2017).
12. De Wit, P. et al. Spatial genetic structure in a crustacean herbivore highlights the need for local considerations in Baltic Sea biodiversity management. *Evol. Appl.* **13**, 640–654. https://doi.org/10.1111/eva.12914 (2020).
13. Knöbel, L. et al. Salinity driven selection and local adaptation in Baltic Sea mytilid mussels. *Front. Mar. Sci.* **8**, 692078. https://doi.org/10.3389/fmars.2021.692078 (2021).
14. Geburzi, J. C. et al. An environmental gradient dominates ecological and genetic differentiation of marine invertebrates between the North and Baltic Sea. *Ecol. Evol.* **12**, e8868. https://doi.org/10.1002/ece3.8868 (2022).
15. Dahlgren, T. G., Weinberg, J. R. & Halanych, K. M. Phylogeography of the ocean quahog *Arctica islandica*: influences of paleoclimate on genetic diversity and species range. *Mar. Biol.* **137**, 487–495. https://doi.org/10.1007/s002270000342 (2000).
16. Butler, P. G., Wanamaker, A. D., Jr, Scourse, J. D., Richardson, C. A. & Reynolds, D. J. Variability of marine climate of the North Icelandic shelf in a 1357-year proxy archive based on growth increments in the bivalve *Arctica islandica*. *Palaeogeogr Palaeoclimatol Palaeoecol*. **373**, 141–151. https://doi.org/10.1016/j.palaeo.2012.01.016 (2013).
17. Brey, T., Arntz, W. E., Pauly, D. & Rumohr, H. Arctica (Cyprina) islandica in Kiel Bay (western Baltic): growth, production, and ecological significance. *J. Exp. Mar. Biol. Ecol.* **136**, 217–235. https://doi.org/10.1016/0022-0981(90)90162-6 (1990).
18. Witbaard, R., Duineveld, G. C. A. & de Wilde, P. A. W. Geographical differences in growth rates of *Arctica islandica* (Mollusca: Bivalvia) from the North Sea and adjacent waters. *J. Mar. Biol. Assoc. U K*. **79**, 907–915. https://doi.org/10.1017/S0025315499002145 (1999).
19. Begum, S. et al. Growth and energy budget models of the bivalve *Arctica islandica* at six different sites in the Northeast Atlantic realm. *J. Shellfish Res.* **29**, 107–115. https://doi.org/10.2983/035.029.0103 (2010).
20. Begum, S., Brey, T. & Held, C. Lack of association between genetic and morphological variation in the bivalve *Arctica islandica* from six different sites in the NE Atlantic Ocean. *Estuar. Coast Shelf Sci.* **212**, 34–39. https://doi.org/10.1016/j.ecss.2018.06.014 (2018).
21. Pace, S. M., Powell, E. N., Mann, R. & Long, M. C. Comparison of age-frequency distributions for ocean quahogs *Arctica islandica* on the western Atlantic US continental shelf. *Mar. Ecol. Prog Ser.* **585**, 81–98. https://doi.org/10.3354/meps12384 (2017).
22. Zettler, M. L., Bönsch, R. & Gosselck, F. Distribution, abundance and some population characteristics of the ocean quahog, *Arctica islandica* (Linnaeus, 1767), in the Mecklenburg Bight (Baltic Sea). *J. Shellfish Res.* **20**, 161–169 (2001).

