Manuscript, August 2023

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Heterogeneous microgeographic genetic structure of the common cockle (*Cerastoderma edule*) in the Northeast Atlantic Ocean: biogeographic barriers and environmental factors

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Running title: Fine-scale genetic structuring of common cockle

Word count (excluding references, tables and figures): 6,834

Abstract

Knowledge of genetic structure at the finest level is essential for conservation of genetic resources. Despite no visible barriers limiting gene flow, significant genetic structure has been shown in marine species. The common cockle (*Cerastoderma edule*) is a bivalve of great commercial and ecological value inhabiting the Northeast Atlantic Ocean. Previous population genomics studies demonstrated significant structure both across the Northeast Atlantic, but also within small geographic areas, highlighting the need to investigate fine-scale structuring. Here, we analysed two geographic areas that could represent opposite models of structure for the species: 1) the SW British Isles region, highly fragmented due to biogeographic barriers, and 2) Galicia (NW Spain), a putative homogeneous region. 9,250 SNPs genotyped by 2b-RAD on 599 individuals from 22 natural beds were used for the analysis. The entire SNP dataset mostly confirmed previous observations related to genetic diversity and differentiation, however, neutral and divergent SNP outlier datasets enabled disentangling physical barriers from abiotic environmental factors structuring both regions. While Galicia showed a homogeneous structure, the SW British Isles region was split into four reliable genetic regions related to oceanographic features and abiotic factors, such as sea surface salinity and temperature. The information gathered supports specific management policies of cockle resources in SW British and Galician regions also considering their particular socio-economic characteristics; further, these new data will be added to those recently reported in the Northeast Atlantic to define sustainable management actions across the whole distribution range of the species.

Introduction

Knowledge of genetic diversity distribution is crucial for the sustainable management and conservation of natural resources (Leary et al. 2009; Sa-Pinto et al. 2012). This distribution is affected by larval connectivity, demographic parameters and selective processes operating on species populations. Scarcity of physical barriers in marine environments is expected to promote higher connectivity among populations in comparison to terrestrial species (Waples 1998). Moreover, marine species usually show large population sizes, which along with pelagic larval stages, often lasting several weeks, facilitate population genetic homogenization across wide regions (Sa-Pinto et al. 2012; do Prado et al. 2018). Despite these general features, genetic studies on marine organisms have frequently detected genetic differentiation, even at local scales (i.e., below the geographic scale of effective dispersal of the species studied, known as chaotic genetic patchiness (CGP); see Eldon et al. 2016), which can be explained by historical and reproductive/demographic factors (e.g. high fecundity and high mortality in early life stages, sweepstakes reproductive success; see Parrondo et al. 2022), natural selection associated with environmental conditions (Vilas et al. 2015; do Prado et al. 2018; Vera et al. 2019) and oceanic features such as residual currents, bathymetry, coastline shape, upwelling, fronts, gyres and eddies (Vera et al. 2016; Coscia et al. 2020; Handal et al. 2020; Fisher et al. 2022; Vera et al. 2022).

Different types of ocean fronts have been described across the Northeast Atlantic region, encompassing tidal mixing fronts, shelf break fronts, and freshwater fronts separating estuarine freshwater and higher salinity coastal waters (Sharples and Simpson 2019). Examples of these frontal systems on the NW European Shelf include the Celtic Sea Front (NE Celtic Sea), the Irish Sea Front (NW Irish Sea), the Alderney Race (with one of the strongest current in Europe) and the Ushant Front (W English Channel) (Suberg et al. 2019). These fronts may influence genetic structure acting as barriers to cross-front planktonic dispersal and as conduits through along-front dispersal by frontal jets, with important influences on the pelagic distribution of larvae of marine species (Galarza et al. 2009). Biogeographical barriers can also limit dispersal in marine environments. In the Northeast Atlantic region, Cape Finisterre, the Cornwall Peninsula, the tip of Brittany, the Llyn Peninsula, and the Alderney race along Cotentin Peninsula have been identified as potential barriers to the connectivity of marine organisms due to their oceanographic features, including fish (Abaunza et al. 2008; Larmuseau et al. 2009) and molluscs (Dupont et al. 2007; Piñeira et al. 2008; Martinez et al. 2015; Handal et al. 2020; Vera et al. 2022).

The common cockle, *Cerastoderma edule*, is a bivalve mollusc naturally distributed throughout the Northeast Atlantic coast, from Senegal, West Africa, to Norway, northern Europe, where it inhabits on intertidal and shallow subtidal soft sediments (Hayward and Ryland 1995). The species is commercially exploited and provides a wealth of services to coastal communities mainly in Ireland, United Kingdom, France, Spain and Portugal, where it is harvested (Flach and de Bruin 1994; Carss et al. 2020; Jackson-Bue et al. 2022). Cockle harvest has been reduced since the 1980s (> 100,000 tonnes) to nowadays (~ 25,000 tonnes in 2019) due to changes in fisheries policies, overfishing, variable recruitment and mass mortalities produced by pollution, climate events and parasites (Villalba et al. 2014; Mahony et al. 2020; Pampin et al. 2023). Furthermore, cockles are considered keystone for ecosystem due to their role as reef engineers, agents of carbon sequestration and their linking between primary producers and higher trophic levels (Norris et al. 1998; Carss et al. 2020). The species is dioecious and can live up to 10 years displaying fast sexual maturation (reached in the first year of life) and high fecundity (Honkoop and van der Meer 1998). The reproductive period occurs from April to August (Malham et al. 2012), but it can be extended to September in more southern European countries such as Portugal (Mahony et al. 2021), and planktonic larvae can remain in the water column for 30 days facilitating widespread dispersal (de Montaudouin et al. 2003; Dare et al. 2004).

Genetic studies throughout the natural cockle's distribution have identified three main population genetic units: i) a southern group encompassing the Atlantic coast from Morocco to the Bay of Biscay; ii) a central group comprising of the Celtic and Irish Seas, the English Channel and the southern North Sea; and iii) a northern group consisting of the northern North Sea (Beaumont et al. 1980; Hummel et al. 1994; Martínez et al. 2013; 2015). These results have been recently confirmed by Vera et al. (2022) through a wide genome scan (~10,000 single nucleotide polymorphisms, SNPs), but additionally enabled identifying substructure within the main genetic groups using outlier loci under divergent selection, mostly in accordance with residual current patterns and environmental variables.

