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RESOURCE ARTICLE

Evolutionary history and seascape genomics of Harbour porpoises (*Phocoena phocoena*) across environmental gradients in the North Atlantic and adjacent waters

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Abstract

The Harbour porpoise (*Phocoena phocoena*) is a highly mobile cetacean species primarily occurring in coastal and shelf waters across the Northern hemisphere. It inhabits heterogeneous seascapes broadly varying in salinity and temperature. Here, we produced 74 whole genomes at intermediate coverage to study Harbour porpoise's evolutionary history and investigate the role of local adaptation in the diversification into subspecies and populations. We identified ~6 million high quality SNPs sampled at eight localities across the North Atlantic and adjacent waters, which we used for population structure, demographic and genotype–environment association analyses. Our results suggest a genetic differentiation between three subspecies (*P.p. relicta*, *P.p. phocoena* and *P.p. meridionalis*), and three distinct populations within *P.p. phocoena*: Atlantic, Belt Sea and Proper Baltic Sea. Effective population size and Tajima's D suggest population contraction in Black Sea and Iberian porpoises, but expansion in the *P.p. phocoena* populations. Phylogenetic trees indicate post-glacial colonization from a southern refugium. Genotype–environment association analysis identified

salinity as major driver in genomic variation and we identified candidate genes putatively underlying adaptation to different salinity. Our study highlights the value of whole genome resequencing to unravel subtle population structure in highly mobile species, shows how strong environmental gradients and local adaptation may lead to population differentiation, and how neutral and adaptive markers can give different perspectives on population subdivision. The results have great conservation implications as we found inbreeding and low genetic diversity in the endangered Black Sea subspecies and identified the critically endangered Proper Baltic Sea porpoises as a separate population.

KEYWORDS
conservation, genetic structure, genomics, harbour porpoise, local adaptation

1 | INTRODUCTION

The well-being of populations depends on an array of extrinsic, as hunting, habitat destruction or pathogens, and intrinsic factors, as effective population size and genetic diversity. Reduction of genetic diversity in a population can lead to detrimental outcomes such as loss of adaptive potential and inbreeding depression, produced by the accumulation of slightly deleterious mutations due to reduced efficiency of purifying selection (Tanaka, 2000). Understanding the processes that influence current genetic variation is essential for the management and conservation of the diversity of a species (Kardos et al., 2021). Variation in genetic diversity is the result of historical and present demographic, geographic, ecological and behavioural mechanisms that influence gene flow, genetic drift and/or selection levels (Stange et al., 2021). Overarching processes such as glacial contractions and post-glacial expansions have influenced the current patterns of genetic structure and diversity in many European species, creating population subdivisions and hybrid zones by secondary contact (Hewitt, 1999, 2000, 2001). However, neutral evolutionary processes are not the only factor contributing to population subdivisions, as selective processes such as local adaptation could also produce different evolutionary trajectories (Barret & Schluter, 2008). Therefore, both neutral and adaptive processes must be considered when studying genetic diversity and population structure. Dispersal ability over vast geographical distances may facilitate gene flow among distant locations and hence hinder population differentiation (Slatkin, 1987). The marine habitat is a perfect example of an environment where a lack of physical barriers offers a continuous environment such that highly mobile species could present large homogenous populations and an absence of genetic structure. Yet, several cetacean species show fine-scale population structure, as for instance Northern bottlenose whale (*Hyperoodon ampullatus*) (de Greef et al., 2022), Finless porpoises (*Neophocaena asiaeorientalis*, *N. phocaenoides and N. sunameri*) (Zhou et al., 2018), Killer whale (*Orcinus orca*) (Foote et al., 2016) and bottlenose dolphins (*Tursiops truncatus*) (Louis et al., 2021), which may be attributed to philopatry, local adaptation and/or reduced migration ability, among other factors.

The Harbour porpoise (*Phocoena phocoena*) is a great example of complex genetic differentiation in a highly mobile cetacean species. Harbour porpoises inhabit coastal and shelf waters across the Northern hemisphere and at least three subspecies have been described (Committee on Taxonomy, 2022): *P.p. vomeria* in the North Pacific, *P.p. phocoena* in the North Atlantic and *P.p. relicta* in the Black Sea. A fourth subspecies near the Iberian Peninsula and in Mauritanian waters (*P.p. meridionalis*) has been proposed (Fontaine et al., 2007, 2014), although a formal description has not yet been made. The North Atlantic subspecies (*P.p. phocoena*) has a continuous distribution in the North Atlantic extending from the French Biscayan waters to the Baltic and Barents Sea and from the Norwegian Sea to the western North Atlantic coast of Canada and the United States, crossing Faroese, Icelandic and Greenlandic waters (Gaskin, 1992; Read, 1999). The genetic structure of North Atlantic Harbour porpoises has been widely studied (Alfonsi et al., 2012; Fontaine et al., 2007; Luna et al., 2012; Quintela et al., 2020 among others) and microsatellite data suggest that both sides of the Atlantic belong to the same population (Ben Chehida, Loughnane, et al., 2021; Ben Chehida, Stelwagen, et al., 2021). However, genetic data, diet compositions, movement behaviour and morphology suggest the presence of different ecotypes or populations on the peripheral waters of West Greenland (Olsen et al., 2022) and the Baltic Sea (Lah et al., 2016; Tiedemann et al., 1996; Wiemann et al., 2010).

The Baltic Sea is a remarkable sub-basin of the Atlantic Ocean formed less than 10,000 years before present (BP) as a postglacial aquatic environment. Baltic populations of several marine organisms are genetically distinct from conspecifics from the North Sea and the Atlantic, possibly due to isolation, bottlenecks and local adaptation (Wennerström et al., 2013). A series of small basins are separated by shallow underwater ridges ranging from the North Sea through Skagerrak, Kattegat, Belt Seas to the entrance of the proper Baltic Sea, presumably limiting dispersal and gene flow (Johannesson & André, 2006). Moreover, the Baltic Sea is an extreme marine environment with low winter temperatures and one of the strongest

salinity gradients in the world, ranging from ~34 practical salinity units (psu) in the Skagerrak to ~2 psu in the innermost parts of the Baltic (Feistel et al., 2010). These conditions make Baltic species a prime system to study local adaptation (DeFaveri & Merilä, 2014; Sjöqvist et al., 2015; Wrange et al., 2014) and speciation in the marine environment (Pereyra et al., 2009; Riginos & Cunningham, 2005; Stuckas et al., 2009). Passive acoustic (Carlén et al., 2018), telemetry (Sveegaard et al., 2015), morphological (Galatius et al., 2012; Huggenberger et al., 2002) and genetic data (Lah et al., 2016; Tiedemann et al., 1996; Wiemann et al., 2010) suggest the presence of three Harbour porpoise populations in the Baltic region: one in the North Sea, Skagerrak and northern parts of Kattegat (North Sea population, NOS), another in southern parts of Kattegat and Belt Seas (Belt Sea population, BES) and a third one in the Baltic Proper (Proper Baltic Sea population, PBS). Although overlap between the three populations has been reported based on both genetic (Lah et al., 2016; Wiemann et al., 2010) and satellite tracking data (Sveegaard et al., 2015), borders among them have been postulated based on geographical separation during the reproductive season (Amundin et al., 2022; Carlén et al., 2018; Sveegaard et al., 2015).

Harbour porpoise abundance estimates vary greatly among regions: Black Sea porpoise population size is unknown, but declined by ~90% between the 1930s and the 1980s (Birkun Jr., 2002); the European Atlantic Shelf is estimated to be inhabited by ~375,000 individuals (Hammond et al., 2013), ~20,000 animals are estimated in the Belt Sea and only ~500 in the Proper Baltic Sea (Amundin et al., 2022). The Black Sea subspecies and the Proper Baltic Sea population are considered endangered and critically endangered respectively. Porpoises are mainly affected by incidental bycatch (Brownell Jr et al., 2019), pollutants such as PCBs (Berggren et al., 1999; Karlson et al., 2000), pathogens (Dzido et al., 2021; Reckendorf et al., 2021; Ryeng et al., 2022) and noise pollution issued from offshore infrastructure developments, shipping routes and underwater explosions (Siebert et al., 2022). To date, no assessment of genetic diversity, effective population size (N_e) or population structure has been conducted on North Atlantic porpoises at the whole-genome level and very little is known about putative genetic adaptations. Historically, conservation and evolutionary geneticists have leaned on a handful of molecular markers, such as mitochondrial DNA and microsatellites, for the study of genetic variation among populations (Schweizer et al., 2021). However, with the development of high-throughput sequencing, there has been a transition from genetics to genomics (Formenti et al., 2022). The ever-decreasing cost of reduced representation and whole genome sequencing methods has positioned conservation genomics as a prominent tool for the characterization of biodiversity and preservation of species (Fuentes-Pardo & Ruzzante, 2017). Nowadays, the democratization of sequencing costs allows to resequencing the genome of a set of individuals to assess genetic variation across thousands or millions of markers and address long-standing questions in evolutionary biology not fully resolved with traditional markers or reduced representation methods (Foote et al., 2021; Robinson et al., 2022; Wolf et al., 2022). This increase of statistical power to unravel subtle patterns not fully captured by less dense data sets has had and will continue to have a remarkable impact in the field of conservation genomics (Lou et al., 2021; Szarmach et al., 2021).