23. Schulz, L. A. et al. Recent distribution and population structure of the ocean quahog, *Arctica islandica* (Linnaeus, 1767), in the German waters of the Baltic Sea – ecological insights and relevance for conservation. *J. Sea Res.* **208**, 102630. https://doi.org/10.1016/j.seares.2025.102630 (2025).
24. Basova, L. et al. Age-dependent patterns of antioxidants in *Arctica islandica* from six regionally separate populations with different lifespans. *Aquat. Biol.* **14**, 141–152. https://doi.org/10.3354/ab00387 (2012).
25. Basova, L. et al. Lipofuscin accumulation in tissues of *Arctica islandica* indicates faster ageing in populations from brackish environments. *Mar. Biol.* **164**, 72. https://doi.org/10.1007/s00227-017-3110-4 (2017).
26. Hiebenthal, C., Philipp, E. E. R., Eisenhauer, A. & Wahl, M. Interactive effects of temperature and salinity on shell formation and general condition in Baltic Sea *Mytilus edulis* and *Arctica islandica*. *Aquat. Biol.* **14**, 289–298. https://doi.org/10.3354/ab00405 (2012).
27. Hiebenthal, C., Philipp, E. E. R., Eisenhauer, A. & Wahl, M. Effects of seawater pCO_2 and temperature on shell growth, shell stability, condition and cellular stress of Western Baltic Sea *Mytilus edulis* (L.) and *Arctica islandica* (L). *Mar. Biol.* **160**, 2073–2087. https://doi.org/10.1007/s00227-012-2080-9 (2013).
28. Philipp, E. E. R. et al. Gene expression and physiological changes of different populations of the long-lived bivalve *Arctica islandica* under low oxygen conditions. *PLoS One*. **7**, e44621. https://doi.org/10.1371/journal.pone.0044621 (2012).
29. Darr, A., Gogina, M. & Zettler, M. L. Detecting hot-spots of bivalve biomass in the south-western Baltic Sea. *J. Mar. Syst.* **134**, 69–80. https://doi.org/10.1016/j.jmarsys.2014.03.003 (2014).
30. Gogina, M. et al. Interregional comparison of benthic ecosystem functioning: community bioturbation potential in four regions along the NE Atlantic shelf. *Ecol. Indic.* **110**, 105945. https://doi.org/10.1016/j.ecolind.2019.105945 (2020).
31. Gogina, M., Renz, J. R., Forster, S. & Zettler, M. L. Benthic macrofauna community bioirrigation potential (BIPc): regional map and utility validation for the south-western Baltic Sea. *Biology* **11**, 1085. https://doi.org/10.3390/biology11071085 (2022).
32. Rachor, E. et al. Dezember. Rote Liste und Artenlisten der bodenlebenden wirbellosen Meerestiere – 4. Fassung, Stand einzelne Aktualisierungen bis 2012. in *Rote Liste gefährdeter Tiere, Pflanzen und Pilze Deutschlands, Band 2: Meeresorganismen* (eds Becker, N. et al.) 81–176 (Landwirtschaftsverlag, Münster, 2013). (2007).
33. HELCOM. Biotope information sheet – AB.H3L3: Baltic aphotic muddy sediment dominated by ocean quahog (Arctica islandica) & HELCOM. ((2013). https://helcom.fi/wp-content/uploads/2019/08/HELCOM-Red-List-AB.H3L3.pdf
34. Turra, A., Corte, G., Amaral, A. C. Z. & Denadai, M. Non-linear curve adjustments widen biological interpretation of relative growth analyses of the clam *Tivela mactroides* (Bivalvia, Veneridae). *PeerJ* **6**, e5070. https://doi.org/10.7717/peerj.5070 (2018).