However, due to the limited number of markers and/or the scale of sample collection, a comprehensive picture of population connectivity in the common cockle is still incomplete. Information at the microgeographic level, always considering the dispersal capacity of the species (Eldon et al. 2016; Vera et al. 2022), is relevant for the management of fisheries (Bernatchez et al. 2017). Using a wide SNP genomic screening, Coscia et al. (2020) identified three genetic clusters (global F_{ST} = 0.021) of cockles in the Celtic and Irish seas and that could be associated with residual ocean currents, salinity and geographical proximity using information on larval dispersal.

This study aimed to analyse the genetic structure of the common cockle at a microgeographic scale using 2b Restriction Associated DNA sequencing (2b-RADseq). Two regions were investigated: (1) the SW British Isles and the English Channel, characterised by putative habitat fragmentation due to tidal mixing fronts and biogeographical barriers; and (2) the Northwest coast of Spain (Galicia), representing a quite homogeneous region according to previous information on other mollusc species

(Diz and Presa 2009; Vera et al. 2016). The results confirmed the significant differentiation of cockles' populations at microgeographic scale, but also the power of larval dispersal to homogenize rather wide coastal areas, thus providing essential information for proper management of this valuable resource.

Material and methods

Sample area and oceanography

Two geographic areas along the Northeast Atlantic coast were investigated (Fig. 1). The first was focused on the British Isles and English Channel (hereafter called the SW British Isles region), where previous, though incomplete information, supported significant genetic sub-structuring (e.g. Coscia et al. 2020; Vera et al. 2022). The second area was Galicia (Northwest Spain), which may be genetically homogeneous according to information in other mollusc species (Diz and Presa 2009; Vera et al. 2016).

Over the cockle reproductive season (May to September; Mahony et al. 2020), the coastline of Galicia is characterised by wind-driven upwelling of cold waters resulting in sea surface temperatures (SSTs) that are several degrees colder than off-shore SSTs (Supplementary Fig. 1b). Also driven by the predominantly northerly winds in the summer months, the Portugal coastal current transports waters southwards along the coastline of Iberia (Teles-Machado et al. 2016) with residual current strengths along the Galician coastline exceeding 0.15 m/s (Supplementary Fig. 1d). The SW British Isles region is divided into distinct oceanographic regions (the English Channel, the Celtic Deep, the Celtic Sea and the Irish Sea) by diverging current or seasonal frontal systems (Galparsoro et al. 2014). Several tidal mixing fronts separate seasonally stratified and mixed waters (Supplementary Fig. 1a): the Ushant Front (Group "Grepma", 1988), the Celtic Sea Front, and the Irish Sea Front (Simpson and Pingree, 1978). The Celtic Sea is characterised by northward flow along the western coast of Cornwall which merges into the Celtic Sea Front jet and links into the Irish Coastal Current which transports water clockwise along the south and west coast of Ireland (Supplementary Fig. 1c; Brown et al. 2003; Fernand et al. 2006). Northward currents along the Ushant Front link the Amorican Shelf with the Celtic Sea. The southern English Channel coast is dominated by northeastward flow, with the strongest currents occurring around the Cotentin Peninsula.

Sample collection

A total of 374 cockles from 14 wild natural beds were collected across the aforementioned two regions in the period 2017-2020 and stored in 100% ethanol for analyses (Table 1). Additionally, 231 cockles from eight beds previously analysed (Vera et al. 2022: identified as IDA_18, IDC_18, WDE_17, WBY_17, FBS_17, FAR_17, SNO_17 and SLO_17, where 17 and 18 in the codes represent 2017 and 2018, respectively) were included in the analysis to achieve a comprehensive picture of the areas studied, thus providing an overall total of 605 cockles. To avoid generation overlapping, all samples belonged to the 0+ year age class of their sampling year. No temporal replicates were included considering the temporal genetic stability previously reported by Vera et al. (2022).

Single Nucleotide Polymorphism (SNP) genotyping

Total DNA was extracted from gills using the E.Z.N.A. E-96 mollusc DNA kit (OMEGA Bio-tek), following manufacturer recommendations. 2b-RAD libraries (~ 90 cockles per run) were constructed using the AlfI IIb restriction enzyme and sequenced in an Illumina NextSeq 500 platform following Maroso et al. (2018; 2019). Bowtie 1.1.2 (Langmead et al. 2009) was used to align reads to the cockle's genome (Bruzos et al. 2022) allowing a maximum of three mismatches and a unique valid alignment (-v 3 -m 1). The reference-based mode with default parameters in the gstacks module of STACKS 2.0 (Catchen et al. 2013) was used for SNP calling. For genotyping, SNPs were filtered following Vera et al. (2022): *i*) SNPs genotyped in > 60% individuals; *ii*) MAC (minimum allele count) ≥ 3; iii) conformance to Hardy-Weinberg expectations (i.e. SNPs with significant F_{IS} values ($P < 0.05$) in at least 25% of the populations were removed); and *iv*) the most polymorphic SNP within each RAD-tag was retained. Individuals with less than 250,000 reads were discarded.

Genetic diversity and population structure

Estimates of genetic diversity (i.e. mean number of alleles per locus (Na), observed (Ho) and expected (He) heterozygosity, proportion of polymorphic loci), departure from Hardy–Weinberg equilibrium (HWE) and inbreeding coefficients (F_{IS}) were estimated using GENEPOP v4.0 (Rousset 2008) and ARLEQUIN v3.5 (Excoffier and Lischer 2010). Because a minimum allele frequency (MAF) filtering was not applied, ARLEQUIN was also used to estimate Ho, He and F_{IS} exclusively with polymorphic loci (Minimum Allele Frequency (MAF) > 0.017 according to sample size) for comparison with previous studies.