Here, we used genomics approaches to study the population structure, genetic diversity, evolutionary history and local adaptation of the Harbour porpoise (*Phocoena phocoena*). We generated the most comprehensive data set of North Atlantic Harbour porpoises so far, by resequencing the whole genome of 74 Harbour porpoises from eight regions across the North Atlantic and adjacent waters. Our results shed light on the expansion of Harbour porpoise populations across the North Atlantic, demonstrate that genome-wide data can unravel subtle population structure and contribute to understanding how marine species adapt to their local environment. The results have great conservation implications as we found inbreeding and low genetic diversity in the endangered Black Sea subspecies and identified the critically endangered Proper Baltic Sea porpoises as a separate population.

2 | MATERIALS AND METHODS

2.1 | Sampling and laboratory procedures

The study was based on 74 tissue samples collected in eight different regions across the North Atlantic and adjacent waters (Figure 1): eastern Canada (CA), Iceland (ICE), Barents Sea (BAS), North Sea (NOS), Belt Sea (BES), Proper Baltic Sea (PBS), Iberia (IBE) and Black Sea (BLS). The NOS–BES border was located at the latitude 56.95° N, as a straight line from Denmark to Sweden (Sveegaard et al., 2015), while the BES–PBS border was placed as a diagonal line from the Swedish Hanö island (56° N 14.7° E) to the village of Jarosławiec in Poland (54.5° N 16.5° E) (Amundin et al., 2022; Carlén et al., 2018). All sampling was performed on bycaught or stranded carcasses, and no live Harbour porpoise has been targeted in the scope of this study.

We extracted total genomic DNA from skin or muscle tissue using one of the three following methods: NucleoSpin Tissue Kit, DNeasy Blood & Tissue Kit or phenol–chloroform extraction. DNA concentration and quality were measured using a Qubit fluorometer and fragment analyser to ensure that chosen samples were not fragmented and at least 300 ng of DNA per sample was available. Library preparation and whole-genome resequencing was performed at GENEWIZ from Azenta Life Sciences in Leipzig, Germany. Briefly, genomic DNA was fragmented by acoustic shearing, then fragmented DNA was end repaired and adenylated. Adapters were ligated after adenylation of the 3′ ends followed by enrichment by limited cycle PCR. The libraries were then multiplexed on a flow cell and sequenced using 2×150 paired-end reads in a Illumina NovaSeq 6000. Raw sequencing data (*bcl* files) were converted into *fastq* files and de-multiplexed using Illumina's *bcl2fastq* software.

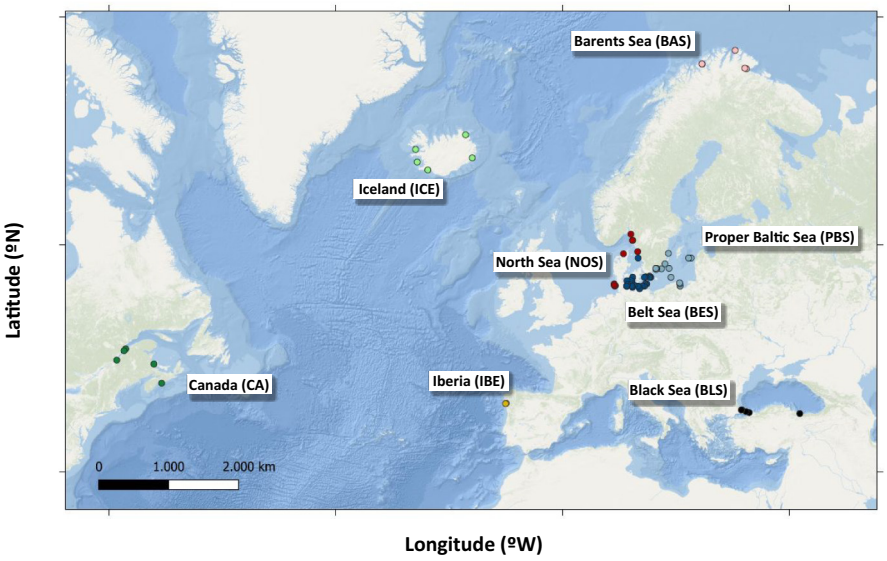

FIGURE 1 Map of sampling locations of Harbour porpoise individuals coloured according to origin: Canada (CA) dark green, Iceland (ICE) light green, Barents Sea (BAS) pink, North Sea (NOS) red, Belt Sea (BES) dark blue, Proper Baltic Sea (PBS) light blue, Iberia (IBE) yellow and Black Sea (BLS) black.

2.2 | Genomic data processing

Fastq files were processed with the software *Fastp* (v.0.23.2) (Chen et al., 2018) to trim residual adapter sequences and poly G tails as well as to filter out bad/low quality (<15Q) and too short (<75 bp) reads. The remaining filtered reads were mapped to the Harbour porpoise reference genome assembly (originating from a Belt Sea Harbour porpoise; Autenrieth et al., 2018) using the *Bwa mem* algorithm (v.0.7.17) (Li & Durbin, 2009) with default settings. Recently, a chromosome-level assembly of a Pacific Harbour porpoise (*P.p. vomeria*) has been released (https://www.dnazoo.org/assemblies/Phocoena_phocoena). We compared the mapping rate for five specimens representing all populations/subspecies (North Atlantic, Belt Sea, Proper Baltic Sea, Iberia, Black Sea). On average, 99.73% of the reads were mapped to our reference genome [range 99.69%–99.76%]. The mapping rate slightly increased, when reads were mapped to the novel chromosome-level genome [average 99.90%; range 99.86%–99.91%]. Alignment *sam* files were converted to *bam* files and sorted by its leftmost coordinate with *Samtools* (v.1.15) (Danecek et al., 2021). *Picard tools* (v.2.27.2) was used to add read groups and to remove PCR and sequencing duplicates. Thereafter, *bam* files were realigned around indels with *GATK* (v.3.8.1) (Van der Auwera et al., 2013).

We used *RepeatMasker* (v.4.1.2) (Smit et al., 2013) and the *dfam 3.6* (Storer et al., 2021) database to identify repetitive sequences and interspersed repeats were removed from the *bam* files using *Samtools*. Then, we identified sex-linked scaffolds with the software *SATC* (Nursyifa et al., 2022) and used *Samtools* to remove them. Additionally, we removed reads of mapping quality <30 and regions of low (1/3 mean coverage) and excessive (2× mean coverage) depth, previously estimated with ANGSD (v.10.2.0) (Korneliussen et al., 2014). Since some population genomics analyses can be affected by the presence of first-degree relatives, we calculated relatedness statistics with the software *NgsRelate* (v.2.1) (Hanghøj et al., 2019), which uses genotype likelihoods as input. Subsequently, we removed one sample from the only pair of first-degree relatives found in our data set from the downstream analyses.

2.3 | SNP calling: Genotype likelihoods and genotype calls

We called SNPs in two different ways: calculating genotype likelihoods with *ANGSD* and calling genotypes (generation of a *vcf* file) with *Bcftools* (v.1.11). Genotype likelihoods take into account genotype uncertainty and allow to obtain reliable SNPs at very low coverages (Lou et al., 2021). We calculated genotype likelihoods in two data sets, one including Black Sea (BLS) individuals and another without BLS individuals using the *Samtools* model (GL 1), keeping SNPs with a minimum minor allele frequency (MAF) of 0.05, having data in a minimum 75% of the individuals and a SNP *p*-value<$1e^{-6}$. The beagle file generated with *ANGSD* was used as an input in the population structure analysis and to calculate population genomics summary statistics. Genotypes were called with *Bcftools* commands *mpileup* and *call*, with the multiallelic and rare-variant calling option *−m*, in alignments with minimum mapping *(−q)* and minimum base *(−Q)* quality of 30. We also used *Bcftools* to subsequently retain only high-quality SNPs: We removed non-biallelic sites, indels, SNPs with MAF below 0.05 and SNPs that did not yield genotype information in at least 75% of the individuals, as a compromise between having too much missing data and removing too many SNPs. Our filtering scheme is similar to those used in similar WGS projects in cetaceans (Louis et al., 2021; Robinson et al., 2022). The *vcf* file generated was used as input in the demographic history and seascape genomics analysis.

2.4 | Population structure analysis

We studied the genetic structure of North Atlantic Harbour porpoises by performing PCAs and admixture analyses on a set of

unlinked SNPs. We used the software *ngsLD* (Fox et al., 2019) to prune our data of linked SNPs, considering that SNPs are in linkage disequilibrium (LD) if they are on the same chromosome/scaffold within less than 20 kb and using a minimum weight of 0.5. The PCAs were calculated with *PCAngsd* (Meisner & Albrechtsen, 2018), while the admixture analyses were run in *NGSAdmix* (Skotte et al., 2013). To assess convergence, we performed 20 independent runs, with the number of assumed populations (K) ranging from 2 to 8, a minimum tolerance for convergence of 1×10^{-10} and a minimum likelihood ratio value of 1×10^{-6}.