35. García-Souto, D. & Pasantes, J. J. Cytogenetics in *Arctica islandica* (Bivalvia, Arctidae): the longest lived non-colonial metazoan. *Genes* **9**, 299. https://doi.org/10.3390/genes9060299 (2018).
36. Kearse, M. et al. Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* **28**, 1647–1649. https://doi.org/10.1093/bioinformatics/bts199 (2012).
37. Paradis, E. & Schliep, K. ape 5.0: an environment for modern phylogenetics and evolutionary analyses. *R Bioinformatics*. **35**, 526–528. https://doi.org/10.1093/bioinformatics/bty633 (2019).
38. Leigh, J. W. & Bryant, D. popart: full-feature software for haplotype network construction. *Methods Ecol. Evol.* **6**, 1110–1116. https://doi.org/10.1111/2041-210X.12410 (2015).
39. Excoffier, L. & Lischer, H. E. L. Arlequin suite ver 3.5: a new series of programs to perform population genetics analyses under Linux and Windows. *Mol. Ecol. Resour.* **10**, 564–567 (2010).
40. Tajima, F. Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. *Genetics* **123**, 585–595 (1989).
41. Fu, Y. X. Statistical tests of neutrality of mutations against population growth, hitchhiking and background selection. *Genetics* **147**, 915–925 (1997).
42. Glöckner, G., Heinze, I., Platzer, M., Held, C. & Abele, D. The mitochondrial genome of *Arctica islandica*: phylogeny and variation. *PLoS One*. **8**, e82857. https://doi.org/10.1371/journal.pone.0082857 (2013).
43. Dégletagne, C. et al. Presence of male mitochondria in somatic tissues and their functional importance at the whole animal level in the marine bivalve *Arctica islandica*. *Commun. Biol.* **4**, 1104. https://doi.org/10.1038/s42003-021-02593-1 (2021).
44. Lutz, R. A., Mann, R., Goodsell, J. G. & Castagna, M. Larval and early post-larval development of Arctica islandica. *J. Mar. Biol. Assoc. U K*. **62**, 745–769. https://doi.org/10.1017/S0025315400070314 (1982).
45. Zouros, E. Biparental inheritance through uniparental transmission: the doubly uniparental inheritance (DUI) of mitochondrial DNA. *Evol. Biol.* **40**, 1–31. https://doi.org/10.1007/s11692-012-9195-2 (2013).
46. Smith, C. H. et al. A tale of two paths: the evolution of mitochondrial recombination in bivalves with doubly uniparental inheritance. *J. Hered*. **114**, 199–206. https://doi.org/10.1093/jhered/esad004 (2023).
47. Ye, Y. Y., Wu, C. W. & Li, J. J. Genetic population structure of *Macridiscus multifarius* (Mollusca: Bivalvia) based on mitochondrial markers: strong population structure in a species with a short planktonic larval stage. *PLoS One*. **10**, e0146260. https://doi.org/10.1371/journal.pone.0146260 (2015).
48. Xu, T. et al. Population genetic structure of the deep-sea mussel *Bathymodiolus platifrons* (Bivalvia: Mytilidae) in the Northwest Pacific. *Evol. Appl.* **11**, 1915–1930. https://doi.org/10.1111/eva.12696 (2018).

49. Shanks, A. L., Grantham, B. A. & Carr, M. H. Propagule dispersal distance and the size and spacing of marine reserves. *Ecol. Appl.* 13, 159–169 (2003). https://doi.org/10.1890/1051-0761(2003)013%5B0159:PDDATS%5D2.0.CO;2.

50. Neumann, T., Radtke, H. & Seifert, T. On the importance of Major Baltic inflows for oxygenation of the central Baltic Sea. *J. Geophys. Res. Oceans*. **122**, 771–783. https://doi.org/10.1002/2016JC012525 (2017).

51. Weigelt, M. Short- and long-term changes in the macrobenthic community of the deeper parts of Kiel Bay (Western Baltic) due to oxygen depletion and eutrophication. *Meeresforschung* **33**, 197–224 (1991).

52. Meier, H. E. M. et al. Modeling the combined impact of changing climate and changing nutrient loads on the Baltic Sea environment in an ensemble of transient simulations for 1961–2099. *Clim. Dyn.* **39**, 2421–2441. https://doi.org/10.1007/s00382-012-1339-7 (2012).

53. Reusch, T. B. H. et al. The Baltic Sea as a time machine for the future coastal ocean. *Sci. Adv.* **4**, eaar8195. https://doi.org/10.1126/sciadv.aar8195 (2018).

54. Hinz, H., Törnroos, A. & de Juan, S. Trait-based indices to assess benthic vulnerability to trawling and model loss of ecosystem functions. *Ecol. Indic.* **126**, 107692. https://doi.org/10.1016/j.ecolind.2021.107692 (2021).

55. Witbaard, R. & Klein, R. Long-term trends on the effects of the southern North Sea beamtrawl fishery on the bivalve mollusc Arctica islandica L. (Mollusca, Bivalvia). *ICES J. Mar. Sci.* **51**, 99–105. https://doi.org/10.1006/jmsc.1994.1014 (1994).

56. Witbaard, R. et al. The distribution and population structure of the bivalve Arctica islandica L. in the North Sea: what possible factors are involved? J. Sea Res. 50, 11–25 https://doi.org/10.1016/S1385-1101(03)00055-157. Strong genetic differentiation of the clam *Meretrix lamarckii* in the China Sea revealed by a mitochondrial DNA marker. *Mol. Biol. Rep.* 47, 693–702 (2020). https://doi.org/10.1007/s11033-019-05177-9 (2003).