Global and pairwise coefficients of population differentiation (F_{ST}) between cockle beds were calculated with ARLEQUIN v3.5 using 10,000 permutations to test for significance. The variational Bayesian clustering method implemented in the package fastSTRUCTURE v2.3.4 (Raj et al. 2014) was used to estimate the number of genetic population units (K) in the whole studied area and in each region testing from K = 1 to K = number of beds + 1, with an admixture ancestry model, convergence criterion of 1×10^{-8}, five cross-validated sets and the simple prior (flat-beta prior). The most likely number of K was estimated using the "chooseK.py" program included in the fastSTRUCTURE which gives the best K value and the K corresponding with weak population structure in the data using heuristic scores. Summarised outputs were carried out using the software POPHELPER (Francis 2017). Discriminant analyses of principal components (DAPC) were run in ADEGENET package (Jombart et al. 2010; Jombart and Ahmed 2011) for the R platform (R Development Core Team, 2014; http://www.r-project.org) with the whole dataset and for each region. Data were transformed using PCA (Principal Component Analysis) and the optimal number of principal components (PC) was calculated using the optim.a.score() command (see Miller et al. 2020). Isolation by distance (IBD) was checked by the correlation between geographical (measured as the shortest oceanic distance between two beds in Km) and genetic distance (measured as $F_{ST}/1-F_{ST}$; Rousset 1997) matrices using a Mantel test with 10,000 permutations using NTSYS v.2.1 (Rohlf 1993).

Outlier tests

The Bayesian F_{ST} –based method implemented in BAYESCAN v2.1 (Foll and Gaggiotti 2008) was used to identify outlier loci subjected to selection. BAYESCAN was run using default parameters (i.e. 20 pilot runs; prior odds value of 10; 100,000 iterations; burn-in of 50,000 iterations and a sample size of 5,000, hereafter "BY10"), but we also explored increasing prior odds value to 1000 (hereafter "BY1000"). Despite high prior odds tend to remove false positives, they also reduce the power for detection loci under selection (Foll 2012). Loci with a False Discovery Rate (FDR, q-value) < 0.05 were considered as outliers. Moreover, the principal components-based method implemented in R package PCADAPT v4.0 (Luu et al. 2017; Prive et al. 2020) was also applied. This method renders low false-positive rates and uses individual information, not requiring *a priori* population assignment. For the analysis, the number of principal components (PC) retained was performed with the "chooseK" option. The outlier identification was carried out with an FDR < 0.05. We considered as outliers those loci identified by any of the two approaches, but additionally those shared between all approaches as the most confident ones.

Seascape analyses

Effects of spatial (latitude and longitude) and relevant abiotic factors in coastal and marine environments (sea surface temperature (SST, ºC); sea bottom temperature (SBT, ºC); sea surface salinity (SSS, psu); sea bottom salinity (SBS, psu); bottom shear stress (BSS, $N \cdot m^{-2}$); net primary productivity (NPP, $mg \cdot m^{-3} \cdot day^{-1}$); see Coscia et al. 2020 and Vera et al. 2022) shaping genetic differentiation across beds in the studied areas were assessed using a canonical redundancy analysis (RDA) implemented in the VEGAN software (Oksanen 2015) in R. This abiotic information was retrieved as monthly averages from the IBI_REANALYSIS_PHYS_005_002 ocean reanalysis model (https://resources.marine.copernicus.eu/?option=com_csw&task=results?option=com_csw&view=details&product_id=IBI_REANALYSIS_PHYS_005_002") and IBI_REANALYSIS_BIO_005_003 model (https://resources.marine.copernicus.eu/?option=com_csw&task=results?option=com_csw&view=details&product_id=IBI_REANALYSIS_BIO_005_003) for the period 2014-2018 (Supplementary Table 1), respectively. The nearest model cell classified as ocean was selected to extract the data (average distance between the sampling location and centre of the nearest model grid cell edge = 11.6 km). Then, averages for the spawning season (i.e., from April to September, see Malham et al. 2012; Mahony et al. 2020), winter (i.e., from January to March) and summer (i.e., from July to September), were calculated for each bed. Allele frequencies were calculated for each bed with ADEGENET package using the “makefreq” option. Loci with missing values were removed from the analysis. The significance of the variance associated to the different variables was tested with 1,000 random permutations. Variance inflation factor (VIF) was estimated to explore collinearity (correlation) between seascape variables in the dataset, with VIF values > 10 suggesting important collinearity problems (Marquardt, 1970). The selection model was performed using automatic stepwise model building algorithm based on permutation p-values tests. This procedure was performed with the *ordistep* function included in VEGAN. The reduced panel of explanatory variables was used to recalculate the total proportion of genetic variation in the variance partitioning. The weight of the different loci on the significant environmental vectors was calculated using VEGAN. All these analyses were performed separately for the whole, neutral and divergent outlier SNP datasets in the regions studied.

Potential correlations between allele frequencies and seascape variables were investigated with BAYENV2 (Coop et al. 2010; Gunther and Coop 2013) and results were compared with the mentioned RDA analyses. The method implemented in this software allows controlling the neutral genetic structure, because the fit improvement for a given genetic variant between a model including the environmental factor and a model including only neutral genetic structure is tested (Rellstab et al. 2015). BAYENV2 was carried out using the whole SNP datasets from SW British Isles and Galicia, respectively. First, analyses were performed with 100,000 iterations across five independent runs to obtain the average covariance matrix for each subset. Secondly, the correlation between each SNP and the different variables was calculated using 100,000 iterations to obtain Bayes factors (BF). As in the previous step, five independent runs were used. Only SNPs with a BF > 10 and Spearman's coefficient (rho, ρ) thresholds > 1% for any variable in all runs were considered as a well-supported environment-associated SNPs. Finally, significantly correlated SNPs were compared with the outliers identified in the BAYESCAN and PCADAPT analyses.