To remove the genetic signal created by other subspecies and study only the population structure of the *P.p. phocoena* subspecies, we excluded BLS samples and repeated the PCA and admixture analysis, with K ranging from 2 to 7. In addition, we examined the local population structure in the Baltic region by including only samples from NOS, BES and PBS in an independent PCA and admixture analysis with K ranging from 2 to 3. Finally, we calculated the rate of likelihood change or Delta K (Evanno & Goudet, 2005) for the three data sets to find the most likely K.

2.5 | Population genomic summary statistics

A series of diversity and demographic statistics were estimated from the folded site frequency spectrum (SFS) with *ANGSD*. Genome-wide heterozygosity was estimated per sample by first computing the folded site allele frequency likelihood using the reference genome as ancestral state and then calculating the folded SFS. The folded SFS was calculated independently for each sampling site after removing admixed (less than 70% ancestry to any cluster under K4) and migrant individuals (individuals whose ancestry was different from the prevalent cluster of their sampling location). Then, we estimated both Watterson's theta and Tajima's D, using a sliding window approach with window size of 50 kb and a step size of 10 kb. Individual inbreeding coefficients (*F*) were estimated with the software *ngsF (v.1.2.0)* (Vieira et al., 2013). First, approximate *F* were obtained in an initial run using the *-aprox_EM* method, with a maximum root mean squared difference between iterations of 1×10^{-5}*(–min_epsilon)* and random initial values. From the output of this first run, the initial parameters for the final run were derived, where the *-min_epsilon* value was decreased to 1×10^{-7} to assume convergence. To avoid convergence to local maxima, this two-step analysis was repeated 10 times, as suggested by the authors (Vieira et al., 2013). To check for significance on the population summary statistics, we ran an ANOVA and a post hoc Tukey test.

2.6 | Demographic history analysis

To reconstruct historical relationships among North Atlantic Harbour porpoises, we inferred a maximum likelihood bifurcating population tree using *Treemix* (v.1.13) (Pickrell & Pritchard, 2012). The genotypes (*vcf*) were filtered to retain only sites with no missing data. We performed the *Treemix* analysis 1000 times at the population level with a window size of 1000 SNPs, specifying the Black Sea subspecies as outgroup and with the option *-noss* to turn off sample size correction, as suggested by the authors. We obtained a consensus tree and bootstrap values with the R package *BITE* (Milanesi et al., 2017).

We also inferred changes in effective population sizes (N_e) through time with the software *SMC++* (v.15.2) (Terhorst et al., 2017). This analysis was run only using scaffolds larger than 1Mba (160 scaffolds) and we filtered singletons on the *vcf*. As repetitive and excessive coverage regions were removed from the *bam* files, these uncalled regions were marked as missing data, as suggested by the authors (Terhorst et al., 2017). These regions could be misidentified as very long runs of homozygosity, erroneously decreasing the N_e estimate, and hence compromising the power to infer true population contractions. In addition, we formed composite likelihoods by varying the distinct individual (*–d*), also as suggested by the authors. Then, the population size histories were computed by using the option *estimate* with the default settings, a generation time of 11.9 years (Taylor et al., 2007) and a mutation rate of 2.56×10^{-8} (Yim et al., 2014). We investigated the effect of imbalanced population sample sizes by running *SMC++* again on a reduced data set including three randomly chosen individuals per population, except for PBS and IBE where we used the three same individuals for the former and one for the latter. Furthermore, to evaluate uncertainty of our *Ne* estimates, we performed jackknife resampling over specimens (Sokal & Rohlf, 1995).

2.7 | Genotype–environment associations: Seascape genomics

To assess how environmental variables shaped the genetic structure of North Atlantic and Black Sea Harbour porpoises, we developed a seascape genomics approach. Specifically, we studied genotype–environment associations (GEA) to identify putative SNPs underlying local adaptation by carrying out a redundancy analysis (RDA) with the R package *vegan* (Oksanen, 2007). RDA is a multivariate method that finds linear dependencies between response (genotypes) and explanatory variables (environmental predictors). Previous authors (Capblancq et al., 2018; Forester et al., 2018) have found multivariate GEA analyses, especially constrained ordination approaches such as RDA, to detect more effectively multilocus selection than univariate methods and to have a superior combination of low false-positive and high true-positive rates (Capblancq & Forester, 2021). RDA was carried out at the individual level using two data sets, with and without BLS. To control for spatial autocorrelation and other demographic processes as population subdivision and potential isolation-by-distance, pairwise oceanic distances were calculated from the coordinates of the samples with the R package *marmap* (Pante & Simon-Bouhet, 2013). Subsequently, pairwise oceanic distances

were transformed to distance-based Moran's eigenvector maps (*dbMEMs*) with the R package *adespatial* (Dray et al., 2012) and used as the space variable in the RDA.

Previous seascape genomics studies on Common (*Delphinus delphis*) and Bottlenose dolphins (*Tursiops truncatus*) considered nine environmental variables which had been previously discussed to be relevant for their respective species (Barceló et al., 2022; Pratt et al., 2022; and references therein). They identified the same five environmental variables associated with genomic variation in both species. These variables were selected in our study as potential predictors of Harbour porpoise genomic variation: sea surface temperature (SST), sea surface salinity (SSS), sea current velocity (SCV), sea chlorophyll-*a* concentration (SCA) and sea primary productivity (SPP). For each of the variables, the annual maximum, mean, minimum and range values were downloaded from the database *BioOracle (v.2.2)* (Assis et al., 2018; Tyberghein et al., 2012). SCVmax and SPPmax were not available in this database, yielding altogether 18 variables. As genomic input we used a set of unlinked called genotypes, identified by *Plink (v.1.9)* (Purcell et al., 2007) with a window size of 20 kb, a step size of 10 kb and a r^2 threshold of 0.1.

To maximize the genetic variance explained by our set of environmental predictors, we performed a forward selection with the function *forward.sel* of the R package *adespatial*. The forward selection was carried out for the environmental variables and *dbMEMs* separately, and only variables explaining a significant proportion ($p < .05$) of the genomic variation were retained. To control for multicollinearity, only predictors with a highly conservative variance inflation factor (VIF) < 3 and $r < |0.7|$ were retained. An RDA-based variance partitioning (Capblancq & Forester, 2021) was performed to estimate the independent contribution of the environmental and spatial variables. First, we ran an unconstrained RDA with the retained environmental and spatial variables as predictors to find the variance explained by the full model. Then, we calculated the variance explained by the environmental variables once the influence of spatial variables had been removed by applying a constrained pRDA. Finally, we checked the significance of the RDAs and pRDAs as well as the significance of the environmental variables by an analysis of variance (ANOVA) with 1000 permutations.

Candidate loci under selection were identified by applying a three standard deviation cut-off ($p = .0027$) on the SNPs loading scores (Forester et al., 2018) from the two first redundancy axes and we determined to which environmental variable each candidate SNPs is most associated. To further control for false positives, we carried out an additional selection genome scan based on individual genotypes with the R package *Pcadapt* (Privé et al., 2020). We used four principal components (K), identified by computing a scree plot and choosing the K that minimized the genomic inflation factor (GIF). Then, we transformed the *p*-values in *q*-values with the R package *qvalue* and applied a false discovery rate of 0.1 to control for false positives.

We performed a functional enrichment analysis by extracting the gene ontology (GO) terms of the candidate SNPs detected by the three methods (RDA-pRDA-Pcadapt) on the data set without BLS (952) by making use of the draft annotation (Autenrieth et al., 2018). Then, with a Fisher's exact test with an α value of .05, we identified GO terms that were overrepresented in the environmentally adapted SNP data set compared with the entire genome. Additionally, we identified putative candidate genes locally adapted to salinity by using only the candidate SNPs detected by the three methods RDA-pRDA-Pcadapt on the data set without BLS and that were associated with salinity (271). We extracted 300 bp of flanking sequences for each candidate SNP resulting on 601 bp long sequences, each containing a single SNP. We then performed a basic local alignment with *BLASTN* using the nucleotide database of NCBI with an e-value of 1×10^{-3}. After extracting hits per query, we identified gene function and influenced biological function with the PubMed and GeneCards (Stelzer et al., 2016) databases.

2.8 | Neutral and adaptive diversity

To get further insights into how adaptive processes shaped the genetic structure of North Atlantic Harbour porpoises, we analysed separately the neutral and inferred adaptive SNPs. The neutral data set consisted of the SNPs not found under selection in the *Pcadapt* genome scan and that were in Hardy–Weinberg Equilibrium (HWE), while the adaptive data set comprised the outlier SNPs identified by the *Pcadapt* genome scan. We performed a PCA with the R package *adegenet* (Jombart & Ahmed, 2011), estimated mean pairwise-weighted *Fst* across populations using *vcftools (v.0.1.16)* (Danecek et al., 2011) and performed a paired *t*-test to test for significance among SNP data sets. To test for spatial autocorrelation/isolation-by-distance (IBD) and to overcome limitations of the frequently used Mantel test (Legendre et al., 2015), a redundancy analysis was run on the neutral and adaptive data set without BLS samples using the retained dbMEMs as spatial variables. The outcome was evaluated for significance using an ANOVA with 1000 permutations.