57. Feng, J. et al. Strong genetic differentiation of the clam *Meretrix lamarckii* in the China Sea revealed by a mitochondrial DNA marker. *Mol. Biol. Rep.* **47**, 693–702. https://doi.org/10.1007/s11033-019-05177-9 (2020).

58. Wei, X., Fu, Z., Li, J., Guo, B. & Ye, Y. Genetic structure and phylogeography of commercial *Mytilus unguiculatus* in China based on mitochondrial COI and Cytb sequences. *Fishes* **8**, 89. https://doi.org/10.3390/fishes8020089 (2023).

59. Messer, P. W., Ellner, S. P. & Hairston, N. G. Can population genetics adapt to rapid evolution? *Trends Genet.* **32**, 408–418. https://doi.org/10.1016/j.tig.2016.04.005 (2016).

60. Galtier, N., Nabholz, B., Glémin, S. & Hurst, G. D. D. Mitochondrial DNA as a marker of molecular diversity: a reappraisal. *Mol. Ecol.* **18**, 4541–4550. https://doi.org/10.1111/j.1365-294X.2009.04380.x (2009).

Figures

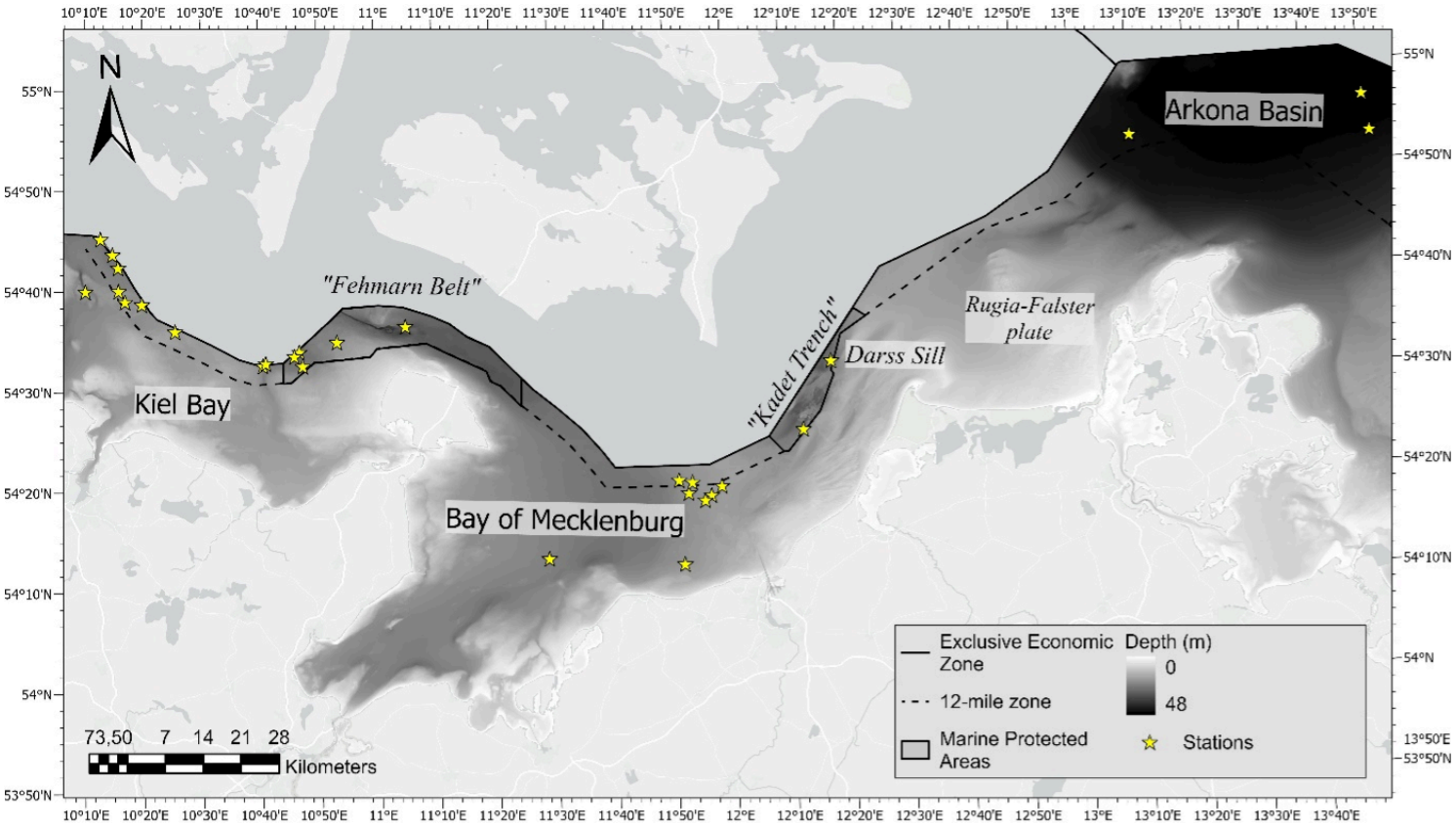

Figure 1

Sampling locations of Arctica islandica specimens collected in 2023 and 2024 in the German waters of the Baltic Sea. Sampling sites represent the regions analysed for mitochondrial COI and CytB variation. Bathymetry follows Tauber [8].

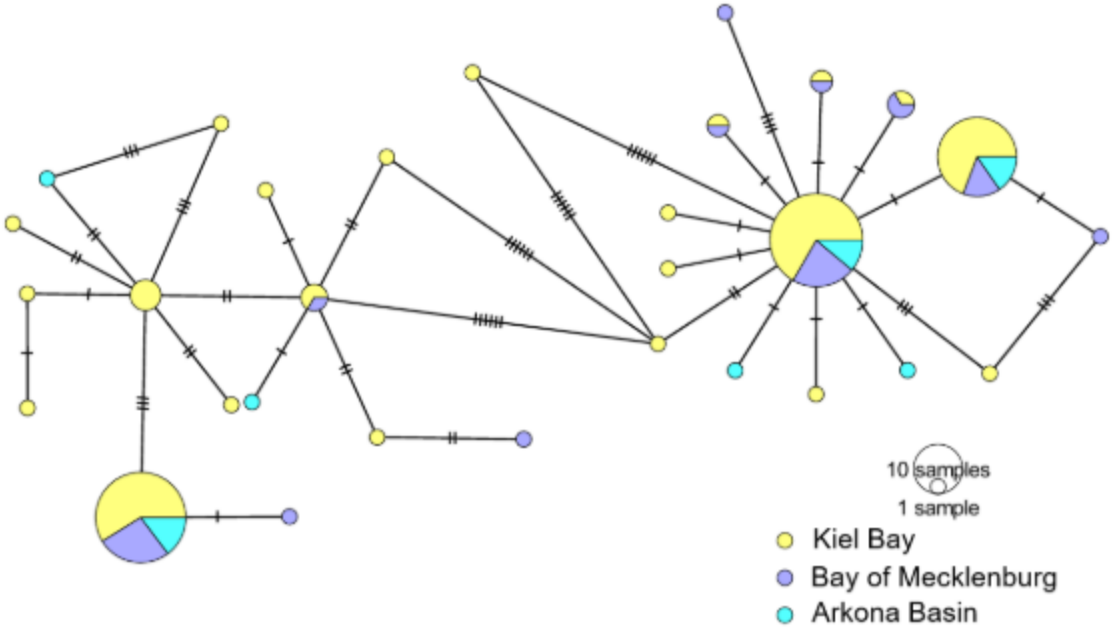

Figure 2

Minimum spanning haplotype network based on concatenated mitochondrial COI-CytB sequences (n = 128) of *Arctica islandica*from the German waters of the Baltic Sea. Circle size is proportional to haplotype frequency, and pie-chart segments indicate the distribution of haplotypes among sampling regions. Hash marks on branches represent mutational steps between neighbouring haplotypes.