Gene mining and functional enrichment

RAD-tags including divergent outlier SNPs were mapped in the *C. edule* genome (Bruzos et al. 2022) and their position compared with the consistent genomic windows under divergent selection previously reported by Vera et al. (2022) in the Northeast Atlantic Ocean. The very low genetic differentiation with neutral markers in the studied areas precluded the detection of consistent genomic regions under stabilizing selection. Thus, we could verify in more restricted geographical scenarios (SW British Isles and Galicia) the consistency of the genomic regions under divergent selection previously detected. Additionally, we looked for new regions under selection considering the singularity of the new sample collections of this study following a similar methodology to that proposed by Vera et al. (2022). Briefly, we defined a consistent window when ≥ 2 consecutive outliers were detected; then, we expanded the region ± 250 kb from the external outliers of the seed to define a genomic window for mining. Genes included in those genomic windows were identified using the cockle's transcriptome assembled and annotated by Pardo et al. (2022), which was used as reference to detect Gene Ontology (GO) functional enrichment of the genomic regions under selection (FDR 5%) using GOfuncR (Grote 2022). Furthermore, we also analysed genomic windows around the SNPs correlated with environmental variables for mining; since we could not identify consecutive SNPs as with outliers, we were more conservative and defined smaller windows around each SNP (± 100 kb).

Results

Genetic diversity and differentiation: whole sample and SNP dataset

A total of 599 cockles were analysed, since six specimens that exhibited a low number of reads (< 250.000 reads) from WDE_17 (two individuals), SAN_17 (one individual), SVI_17 (two individuals) and SMO_17 (one individual), were removed. After quality filtering, the number of SNPs retained in the whole dataset was 9,250. This number was slightly lower than the number used in the macrogeographical study carried out by Vera et al. (2022) (9,309 markers), because 59 of these markers were monomorphic in the studied regions. All the 9,250 markers were included in the "9,309 markers" dataset and their genomic information is available at https://onlinelibrary.wiley.com/doi/10.1111/eva.13340, where the SNP code from Vera et al. (2022) has been maintained for comparison between studies.

Observed (Ho) and expected (He) heterozygosities ranged respectively from 0.070 (SMO_17, Spain) to 0.080 (IWC_20, IGC_20 and IKF_20, Ireland; mean ± SD = 0.075 ± 0.003) and from 0.076 (WDE_17, Wales) to 0.087 (SNO_17, Spain and IKF_20, Ireland; mean ± SD = 0.082 ± 0.003) (Table 1). All F_{IS} values per locus and bed were positive, suggesting heterozygote deficit, but low (always < 0.115) and not significant;and all beds met to HW expectations (P < 0.0022; 0.05/22 populations), an expected outcome considering the HW filtering applied to retain SNPs. The percentage of polymorphic loci ranged from 25.5 % in SMO_17 (Spain) to 52.8 % in SNO_17 (Spain) (mean ± SD = 41.3 ± 7.2%). When only polymorphic loci within each bed were considered, Ho ranged from 0.137 in SLO_17 (Spain) to 0.181 in SMO_17 (Spain) (mean ± SD = 0.155 ± 0.014), showing these two beds also the lowest (0.156) and highest (0.200) He (mean ± SD = 0.171 ± 0.012). No differences in genetic diversity were found between the SW British Isles and Galician regions (Mann-Whitney U tests P > 0.250 for Ho, He with all loci and with polymorphic loci). Genetic diversity was in the range of previous values reported by Vera et al. (2022) for the whole Atlantic area using the same methodology.

Global F_{ST} for all beds was 0.02118 (P < 0.001), pairwise F_{ST} ranged from 0 (non-significant ≠ 0) for many bed pairs up to a maximum of 0.05040 (P < 0.001) between

IDC_18 and SVI_17 (Supplementary Table 2). Most pairwise comparisons were significant excluding those from Galicia. Average pairwise F_{ST} between the SW British Isles and Galicia was 0.03400 ($P < 0.001$), while 0.01374 ($P < 0.001$) within the SW British Isles and -0.00529 ($P = 1.000$) within Galicia. The two beds from the Cotentin Peninsula (FBV_19 and FGO_19, SW British Isles region), separated by 190 kilometres, showed significant genetic differentiation ($F_{ST} = 0.01207$, $P < 0.001$). The most likely K values inferred by fastSTRUCTURE were 1 and 3. When K = 3 was plotted, two main groups were identified differentiating the SW British Isles (IGC_20, IKF_20, IWC_20, IDA_18, IDC_18, WDE_17, WBY_17, ECE_20, FBS_17, FBV_19 and FGO_19) from Galicia (plus Arcachon) (FAR_17, SBA_17, SMI_17, SAN_17, SNO_17, SLO_17, SSA_17, SVI_17, SCA_17, SMO_17, SBI_18) (Fig. 2A). FGO_19 (France, Cotentin Peninsula) showed a high component of the southern group, also detectable in all samples from the English Channel (ECE_20, FBS_17 and FBV_18), suggesting some introgression between the two groups. The DAPC representation on the SW British Isles also suggested differentiation of the English Channel samples from the northernmost populations across the second component, while the first one, indicated a remarkable divergence of the IKF_20 sample from the remaining ones (Fig. 3A). The DAPC from Galicia showed most of the samples grouped excluding SNO_17, in the middle of the distribution, below Cape Finisterre, and SBI_18, the southernmost one (Fig. 3B).

Genetic structure within regions: demographic and selective factors

To understand the factors underlying genetic differentiation within the SW British Isles and Galician regions, we first identified those loci under selection using three different statistical approaches. BY10, BY1000 and PCADAPT detected 159, 47 and 84 outliers in the SW British Isles, respectively, all of them under divergent selection and representing a total of 186 different outliers (Supplementary Table 3). Thirty-five markers were shared between the three methods. The number of outliers in Galicia was much lower (BY10 = 15, BY1000 = 2, PCADAPT = 39), two of them shared between the three methods and representing a total of 51 outliers, all of them putatively under divergent selection. Among the whole outlier dataset, 15 were shared between SW British Isles and Galicia. Then, by discounting the total number of outliers to the whole dataset in each region, a total of 9,064 neutral markers were identified in the SW British Isles and 9,199 in Galicia, representing the neutral datasets for each region.