3 | RESULTS

To disentangle the evolutionary history and population structure of North Atlantic Harbour porpoises, we resequenced genomes of 74 specimens from eight different regions (Figure 1). Sample biological information, sequencing, filtering and mapping statistics are provided in Table S1. After all filtering steps, one BES individual (Figure S1c) kept a small fraction of the raw reads (6.65%, 2.73X coverage) and was discarded from further analysis. Mean sequencing depth was 10.11X (Figure S1b), which is considered an intermediate coverage level (Bourgeois & Warren, 2021; Fuentes-Pardo & Ruzzante, 2017), and similar depth levels were used in other population genomic studies on cetaceans based on whole genome resequencing (Cerca et al., 2022; de Greef et al., 2022; Zhou et al., 2018). Scaffold coverage comparisons between male and female sequencing data (Figure S2) identified 46 sex-associated scaffolds (122.3 Mb), which were subsequently removed from downstream analysis. Relatedness

analysis (Figure S3) identified one pair of first-degree relatives; thus, we removed the individual (B41-14) with the lower coverage out of the pair, leading to a final sample size of 72 Harbour porpoises. Genotype likelihood estimation rendered 7,337,750 high-quality SNPs, from which 1,745,544 were identified as unlinked. After SNP calling and filtering, we retained a set of 6,186,462 high-quality SNPs (1,320,367 unlinked).

3.1 | Genetic structure

The population structure analysis, *PCAngsd* and *NGSAdmix* (Figure 2), based on a set of ~1.7 million genotype likelihoods, indicated that Harbour porpoise subspecies and populations clustered together. The PCA including all samples (Figure 2a) show two major axes of differentiation: subspecies (PC1) and populations of the North Atlantic subspecies (PC2). The first principal axis, explaining 5.8% of the variance, separates the BLS and one IBE individual from the rest of the samples, suggesting that this IBE individual could belong to the proposed Iberian subspecies (Fontaine et al., 2007, 2014). The second principal component (2.2% explained variance) divides Baltic Sea porpoises (BES and PBS) from the Atlantic porpoises (CA, ICE, BAS, NOS), except for one porpoise bycaught in Latvian waters that clustered with the Atlantic ones. Nine samples (1 NOS, 4 BES and 4PBS) were located between the Atlantic and Baltic clusters, but were more closely related to the Baltic one (Figure 2a). When analysing the PCA without BLS samples (Figure 2c), PC1 (3% variance explained) also divides the Baltic from the Atlantic samples, but in this case, only six individuals were located between the two groups, as the other three PBS samples were separated by PC2 (2% variance explained). The PCA including only porpoises from the Baltic region (Figure S4b) further suggested the presence of three populations in this small area. The admixture results were consistent with the population structure identified in the PCAs. On the

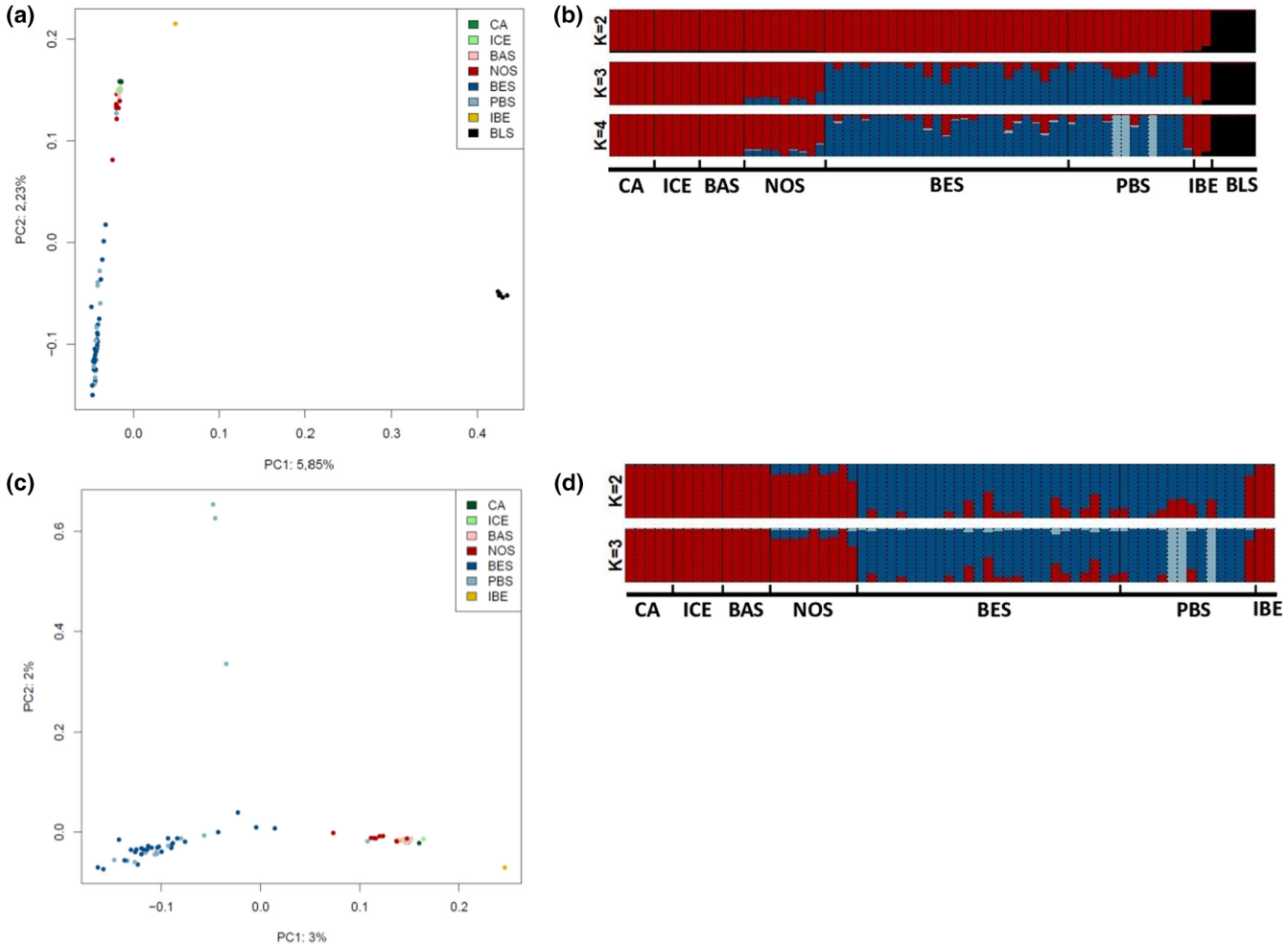

FIGURE 2 Population structure of North Atlantic Harbour porpoises suggesting the existence of five major genetic clusters: Black Sea subspecies, the potential Iberian subspecies, Atlantic, Belt Sea and Proper Baltic Sea populations. (a) Principal component analysis (PCA) of harbour porpoises ($N = 72$) showing the first and second PCs. (b) Admixture analysis of harbour porpoises ($N = 72$), only K ranging from 2 to 4 is shown. (c) PCA of the data set without the Black Sea subspecies ($N = 67$) showing the first and second PCs. (d) Admixture analysis of the data set without the Black Sea subspecies ($N = 67$), only K ranging from 2 to 3 is shown. Each small vertical bar in the admixture analyses represents a Harbour porpoise specimen and the colouring corresponds to its genetic ancestry, Black Sea subspecies in black, Atlantic population in red, Belt Sea population in dark blue and Proper Baltic Sea population in light blue.

data set including BLS samples (Figure 2b), K2 separated BLS porpoises from the others, K3 subdivided the Baltic from the Atlantic and K4 isolated the same three PBS samples from the remainder of the Baltic. The admixture analysis without BLS (Figure 2d) and only Baltic region samples (Figure S4c) first divided Baltic samples from the rest (K2), and then the same three PBS individuals from the remaining of the Baltic (K3). The Delta K method supported K3 (i.e., separate PBS cluster; light blue in Figure 2d; Figure S4b) as the most likely in the data set including only Baltic samples, while in the other two data sets, the K-values without this cluster (K3 all samples; K2 without BLS) yielded slightly higher Delta K scores. It has been recently recommended to complement the Delta K inference with visual plot inspection, in order not to overlook subtle population differentiation (Stankiewicz et al., 2022). Accordingly, based on the genetic structure results (Figure 2a,b), and published telemetry and passive acoustic data, we retained the inferred separate light blue cluster in the Proper Baltic Sea. This corresponds to the K = 4 assignment as the highest level of structure in the data set including all samples and we assigned individuals to a given cluster if the likelihood of membership was ≥75% in the admixture analysis. Sixty-six out of the 72 individuals could be assigned to one of the four clusters. This division resulted in 26 porpoises assigned to the Atlantic population (red cluster), six admixed between Atlantic and BES, 32 assigned to the BES population (dark blue cluster), three assigned to the Proper Baltic Sea population (light blue cluster) and five assigned to the BLS subspecies (black cluster). Both IBE samples clustered with the Atlantic. For the analysis at the population level (*Treemix*, *SMC++* and population summary statistics), we excluded the six specimens admixed between Atlantic and BES, as well as 11 individuals found in the PBS region, but assigned to the Atlantic (red) or BES (dark blue) cluster, such that PBS is represented by the three specimens forming the PBS-specific light blue cluster in Figure 2b,d.