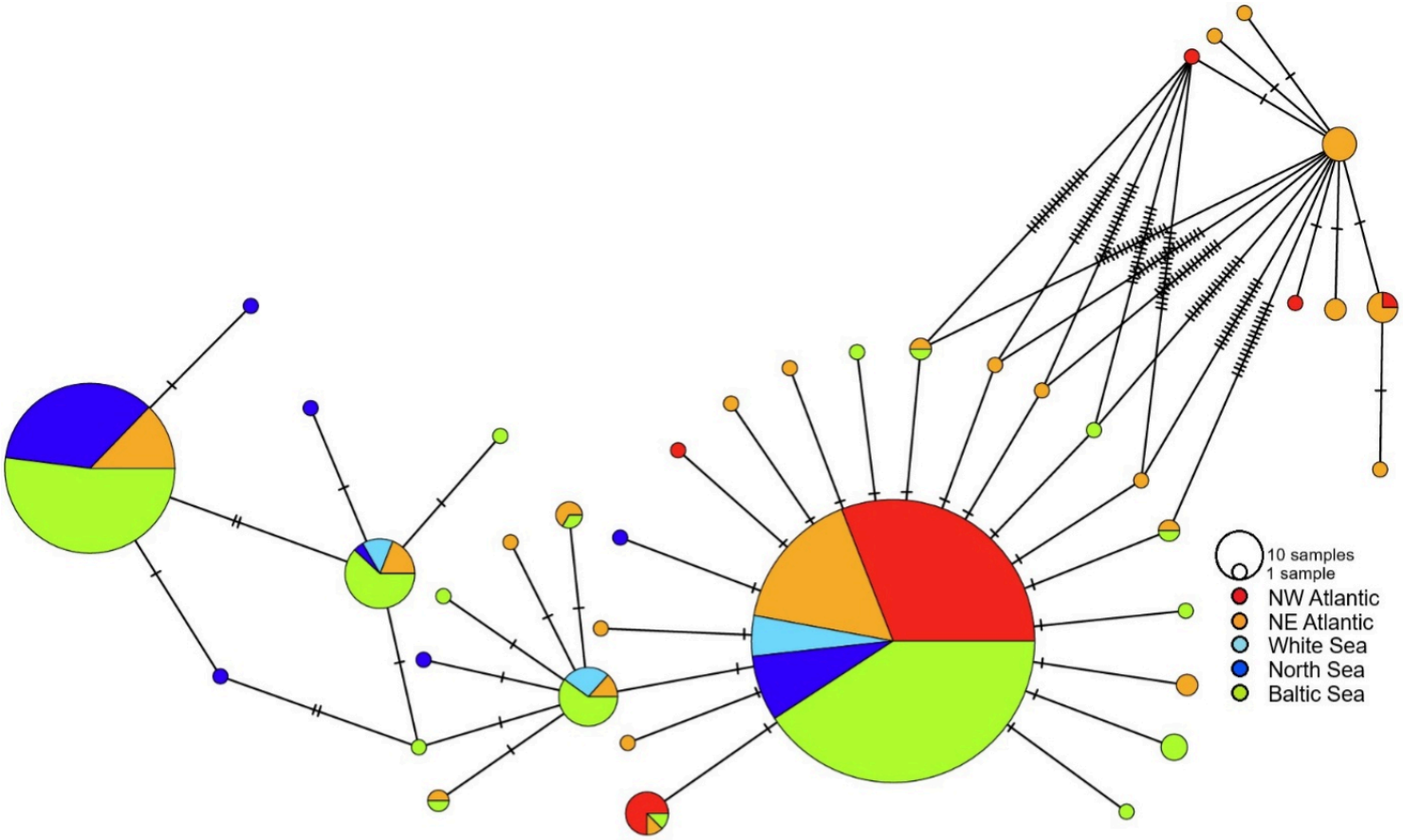

Figure 3

Range-wide minimum spanning haplotype network based on mitochondrial CytB sequences of Arctica islandica. The network includes Baltic Sea specimens analysed in the present study (n = 156) and published reference sequences from across the species' distribution range (n = 401). Sampling regions comprised the northwestern Atlantic (U.S. east coast and Canada; n = 117); northeastern Atlantic (Iceland, Faroe Islands, and northern Norway; n = 107); the White Sea (n = 23); the North Sea (incl. Skagerrak and Kattegat; n = 76); and the Baltic Sea (German waters; n = 243). Circle size is proportional to haplotype frequency, and pie-chart segments indicate haplotype distribution among sampling regions. Hash marks on branches represent mutational steps between neighbouring haplotypes.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- 202607SupplementaryInformation.pdf

- pub20260527Fig.S1COICytBMST.tif
- 202607SupplementaryDataS1metadata.xlsx