Small but significant genetic differentiation was detected among the SW British Isles beds using neutral markers ($F_{ST} = 0.00778$, $P < 0.001$), suggesting limitations to larval dispersion in this area by biogeographical barriers. As expected, the 186 total outliers rendered a much higher global F_{ST} (0.10959, $P < 0.001$), being more accentuated when using the shared set of outliers between methods ($F_{ST} = 0.17411$, $P < 0.001$), which suggests selective factors increasing structuring. Pairwise F_{ST} ranged from -0.03095 (IKF_20 – WDE_17) to 0.02366 (IGC_20 – FGO_19 pair) for neutral markers; from 0.00061 (IDA_18 – IDC_18 pair) to 0.17142 (IDA_18 – FGO_19 pair) for the 186 total outliers; and from -0.00345 (IDA_18 – IDC_18 pair) to 0.27313 (IKF_20 – FBS_17 pair) for the 35 shared outliers (Supplementary Table 4). IBD was significant with the shared and total outlier datasets ($r = 0.63169$ and 0.55136, respectively; $P < 0.001$), but not with the neutral dataset ($r = 0.08578$, $P = 0.330$). These results suggest that correlations could be a by-product of the unequal spatial distribution of the environmental factors responsible of selective forces shaping the cockle’s genome, since IBD patterns should be reflected by the balance between drift and migration on neutral markers. The fastSTRUCTURE analyses identified $K = 1$, $K = 2$ and $K = 3$ as the most likely values for the neutral, 35 shared outlier and 186 total outlier datasets, respectively (Fig. 2B), which consistently differentiated the Celtic Sea and the Northwest Irish cluster (IGC_20, IKF_20 and IWC_20), not studied to date, and the English Channel cluster (ECE_20, FBS_17, FBV_19, FGO_19). In contrast, the Irish Sea appeared as a rather differentiated group with the 186 outliers, which was split into two clusters, the Irish side (IDA_18 and IDC_18) most closely associated with the Celtic and Atlantic Ocean cluster, and the Welsh side (WDE_17 and WBY_17), most closely linked with the English Channel cluster, when using the 35 outlier loci. The differentiation of the Irish Sea from the other samples, and the contrast between the Welsh and Irish (east and west, respectively) samples of the Irish Sea, was shown when exploring a scenario with a larger K value, with both datasets displaying a very similar structure with K = 4 (Supplementary Figures 2 and 3). The DAPC analysis with neutral markers showed a very similar picture to that described with the whole SNP dataset (Supplementary Fig. 4A), however, the 186 and 35 outlier datasets displayed a very distinct picture, both separating the English Channel (ECE_20, FGO_19, FBV_19 and FBS_17) from the Welsh populations, but also from the Irish populations, which were further divided into two groups, the westernmost Northeast Atlantic Ocean group (IWC_20, ICG_20 and IKF_20) and the Irish/Celtic Seas group (IDC_18 and IDA_18) (Supplementary Figs. 4B and 4C).

In contrast to the SW British Isles, no population differentiation was found in Galicia with the neutral dataset (F_{ST} = 0.00552, P = 1.000), also supported by the fastSTRUCTURE (K =1) and DAPC, as previously outlined with whole dataset (Fig. 3B and Supplementary Fig. 4D). However, low but significant differentiation was detected with the 51 outliers (F_{ST} = 0.00870, P < 0.001), the pairwise F_{ST} supporting a significant differentiation of the two northernmost samples (SMI_17 and especially SBA_17; Supplementary Table 5) from the rest. This differentiation was not disclosed with fastSTRUCTURE (K = 1; see Supplementary Fig. 5) and only suggested with DAPC (Supplementary Fig. 4E).

Seascape analysis

RDA analyses in SW British Isles region suggested longitude as the main driver for the observed differentiation with all datasets and seasons (Table 2). Latitude was also supported as driver for many models, especially for those related to the 186 total outliers. Sea bottom salinity (SBS) was suggested for all seasons with the 186 outlier dataset, while bottom shear stress (BSS) was for reproductive and summer seasons using the whole and neutral datasets (Table 2). When longitude and latitude were removed, sea surface temperature (SST) was suggested for all the datasets in the summer season, and in the reproductive and winter seasons only with the whole and 186 outlier datasets, respectively. Sea bottom temperature (SBT) was suggested for the reproductive and summer season with the 186 outlier dataset. SBS and sea surface salinity (SSS) were suggested with the 186 outlier dataset for the summer and winter seasons, respectively. Net primary production (NPP) was suggested for all datasets in the winter season and for the 186 outlier dataset for the reproductive season. Finally, BSS was suggested in all seasons for the neutral dataset and in the reproductive and summer seasons for the complete dataset. In Galician region, no associations were found, except for latitude in all periods analysed using the 51 outliers, and for BSS during winter when latitude and longitude were removed (Table 2). However, VIF values were usually high (> 10), suggesting that results should be taken with caution due to the high collinearity among the variables in many cases.

While no correlations were identified in Galicia with BAYENV2, a total of 54 markers were correlated with different environmental variables in the SW British Isles (Supplementary Table 6). Thirty of these markers (55.6%) were previously identified as outliers by the different methodologies applied. Markers were mainly correlated with latitude, longitude, temperature and salinity. The main variable correlated with genetic markers in the reproductive season and summer scenarios was SBT, while SSS and NPP were in the winter scenario.

Gene mining around outliers and environmental correlated markers

Genetic markers associated with divergent selection or correlated with environmental variables were mapped in the common cockle genome to look for functional interpretation (Supplementary Tables 3 and 6). Outliers identified in the SW British Isles area were scattered across all chromosomes, between one in C18 and 22 in C3, while five chromosomes (C8, C11, C13, C14, C17) did not bear any outlier in Galicia, the maximum being detected in C1 (11 outliers) (Table 3). The 51 outliers detected in Galicia only identified a single consistent genomic region (window) under selection according to our criteria and other five outliers were distributed across four confident genomic windows previously reported by Vera et al. (2022) (Supplementary Tables 7 and 8). However, among the 186 outliers detected in the SW British Isles, 14 defined five new consistent genomic windows under divergent selection and other 45 mapped on genomic windows previously reported by Vera et al. (2022) (Supplementary Tables 7 and 8). Most outliers detected in Galicia were specific to this region, while an important number of outliers from the SW British Isles were shared with the Northern region previously analysed by Vera et al. (2022) (Supplementary Fig. 6). Still, a notable proportion of outliers in the North were specific of each study (North-Vera et al. (2022): 137 vs SW British Isles: 101) suggesting specific evolutionary factors related to each scenario. Among the genes annotated in the five new windows, several related to oxidative stress, hypoxia and immunity were identified in a 200 kb region in C2 and in a 340 kb region in C3 (Supplementary Table 9) (Gerdol and Venier 2015; Grandi et al. 2016; Sokolov et al. 2019). Also, in a 480 kb region in C5, some genes involved in signalling and detoxification (Wang et al. 2018; Kron 2022; Thoma et al. 2022) were identified. Finally, a gene associated with ocean acidification (Lim et al. 2021) was identified in C19. Despite the low number of genes handled, a significantly enriched GO Molecular Function was detected (protein serine/threonine phosphatase activity; GO:0004722) taking as background the common cockle transcriptome reported by Pardo et al. (2022).