3.2 | Evolutionary and demographic history

We explored the post-glacial expansion of North Atlantic Harbour porpoises by inferring the evolutionary relationships among populations, quantifying their genetic diversity and estimating historical variation in effective population size (*Ne*). *Treemix* results (Figure 3a) show how the Harbour porpoise colonized and dispersed across the North Atlantic from a putative southern refugium. The first to split were IBE porpoises, followed by NOS. Thereafter, the ancestral porpoise Atlantic subspecies diverged into Baltic populations and the rest of the Atlantic. All internal nodes had a high bootstrap support (90%–100%), except the branch with NOS porpoises (71%) which presented a lower support, and the ancestral node of CA and BAS localities (49%) which was statistically not supported, such that the ancestry among the northern North Atlantic porpoises of BAS, CA and ICE was not resolved in our analysis.

The *SMC++* results (Figure 3b) indicate that BLS porpoises' inferred N_e was stable until ~100,000 years before present (yBP), followed by a steady population contraction up to ~25,000 yBP, when the N_e started to increase. The porpoise potentially belonging to *P.p. meridionalis* had a very similar trajectory, except that inferred population sizes were slightly higher. The Atlantic and Baltic populations had a related inferred demographic history, with an expansion from ~250,000 yBP until ~50,000 yBP, when populations trajectories started to diverge. The order of inferred population splits remained robust, even if the inference was based on a smaller sample size ($n = 3$ for all populations except IBE; Figure S15). However, after the divergence, estimated N_e trajectories became less precise (as inferred by jackknife-resampling; Figure S16).

Individual genome-wide heterozygosity estimates (Figure 4a) were significantly different among populations (ANOVA: $F_{[8;52]} = 5.095$; $p < .001$), because of lower heterozygosity in BLS porpoises compared to most other populations (CA; ICE; BAS; NOS;

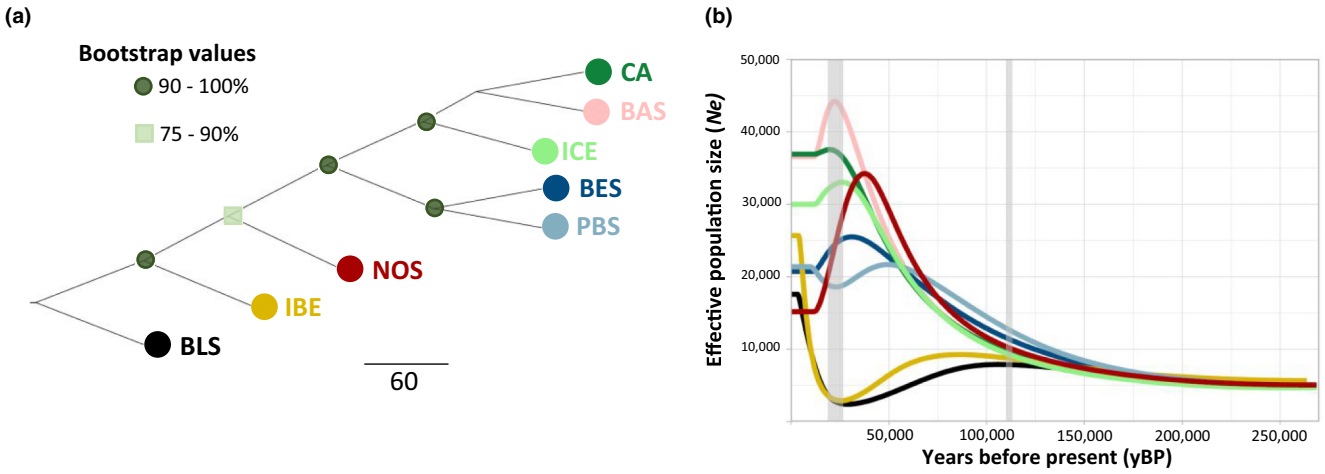

FIGURE 3 Historical relationships and demographic history of North Atlantic Harbour porpoises. (a) Maximum likelihood bifurcating tree inferred by *Treemix* showing the post-glacial colonization of Harbour porpoises. (b) Inferred changes on effective population size (Ne) through time with a mutation rate of 2.56×10^{-8} and a generation time of 11.9 years. The start of the last glacial period (110,000 yBP) and the last glacial maximum (26,500–19,000 yBP) are indicated in grey.

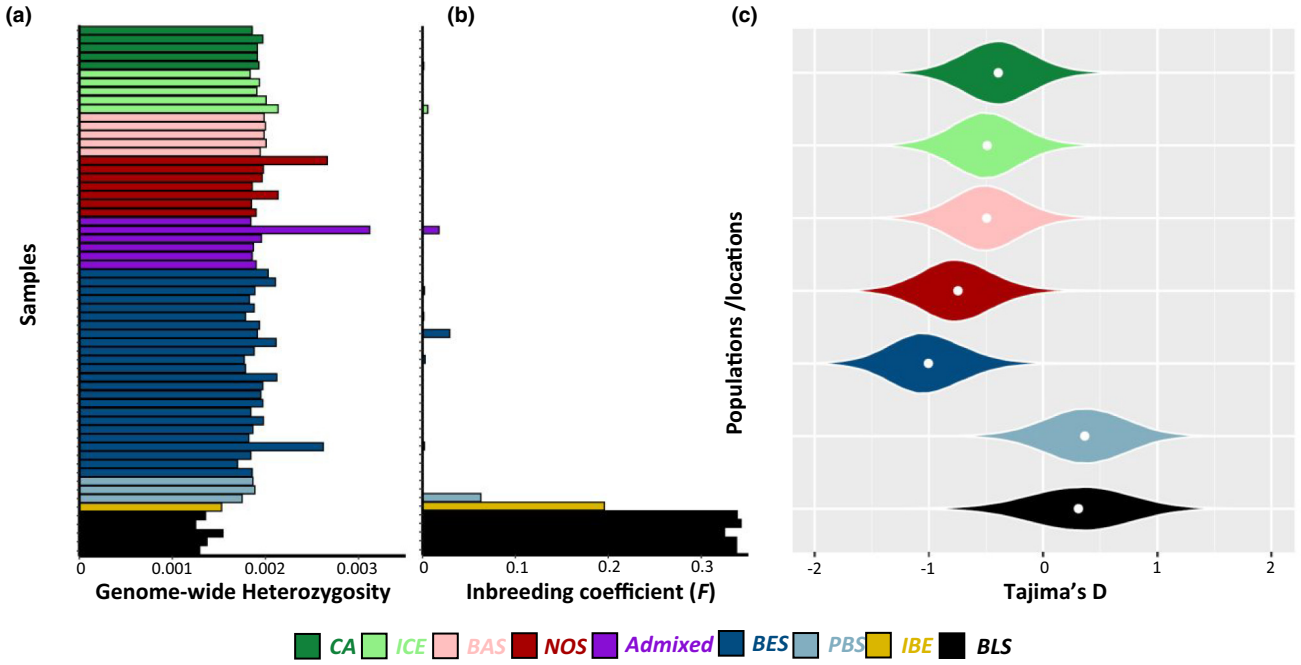

FIGURE 4 Population genomics summary statistics of North Atlantic Harbour porpoises. (a) Individual genome-wide heterozygosity, each sample is coloured according to its sampling locality, admixed BES–NOS individuals are coloured purple and migrants were not included. (b) Individual inbreeding coefficient for each sample. (c) Violin plots of Tajima's D values estimated at population/location level with a sliding window approach with window size of 50 kb and a step size of 10 kb; the white dot indicates the mean value across the 50 kb Windows. No Tajima's D was calculated for the Iberian subspecies due to small sample size ($n = 1$).

BES; Tukey test, all $p < .01$). Among *P.p. phocoena* populations, heterozygosity estimates were not statistically different. Individual inbreeding coefficients (*F*) were also significantly different among populations (ANOVA: $F_{[8;52]} = 894.7$; $p < .001$). They were higher in BLS porpoises (0.32–0.34; significantly different from all other populations; Tukey test, all $p < .001$), in the porpoise potentially belonging to *P.p.meridionalis* subspecies (~0.2; significantly different from all other populations; Tukey test, all $p < .001$) and in PBS porpoises (0–0.06; significantly different from BLS; IBE; BAS; BES; CA; NOS, Tukey test, all $p < .05$; ICE, Tukey test, $p = .071$) than in the Atlantic and Belt Sea populations, that presented inbreeding coefficients close to zero (Figure 4b). Regarding Watterson's theta estimates (Figure S5), the BLS and IBE subspecies as well as the PBS population exhibit low diversity, compared to the BES population and Atlantic locations. Tajima's D estimates (Figure 4c) were negative in all regions, except for the PBS population and the BLS subspecies, where they were positive. No Tajima's D was calculated for the Iberian individual, because of too low sample size ($n = 1$).

3.3 | Seascape genomics

Out of the 18 environmental predictors used in the GEAs (Table S2), forward selection analysis identified five variables significantly associated ($p = .001$) with genomic variation (Table S3): mean SST, mean SSS, minimum SCV, minimum SCA and minimum SPP. The five variables show a heterogeneous seascape in the North Atlantic (Figures S6–S10), especially a pronounced salinity gradient in the Baltic region (Figure S7). Forward selection analysis identified three *dbMEMs* that explained a significant proportion ($p < .05$) of the genomic variation and were used as the spatial variables. After checking for multicollinearity (Figure S11) and assessing the variance inflation factor (VIF), the five environmental variables were retained since they presented a $r < |0.7|$ and VIF <3. We removed one *dbMEM* in the data set including BLS, as it had a large VIF (5.8). In total, the RDA model comprised five environmental variables and two *dbMEMs* for the data set with BLS samples and the five environmental variables and three *dbMEMs* for the data set excluding BLS (Table S4).

In the data set without BLS, the overall RDA model was significant ($p = .001$), with the environmental variables explaining ~8% and the spatial variables ~5% of the genomic variation. In the RDA model, SSS, SST ($p < .001$) and SCV ($p = .023$) were significant, while on the pRDA only SSS ($p < .001$) and SCV ($p = .018$) were significant. By plotting both the RDA and pRDA (Figure 5; Figure S12), we observed that using spatial variables as a condition (pRDA) affected the pattern of the biplots, making the first axis less predominant. In the data set without BLS, RDA1 (Figure 5a) explained 28% of the variance while pRDA1 (Figure 5b) explained 22.7%. The RDA biplots show the variation in the genomic response to the different environmental variables among sampling locations in the North Atlantic. Both RDA1 and pRDA1 divided the Baltic samples from the rest, mostly based on SSS, while RDA2 and pRDA2 were moderately driven by SST and SCV (Figure 5). In the model including BLS porpoises, the five environmental variables were significant and explained 8.7% of

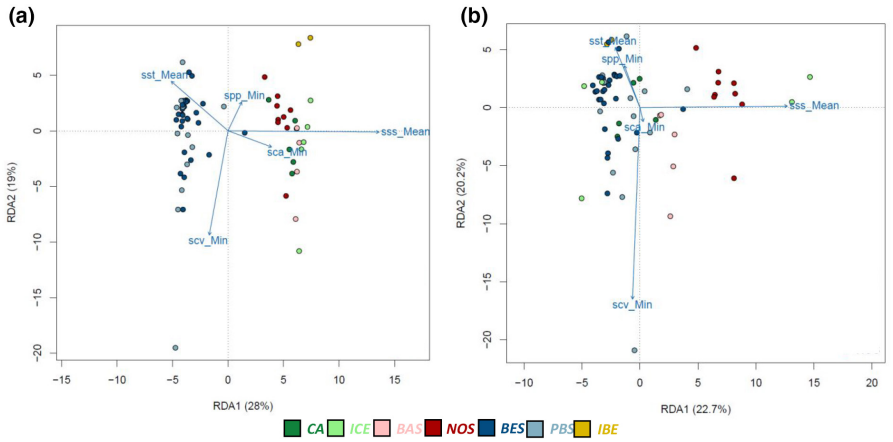

FIGURE 5 Genotype–environment association analysis between the five retained environmental variables and a set of 1,320,367 unlinked SNPs in North Atlantic Harbour porpoises, coloured by sampling locality. (a) RDA biplot of the data set without BLS samples; the overall model was significant ($p = .001$), the environmental variables explained 8.5% of the variance. SST, SSS and SCV were significant (b) pRDA biplot of the data set without BLS, the overall model was also significant ($p = .001$), the spatial and environmental variables explained ~5% and ~8% of the variance respectively. Sea surface salinity and sea current velocity were significant. sca_Min (minimum sea chlorophyll-A concentration), scv_Min (minimum sea current velocity), spp_Min (minimum sea primary productivity), sss_Mean (mean sea surface salinity), and sst_Mean (mean sea surface temperature).

TABLE 1 Analysis of variance (ANOVA) assessing the amount of genomic variation explained by the redundancy analysis (RDA) and partial redundancy analysis (pRDA) models (Black Sea samples excluded).

Variable	RDA	%variance explained RDA	pRDA	% variance explained pRDA	Overlap
SST	1083	19.4***	1351	19.4	154
SSS	1546	26***	1884	22.3***	271
SCV	1092	18.7*	1586	20.1*	141
SCA	2173	18	2617	19.1	222
SPP	1185	17.9	1834	19.1	164
Total	7079	100	9272	100	952

Note: Number of candidate SNPs identified with the RDA, pRDA, *Pcadapt* genome scan and overlapping between RDA, pRDA and the 18,955 outlier SNPs identified by Pcadapt. Percentage explained of each environmental variable and its significance is also shown.
*Significant ($p < .05$).; ***Highly significant ($p < .001$).

the variance, while the spatial variables explained 4.3% (Table S5). Both pRDA1 and RDA1 (Figure S12) separated BLS from the rest based on SST; pRDA2 and RDA2 (~22% variance explained) separated BES and PBS populations from the rest based on SSS.

The PCA loadings of *Pcadapt* (Figure S13c) showed that most of the p-values followed a uniform distribution, but there was an excess of small p-values, indicating the presence of outliers. Using the data set without BLS, *Pcadapt* identified 18,955 candidate SNPs, while the pRDA and RDA identified 9272 and 7079 candidate SNPs, respectively (Table 1). A set of 952 candidate SNPs overlapped in the pRDA, RDA and *Pcadapt*. The number of candidate SNPs inferred to be under selection on the data set with BLS are found in Table S5. Functional enrichment analysis found 13 GO terms significantly ($p < .05$) overrepresented in the putative environmentally adaptive data set compared to the whole genome (Table S6). We successfully mapped and annotated 202 of the 271 candidate SNPs associated with salinity, of which 106 were annotated to known genes. While 48 candidate SNPs had hits to only one gene, the other 58 candidate SNPs had equally good (very low e-value and high bit score) hits to multiple annotated genes (Table S7); thus, the latter candidate genes must be interpreted with caution.

3.4 | Neutral–adaptive population structure and genetic differentiation

Neutral and adaptive SNP data sets revealed a similar population structure (Figure 6; Figure S15). On the data set without BLS, both PCAs of the neutral (Figure 6a) and adaptive SNPs identified with *Pcadapt* (Figure 6b) separated the three North Atlantic populations, that is, Atlantic, BES and PBS. The only difference was that in the neutral set, the three PBS porpoises were separated by PC2 (1.87%) and in the adaptive set by PC1 (15.4%). As to the data set with BLS, the PCA with the set of neutral SNPs (Figure S14a) separated BLS individuals (PC1) and Baltic from Atlantic porpoises (PC2). The PCA inferred with the set of adaptive SNPs (Figure S14b) was however slightly different: PC1 also separated BLS porpoises from the rest, but PC2 divided the three PBS samples (light blue cluster in Figure 2) from the rest.

Genome-wide pairwise *Fst* levels on the neutral data set were moderately low (Figure 6c), ranging from 0 to 0.13. *Fst* levels on the adaptive data set were significantly higher (paired *t*-test; $p = .013$), ranging from 0 to 0.37. Among Atlantic sampling locations (CA, ICE, BAS and NOS), the adaptive data set presented slightly lower *Fst* values than the neutral data set. However, among Baltic (BES and