Markers correlated with environmental variables were scattered across most chromosomes, excluding C7, C14 and C18, and the higher number (seven markers) were detected in two big chromosomes (C2 and C4) (Table 3). An important number of correlated markers were also identified as outliers for divergent selection (55.6 %), some of them associated with consistent genomic windows (Supplementary Table 8). Of note, the three markers detected in one of the most consistent genomic windows in C4. We also mined the cockle genome around the correlated marker dataset (Supplementary Table 10) and detected several genes related to nervous system development and physiology. These genes were mostly clustered at C1 around 142462_31 (correlated with SBT) and C2 around 210318_7 (correlated with SST), respectively. Furthermore, some of these genes were previously associated with temperature stress and oxygen depletion stress or differentially expressed under specific experimental conditions in other mollusc species (Woo et al. 2011; Chen et al. 2022). Another important group of genes scattered around different markers in the cockle genome were related to immunity and defence and had been previously reported in other mollusc species in response to viruses and bacteria (Barbosa et al. 2022; Saco et al. 2023) (Supplementary Table 9).

Discussion

Assessment of the distribution of genetic variability across populations, incorporating historical processes and local adaptation framed within the dispersal range of the focal organism (Richardson et al. 2014), is essential to develop management actions to preserve exploited species (Bernatchez et al. 2017). In the present study, two different patterns of genetic structure at microgeographic scale were identified in two regions within the natural distribution of *C. edule*, highlighting the need to perform analyses at multiple spatial scales (Hoffman et al. 2012), to provide information supporting the management of this valuable resource.

Heterogeneous pattern of microgeographic structure in the common cockle

The two geographic areas studied, the SW British Isles region and Galicia, were selected by their different habitat fragmentation patterns. Both areas were slightly differentiated (F_{ST} = 0.03400), in accordance with their location in the major northern and southern regions of the species' range separated around French Brittany (Vera et al. 2022), but did not show differences in genetic diversity, unlike Vera et al. (2022), who reported a slight, but significant higher diversity in the southern region.

The extensive analysis performed in Galicia (10 natural beds) suggested the presence of a single panmictic unit in this area, as previously reported for other molluscs, with similar pelagic larval periods (*Donax trunculus*, Nantón et al. 2017; *Ensis siliqua*, Arias-Pérez et al. 2012; *Mitilus galloprovincialis*, Diz and Presa 2009; *Ostrea. edulis*, Vera et al. 2016; *Polititapes rhomboides*, Chacón et al. 2021), and for other marine species (*Hippocampus guttulatus*; Lopez et al. 2015; *Pollicipes pollicipes*, Parrondo et al. 2022). Our data does not support Cape Finisterre as a biogeographical barrier for the species as previously suggested (Lopez-Jamar et al. 1992; Piñeira et al. 2008; Martinez et al. 2013; Cruz et al. 2020), since no differentiation was detected between beds at both sides of the Cape with the whole and neutral datasets. However, when using outlier loci, the two northernmost Galician beds showed significant differentiation with the remaining ones, especially the bed closest to the Cantabrian Sea (SBA_17) (average F_{ST} = 0.03145), which could be related to the higher temperature regime in the Cantabrian Sea (Marquina et al. 2015), but a more detailed study in the Cantabrian Sea would be necessary to confirm this observation. Oceanographic dynamics in the Galician coast indicate that the cold-upwelled water usually penetrates estuaries on the west, while it only occurs during very intense events on the north (Alvarez et al. 2010). Thus, water temperature decreases from north to west, with an SST average value of 19.5 ºC in the Cantabrian coast compared with the 18.5 ºC measured in the west coast for the 1985-2005 period (Gomez-Gesteira et al. 2008). Larval dispersal modelling carried out in Vera et al. (2022) (see their Fig. 7) confirmed that cockle beds are well connected with each other by larval transport in Galicia, but the connection between the Rias and the sites to the northeast of Cape Finisterre was weaker, though present. Furthermore, whilst the beds along the northwest coast of the Iberian Peninsula are affected by very similar oceanographic conditions, during the late spring and late summer, temperatures at the most north-easterly site can differ markedly from those at the other beds due to its location at the edge of the upwelling system and at the inception point of the Portugal Coastal Current (STT two degrees higher in the northern beds (mean = 18.51 ºC) than in the southern ones (mean = 16.47 ºC) during the summer; see Supplementary Table 1). Despite the genotype-environment associations methods did not identify sea temperature as driver, latitude, which is highly correlated with temperature, was suggested by the RDA analysis as potential driver in the region.