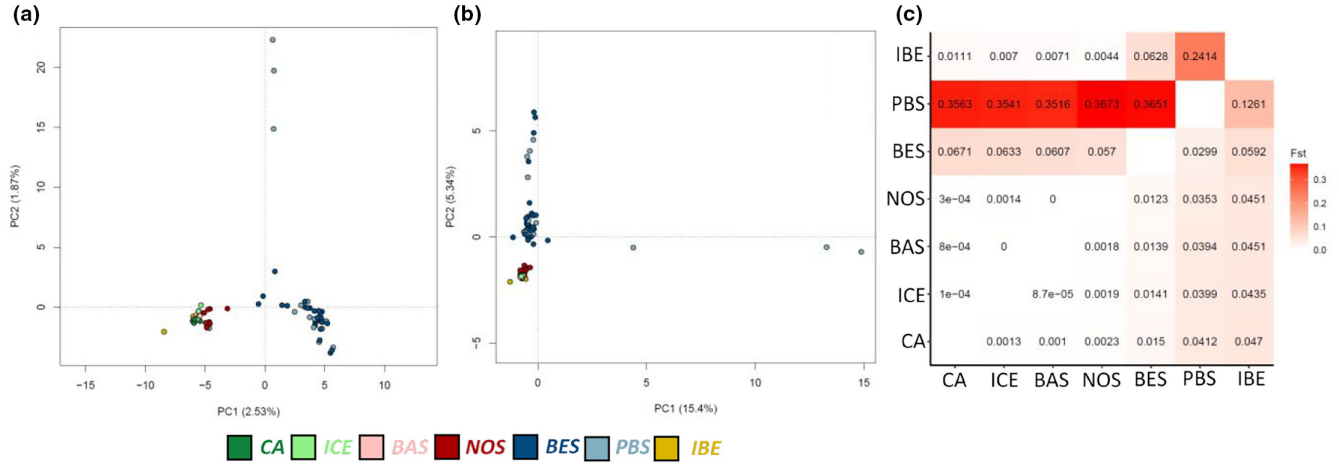

FIGURE 6 Genetic structure of neutral and inferred adaptive SNPs on the data set without BLS. (a) Neutral data set (1,231,060 SNPs). (b) Adaptive data set (18,955 SNPs). The three PBS specimens separated out in A and B are those assigned to be PBS population by the *NGSAdmix* and *PCAngsd* results. (c) Heatmap of mean pairwise-weighted Fst across sampling locations calculated with *vcftools*. Fst estimates using the adaptive set of SNPS (18,955) are on the upper left half of the matrix, while the estimates based on the neutral set (1,231,060) are on the lower right half below the diagonal.

PBS) populations and between Baltic and Atlantic locations, *Fst* was higher in the adaptive data set than in the neutral data set.

The redundancy analysis looking for spatial autocorrelation/isolation-by-distance was significant for the neutral data set (1.2 million SNPs; ANOVA: $F_{[3;63]} = 1.1379$; $p < .001$), and there was also a tendency towards significance for the adaptive data set (18,000 SNPs; ANOVA: $F_{[3;63]} = 1.3378$; $p = .069$).

4 | DISCUSSION

4.1 | Population structure and evolutionary history of Harbour porpoises in the North Atlantic and adjacent waters

Our results support previous population genetic studies based on microsatellites, mitochondrial control region and RAD sequencing data: We identified the separate Black Sea subspecies (*P.p relicta*), found panmixia in the Atlantic (Ben Chehida, Loughnane, et al., 2021; Ben Chehida, Stelwagen, et al., 2021; Fontaine et al., 2007, 2014) and identified a separate Belt Sea population (Lah et al., 2016; Wiemann et al., 2010). Additionally, although our sample size is limited—one and three individuals, respectively—our results point to the existence of the proposed Iberian subspecies (Fontaine et al., 2007, 2014) and a separate population in the Proper Baltic Sea (Lah et al., 2016; NAMMCO, 2019). On the one hand, PCA, admixture analysis (Figure 2) and Fst levels (Figure 6) show that CA, ICE, BAS and NOS porpoises belong to the same population, the so-called Atlantic population. On the other hand, BES and PBS porpoises clustered separately. Between NOS and BES, there is some gene flow (as indicated by partial assignments to the two respective clusters for some specimens; dark blue and red in Figure 2b,d and Figure S4c). Three very distinct individuals from the PBS region stand out in the genetic structure analysis (Figures 2 and 6; Figure S4), which we assigned to the PBS population. This third Baltic cluster was interpreted as the Proper Baltic Sea population for a series of reasons: First, this cluster only includes porpoises of the PBS region (Figures 2 and 6; Figure S4); second, the three porpoises assigned to the PBS population were bycaught in the breeding season, when a separation between putative BES and PBS porpoises occurs (Carlén et al., 2018); third, these three porpoises were bycaught in the easternmost locations (16–18.58 W) and in areas known to be important for the PBS population (Carlén & Evans, 2020): one in the Gdansk Bay and the other two in the waters surrounding the Swedish island of Öland (Figure S4d). These waters present the greatest densities of Harbour porpoises during the breeding season in the PBS region (Amundin et al., 2022) and have been reported as potentially important breeding grounds for the PBS population. PCA results (Figure 2a,c) also show that one Iberian sample (No-2) does not cluster with the Black Sea nor with the Atlantic subspecies. Admixture results group this sample with the Atlantic cluster, possibly since *NGSAdmix* does not create a new cluster for only one sample. Nevertheless, while no other sample had any Black Sea ancestry, this sample had a 10% membership to the Black Sea cluster, further suggesting its distinct evolutionary trajectory. More samples from the Iberian/Mauritanian waters should be resequenced to categorically identify these porpoises as a distinct subspecies.

The result indicating lack of genetic structure over long distances in the open Atlantic is at odds with the fine-scale population structure we observe in the Baltic region. In an area separated by less than ~700 kilometres, we identified three distinct populations (Figure S4d): Atlantic population in the Skagerrak strait, Belt Sea population in the Danish Belts, the Sound and Arkona basin and the Proper Baltic population in the Baltic proper. Our redundancy analysis on neutral SNPS unravelled a weak but significant IBD pattern across the North Atlantic, as had been previously detected (Ben Chehida,

Loughnane, et al., 2021; Ben Chehida, Stelwagen, et al., 2021; Fontaine et al., 2007). This pattern was much less pronounced (below the level of significance) when the adaptive SNP data set was analysed. Hence, the adaptive data set reveals higher population differentiation (in terms of Fst), but is less impacted by IBD, highlighting that geographical distance is not the major driver of the genetic differences found among Harbour porpoises in the North Atlantic and its adjacent waters.

The demographic history analysis shows that North Atlantic Harbour porpoises have been strongly influenced by Pleistocene glaciations, especially since the onset of the Last Glacial Period (LGP) ~115,000 yBP, when multiple rapid climate fluctuations occurred until the end of the Last Glacial Maximum (LGM), ~19,000 yBP (Kindler et al., 2014). The N_e of the Harbour porpoise subspecies were highly correlated until the onset of the LGP (~115,000 yBP) when the Black Sea and potential Iberian subspecies curves split from the North Atlantic subspecies. Our divergence estimate differs from that of previous studies using a portion of the mitogenome (Fontaine et al., 2014) that dated the most recent common ancestor of North Atlantic subspecies during the LGM. Similar differences in divergence estimates have been reported before in the finless porpoise, when a study using mitochondrial control region data (Wang et al., 2008) inferred a much younger divergence than a study using whole-genome resequencing data (Zhou et al., 2018). Further studies focusing on the entire mitogenome of harbour porpoises should determine whether the difference in divergence estimates is real. The Black Sea and potential Iberian subspecies originated from the ancestral North Atlantic population when a small group of individuals may have colonized the Mediterranean and Black Sea after the LGP, which left an imprint in the genome as a founder effect. Both subspecies had low N_e (Figure 3b), which increased sensitivity to genetic drift which in turn leads to loss of genetic variation, high inbreeding levels (Figure 4a; Figure S5) and a positive Tajima's D (Figure 4c). The N_e curves of the *P.p. phocoena* populations started to diverge around ~50,000 yBP, which roughly coincides with two rapid climate fluctuations during that same period (Kindler et al., 2014). This may suggest that BES and PBS populations diverged from the Atlantic population during an interglacial period before the formation of the Baltic Sea at the end of the LGM. After the LGM, the N_e of the PBS population was inferred to increase. This would be compatible with a scenario in which—as the ice sheets retreated from northern regions at the end of LGM—a group of porpoises colonized the newly formed Baltic Sea (~10,000–15,000 yBP), founding the modern PBS population. To take into account that the number of assigned individuals to each population/subspecies is unbalanced and the absolute sample size is small for some populations (IBE, PBS), we repeated the SMC++ analysis choosing randomly three individuals per population/subspecies (Figure S15). The population's specific *Ne* curves' pattern and the inferred split of populations did not change significantly. Previous studies indeed indicated that small sample sizes do not strongly impact genetic estimates in population studies using large numbers of SNPs (Nazareno et al., 2017). However, except for the Black Sea population, the more recent N_e estimates were not very precise (Figure S16), a pattern also observed in other studies applying SMC++ (Chiang et al., 2018) or similar software (Kardos et al., 2023). Presumably, other processes like gene flow and linked selection could be confounding factors in the SMC++ demographic inferences (Mazet et al., 2016; Schrider et al., 2016); thus, these results must be interpreted with caution and time/N_e estimates should not be taken literally.

The maximum likelihood tree inferred with *Treemix* is also compatible with the existence of three subspecies in the North Atlantic and adjacent waters. Previous phylogenies reconstructed with mitochondrial DNA data (Rosel et al., 1999) found that BLS porpoises are a sister group to the North Atlantic population; thus, we were confident rooting our tree with the BLS subspecies. The first split in our graphical representation of historical relationships among North Atlantic Harbour porpoises was the IBE subspecies from the North Atlantic subspecies. Among the North Atlantic subspecies, *Treemix* analysis placed present-day NOS Harbour porpoises as basal, compatible with a northward post-glacial expansion from a southern refugium. As the ice sheets retreated, the ancestral North Atlantic subspecies may have started to colonize novel environments in the Baltic, Iceland, Barents Sea and Canadian waters.