Previous data from the SW British Isles suggested significant structure in *C. edule* related both to current dynamics as well as to abiotic factors, such as salinity and temperature (Coscia et al. 2020; Vera et al. 2022), as reported in other shellfish species such as the horse mussel *Modiolus modiolus* (Gormley et al. 2015) and the great scallop *Pecten maximus* (Vendrami et al. 2019; Hold et al. 2021). However, some regions in this area are still poorly sampled in the common cockle (English Channel) or without information (West Irish coast, North-east Atlantic). Outlier markers showed a moderate pairwise genetic differentiation between beds (F_{ST} = 0.10959 and 0.17411 with the 186 and 35 outlier datasets, respectively), higher than that observed with neutral markers (F_{ST} = 0.00778), as expected, suggesting selective factors shaping specific genomic regions in a small geographic area. An important proportion of divergent outliers (68 markers) were shared with those reported by Vera et al. (2022) for the northern group (210 outliers), which gives robustness to our observations; however, data also suggests specific selective factors shaping the cockle's genome associated with the new sampling in the SW British Isles (117 new outlier loci; 31 within consistent genomic windows). In fact, five new confident genomic windows were identified including relevant genes related to oxidative stress and immunity that would deserve further studies as candidates to explain the association observed with environmental factors. Despite biotic factors, such as pathogens, could not be contemplated in our study, their diversity and distribution (influenced by abiotic factors) are important drivers shaping the genome and distribution of species (Theodosopoulos et al. 2019) and specifically in cockles (Vera et al. 2022; Pampín et al. 2023). Furthermore, we also deepened into the correlation of specific SNPs with environmental factors and could identify, by mining in the cockle genome several genes related to nervous transmission and immunity, arranged in clusters or scattered in different chromosomes, that had been previously reported in other mollusc associated with temperature or oxidative stress (Woo et al. 2011; Barbosa et al. 2022; Chen et al. 2022).

The population structure observed in the SW British Isles region may be in part explained by the residual ocean currents and ocean fronts that characterise this area, but also by selective factors such as salinity gradients, variable bottom shear stress (due to large tidal variability) and sea temperature gradients (driven by ocean currents, stratification and mixing, and latitudinal gradients); however, spatial seascape results should be taken with caution due to the collinearity detected among variables. Both outlier datasets could identify four genetic clusters following two main west-east and north-south axes, which could explain the correlation observed between genetic and geographic distances for outlier loci, but also the identification of longitude and latitude as two main drivers in the seascape analysis. According to the outlier information, the new sampled beds from Western Ireland (IGC_20, IKF_20 and IWC_20) (Northeast Atlantic) would constitute a new cluster. These sites are connected by the Irish coastal current (Brown et al. 2003; Fernand et al. 2006) and larval dispersal modelling (see Fig. 7 in Vera et al. 2022) showed that the beds along the southwest coast of Ireland are well interconnected. The Irish Sea can be split into two different clusters associated with the Irish and Welsh sides, as previously suggested by Coscia et al. (2020). Sites along the southeast coast of the Irish Sea are generally connected by northward currents and sites along the north coast of Wales by eastward currents. In contrast, the two sites on the west coast of the Irish Sea (IDC_18 and IDA_18), appear genetically separated from the remainder of the Irish Sea; This may be driven by the Irish Sea Front acting as a barrier which also drives warmer temperatures in the northwest Irish Sea than in the well-mixed northeast Irish Sea. Finally, the English Channel forms a fourth cluster including the ECE_20 bed from Cornwall with the southern beds limited by the Ushant front. Interestingly, the Cotentin Peninsula, previously identified as a physical barrier to dispersal in other molluscs, such as the slipper limpet *Crepidula fomicata* (Dupont et al. 2007) and *P. maximus* (Nicolle et al. 2016; Handal et al. 2020), showed a significant differentiation between samples on its west and east sides (FGO_19 and FBV_19) with neutral markers (F_{ST} = 0.01045, P < 0.001) and higher with outlier loci (F_{ST} 35 outliers = 0.06654, P < 0.001; F_{ST} 186 outliers = 0.05876, P < 0.001), suggesting additional selective factors differentiating both sides. Oceanic distance between the two Cotentin beds (~ 190 km) is shorter than the longest distance between Galician beds (~ 300 km), where no genetic differentiation was detected with neutral markers. Of note, FGO_19 showed an important genomic component of the South group, suggesting introgression from the south especially in the west coast of the Cotentin Peninsula.

Management implications

The present study represents a refined analysis of the population structure of *C. edule* in two geographic areas of small-medium size representing differentiated models that could aid to obtain a more comprehensive picture for improving the management and conservation of this valuable commercial and ecological resource. Galician beds were suggested to constitute a panmictic population and this region could be managed as a single genetic unit. The fisheries in this region are exclusively commercial and their exploitation management can be through territorial concessions leased by shellfisher guilds or directly by Galician regional government (i.e. free access shellfish areas). This genetic information should be included in the Galician legislation, thus allowing translocations from high production areas (Ría de Noia) to depleted ones by different factors, such as the parasite *M. cochillia* (Ría de Arousa; Villalba et al. 2014). However, caution should be taken considering biotic factors not evaluated in our study, such as emergent pathologies (e.g. marteiliosis), which will require specific recommendations within the general framework depicted in our study. A sharp fragmentation was displayed by the SW British Isles region, especially with divergent outliers, mostly representing adaptive management units (AMU, Bernatchez et al. 2017). Thus, Western (Northeast Atlantic) Irish beds would represent a differentiated group from those previously described, while subtle genetic sub-structuring was identified along the English Channel, with a significant effect at the Cotentin Peninsula representing as a biogeographic barrier. Furthermore, the Irish Sea, a narrow water body mass between Wales and Ireland, appears to represent differentiated units at both sides of the Irish Sea according to our information. All these population units should be individually managed, avoiding translocations between them. Finally, our results could help to improve cockles' production by founding appropriate broodstock to enhance depleted populations and by tracing samples to check undesirable transferences among regions.

Acknowledgements

Authors wish to thank L. Insua, S. Sánchez-Darriba and S. Gómez from the ACUIGEN group (USC) for their technical support. Supercomputing Center of Galicia (http://www.cesga.es) provided computing facilities for genotyping. A. Casanova (ACC) was funded by a Xunta de Galicia-Campus Terra postdoctoral fellow. Authors are also indebted with COCKLES Interreg European project partners who provided samples included in this study. Finally, the authors are grateful to Prof. S. Goodacre, one Associate Editor and three anonymous reviewers for their helpful comments on the earlier version of this manuscript.

Author Contributions

MV, AV and PM designed and supervised the study. DI, AC, KM, FO, SKM, SL performed field collections. PM, SCC, SL, PER, SKM and FO provided funding. FM, MH and AB analysed bioinformatically genomic sequences and created genotyping files. SBW and PER provided information about oceanography, environmental variables and developed geographic maps included in the figures. MV, CB, ACC, AB and PM performed the genetic analyses. MV and PM wrote the manuscript with contributions from all authors. All of them read the manuscript and gave their approval.