4.2 | Local adaptation of Baltic porpoises to low salinity levels

Species and populations inhabiting highly divergent environments are expected to be under different selective pressures, which could cause each local population to evolve traits that provide an advantage under its local environmental conditions (Kawecki & Ebert, 2004). However, the role of ecological specialization on population differentiation and speciation remains poorly understood (Savolainen et al., 2013). This is particularly true for cetacean species, with only a few recent studies attempting to address the genetic basis of local adaptation with population level data (Barceló et al., 2022; de Greef et al., 2022; Louis et al., 2021; Pratt et al., 2022; Zhou et al., 2018). Ecologically and geographically marginal environments often host populations at the edge of the species distribution and under extreme selection regimes (Johannesson & André, 2006). Examples of such populations are the Belt Sea and Proper Baltic Sea Harbour porpoise populations that occur in the peripheral waters of the Baltic Sea, separated from the North Sea by a pronounced salinity gradient.

The genotype–environment association analyses show that including BLS samples in the RDA had a major impact on the outcome of the analysis, especially on the number of putative SNPs inferred to be under selection. The genomic variation of BLS porpoises was highly associated with high temperature (Figure S12), with ~6000 SNPs correlated with SST and only a few associated with the other variables (Table S5). As water temperatures in the Black Sea are significantly higher than in the rest of the locations (Figure S6) and BLS porpoises are highly divergent, we could not discern whether these ~6600 SNPs were indeed associated with temperature or were rather very distinct

for different evolutionary pressures or pronounced genetic drift in BLS porpoises. Thus, to identify candidate genes associated with environmental variables, we focused on the data set without BLS, where the population divergence was not as strong.

Our functional enrichment analysis on the genes containing SNPs significantly associated with environmental variables revealed several overrepresented gene ontology (GO) terms, among them 'transcription factor activity', pointing towards differential gene expression potentially playing a role in porpoises' local adaptation. Indeed, heritable changes in gene expression are discussed as a potential mechanism underlying rapid adaptation to changed environmental conditions (e.g., Hamann et al., 2021).

Our seascape genomics analysis provides statistical support for an influence of salinity on population differentiation in the Baltic Sea (Figure 5; Figure S12). SSS was highly significant in both RDA and pRDA, while SST was significant only in the RDA. The salinity gradient could have contributed to the origin of a soft barrier between the Atlantic and the Baltic, leading to adaptive divergence in BES and PBS porpoises. From 272 inferred candidate SNPs, we annotated 105 genes potentially associated with the salinity gradient in the Baltic Sea (Table S7). Among the 105 genes, we identified eight solute carrier group (SLC) genes, a group of ion transport proteins that have been previously identified as relevant in the adaptation to a freshwater lifestyle in cetacean species, like the finless porpoise (Ruan et al., 2015; Zhou et al., 2018) and the baiji (Zhou et al., 2013) in the Yangtze river. Particularly interesting were the *SLC10A1* gene, a sodium ion transport with a critical role in the osmoregulation of bile acids in the liver (Kubitz & Häussinger, 2007), and *SLC5A3*, a gene that encodes a sodium transporter (*SMIT1*) which is involved in the response to hypertonic stimuli (Barrese et al., 2020; Dai et al., 2016). Another relevant candidate gene is *TMEM72*, annotated from the SNP with the highest NOS-BES-PBS *Fst* value (0.7), which encodes a transmembrane protein involved in kidney development (Ding et al., 2022).

4.3 | Implication on species conservation and future perspectives

The ongoing biodiversity crisis is impacting many organisms across the tree of life, and cetaceans are no exception. From the 134 cetacean species, subspecies or populations assessed by the International Union for Conservation of Nature (IUCN), only 51 are considered of least concern, while 24 are considered critically endangered and 25 are classified as endangered (https://iucn-csg.org/status-of-the-worlds-cetaceans/). In this study, we have analysed whole-genome sequencing data of a critically endangered population, the Proper Baltic Sea Harbour porpoise, and an endangered subspecies, the Black Sea Harbour porpoise.

We identified high levels of inbreeding in the proposed Iberian subspecies, as well as low genetic diversity and N_e compared with the North Atlantic subspecies. Abundance surveys have estimated the Iberian population to ~2900 animals and have presented one of the lowest population densities on the European continental shelf (Hammond et al., 2013). Previous studies have reported gene flow from Iberia to more northern regions, but not from the North Atlantic subspecies to Iberian porpoises (Ben Chehida, Loughnane, et al., 2021; Ben Chehida, Stelwagen, et al., 2021). Therefore, following propositions of previous authors (Fontaine, 2016; Fontaine et al., 2014), we confirm the distinctiveness of Iberian porpoises which may warrant subspecies status. Notwithstanding these taxonomic considerations, measures to guarantee the survival of Harbour porpoises in Iberian waters are needed. Similarly, Black Sea porpoises presented high levels of inbreeding, low genetic diversity and N_e, which imply that Black Sea porpoises are subject to demographic stochasticity due to strong genetic drift (Palstra & Ruzzante, 2008). Although there are no reliable estimates of current population size across the entire Black Sea, Harbour porpoise mortality in the Black Sea is high, with thousands of animals each year incidentally bycaught (Birkun & Frantzis, 2008). In addition, Harbour porpoises and other cetaceans in the Black Sea are highly affected by activities related to fossil fuels extraction, construction work (such as the Kerch Bridge), underwater explosions and different sources of pollution (Carlén et al., 2021). Thus, explicit management policies must be implemented to protect Black Sea Harbour porpoises.

Within the Baltic Sea, our results provide genomic evidence that there is a distinct Proper Baltic Sea population (light blue cluster in Figure 2; Figure S4) and, given the poor status of the population, urgent measures to protect the species must be implemented (Carlén et al., 2021). Previous studies have shown that microsatellite data do not yield enough statistical power to identify the fine population structure of the Harbour porpoise in Baltic waters (Lah et al., 2016; Wiemann et al., 2010). Thus, our results highlight that whole-genome resequencing is a powerful tool to unravel even the most subtle population structure. Moreover, whole-genome resequencing enables to identify adaptive genetic variation related to local environments. Preserving this variation can be crucial for the conservation of endangered local populations.

For the recovery of the Proper Baltic Sea population, a management plan has already been erected and adopted by the Baltic countries in the course of the Agreement on the Conservation of Small Cetaceans of the Baltic, North East Atlantic, Irish and North Seas (ASCOBANS, 'Jastarnia' plan; Carlén & Evans, 2020). The population has been ranked 'critically endangered' by the International Union for Conservation of Nature (IUCN, Hammond et al., 2016) and by the Baltic Marine Environment Protection Commission (Helsinki Commission, HELCOM, 2019). Information from this study will be used to inform the next update of the IUCN population status (Owen, pers. comm.). As a complication for these conservation efforts, the Proper Baltic population is known to seasonally admix with the Belt Sea population and there has been so far no criterion by which single specimens could be assigned to their respective population of origin. Here, we present for the first time genomic evidence allowing individuals to be assigned to the Proper Baltic population of Harbour porpoise. Based on these genomic resources, we discovered highly informative SNPs that differentiate the three populations occurring in Baltic waters and which could be used to design a small SNP

panel to genotype thousands of samples at a moderate price. Such an approach has been previously implemented in plants (Nygaard et al., 2022), terrestrial (von Thaden et al., 2017) and marine species (Jenkins et al., 2019). With such a panel, bycaught and stranded Harbour porpoises could be genotyped and assigned to populations to monitor the conservation status of Baltic porpoise populations. There has been an increased detection rate of porpoises in the Baltic proper in recent years (Owen et al., 2021). With our novel informative SNPs, it will be possible to discern whether this is a sign of recovery of the endangered PBS population or caused by seasonal immigration of Belt Sea porpoises.

AUTHOR CONTRIBUTIONS

E.C. and R.T. designed the study; M.A. assisted with bioinformatic analysis; R.T. provided funding; A.R., I.P., M.Q., U.L., H.B., U.S., C.L., P.B., A.Ö., B.Ö. and V.L. provided samples and associated biological information; E.C. performed laboratory work, executed bioinformatic analyses and analysed the data; E.C. and R.T. interpreted the results, E.C. wrote the draft manuscript with input from R.T and M.A. All authors edited and approved the final manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicting interests.

DATA AVAILABILITY STATEMENT

Raw sequencing reads can be found at the NCBI database under the BioProject PRJNA997110. Genotype likelihoods and genotype files can be found in Dryad public repository (doi:10.5061/dryad.4qrfj6qg6). Table S1 shows sample biological information and Table S4 the environmental data associated with each sample.

BENEFIT-SHARING STATEMENT

Benefits generated: A research collaboration was developed with scientists of North Atlantic countries providing genetic samples, all collaborators are included as co-authors, the results of research have been shared with the provider communities and the broader scientific community (see above), and the research addresses a priority concern, in this case the conservation of Harbour porpoises in North Atlantic waters and especially the critically endangered Proper Baltic Sea populations and the endangered Black Sea subspecies. More broadly, our group is committed to international scientific partnerships, as well as institutional capacity building.

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