Funding

This study has been supported by the COCKLES project (grant number: EAPA_458/2016) of the INTERREG EUROPEAN PROGRAMME and the NERC-SHEAR project (NE/W001217/1).

Conflict of interest

The authors declare no conflict of interest.

Data archiving

Data for this study are available at Dryad Digital Repository (https://doi.org/10.5061/dryad.xpnvx0kmr) and Supplementary material.

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Figure legends:

Figure 1. Geographical distribution of the *Cerastoderma edule* beds analysed in the present study. Location of the study area in Europe (a) and focused on SW British Isles (b) and Galicia (c) regions. Summer sea surface temperatures are shaded. Summer sea surface ocean currents are schematically depicted with magenta-coloured arrows. Tidal mixing fronts are indicated with purple dashed lines. UF Ushant Front, CSF Celtic Sea Front, ISF Irish Sea Front. Location codes are shown in Table 1. Beds previously analysed by Vera et al. (2022) are marked with asterisks.

Figure 2. Population structure of *Cerastoderma edule* at different geographical scales using fastSTRUCTURE. Each vertical bar represents one individual, and the colour proportion of each bar represents the posterior probability of assignment of each individual to the different clusters (K) inferred by the program. The most likely K = 3 using the whole dataset (A), and K = 2 using the 35 shared divergent outliers between methodologies and K = 3 using the total 186 divergent outliers (B) for the SW British Isles are represented. Codes are shown on Table 1. Plots for all the K values tested for the different datasets are shown in Supplementary Figures.

Figure 3. Discriminant Analysis of Principal Components (DAPC) plots using the complete datasets of *Cerastoderma edule* beds belonging to the SW British Isles (A) and Galicia (B). The weight of retained discriminant analysis (DA) and principal components selected are shown on left bottom box and right bottom box, respectively. Codes are shown on Table 1.

Table 1. *Cerastoderma edule* beds analysed in the present study. Location, sampling year, geographical coordinates, code, country, number of individuals collected (N initial) and analysed after quality filtering (N), observed heterozygosity (Ho), expected heterozygosity (He), inbreeding coefficient (F_{IS}) for all dataset and for polymorphic loci are shown. Locations in italics were previously analysed by Vera et al. (2022).

								All dataset			Polymorphic loci (MAF > 0.017)				
Location	**Year**	**Lat (deg N)**	**Lon (deg E)**	**Code**	**Country**	**N initial**	**N**	**Ho**	**He**	**F_{IS}**	**Polymorphic loci**	**% Polymorphic loci**	**Ho**	**He**	**F_{IS}**
Galway Connemara	2020	53.306	-9.846	IGC_20	Ireland	27	27	0.080	0.085	0.067	4205	45.5	0.166	0.179	0.074
Kerry- Feale	2020	52.488	-9.652	IKF_20	Ireland	30	30	0.080	0.087	0.080	4362	47.2	0.161	0.176	0.088
West Cork-Cockle Beach	2020	51.463	-9.744	IWC_20	Ireland	30	30	0.080	0.085	0.064	4294	46.4	0.163	0.175	0.070
Dundalk Bay-Annagassan	*2018*	*53.884*	*-6.341*	*IDA_18*	*Ireland*	*29*	*29*	0.074	0.080	0.082	*2993*	32.4	*0.161*	*0.177*	0.090
Dundalk Bay-Cooley	*2018*	*53.996*	*-6.287*	*IDC_18*	*Ireland*	*22*	*22*	0.077	0.083	0.081	*3493*	37.8	*0.173*	*0.190*	0.087
Dee Estuary	*2017*	*53.343*	*-3.174*	*WDE_17*	*Wales*	*30*	*28*	0.071	0.076	0.074	*2561*	27.7	*0.167*	*0.182*	0.084
Burry	*2017*	*51.643*	*-4.166*	*WBY_17*	*Wales*	*30*	*30*	0.073	0.080	0.091	*3529*	38.2	*0.148*	*0.165*	0.101
Camel Estuary (Cornwall)	2020	50.531	-4.930	ECE_20	England	24	24	0.073	0.081	0.105	3667	39.6	0.159	0.180	0.114
Somme Bay	*2017*	*50.201*	*1.627*	*FBS_17*	*France*	*30*	*30*	0.071	0.080	0.111	*3438*	37.2	*0.147*	*0.167*	0.119
Baie des Veys (Brévands)	2019	49.365	-1.150	FBV_19	France	26	26	0.079	0.081	0.022	3579	38.7	0.169	0.174	0.030
Gouville sur mer	2019	49.105	-1.612	FGO_19	France	23	23	0.077	0.082	0.059	4055	43.8	0.163	0.174	0.063
Arcachon Bay	*2017*	*44.580*	*-1.238*	*FAR_17*	*France*	*30*	*30*	0.074	0.083	0.111	*4335*	46.9	*0.140*	*0.159*	0.120
O Barqueiro	2017	43.722	-7.701	SBA_17	Spain	30	30	0.076	0.085	0.107	4595	49.7	0.140	0.158	0.115
Miño	2017	43.361	-8.206	SMI_17	Spain	30	30	0.073	0.081	0.102	4159	45.0	0.140	0.157	0.110
Anllóns	2017	43.220	-8.943	SAN_17	Spain	30	29	0.073	0.081	0.101	3526	38.1	0.143	0.161	0.110
Ría de Noia	*2017*	*42.790*	*-8.923*	*SNO_17*	*Spain*	*30*	*30*	0.078	0.087	0.099	*4885*	52.8	*0.139*	*0.156*	0.107
Lombos do Ulla	*2017*	*42.629*	*-8.775*	*SLO_17*	*Spain*	*30*	*30*	0.075	0.085	0.113	*4602*	49.8	*0.137*	*0.156*	0.120
Sarrido	2017	42.507	-8.826	SSA_17	Spain	30	30	0.074	0.083	0.103	4317	46.7	0.140	0.158	0.112
Vilanova	2017	42.561	-8.831	SVI_17	Spain	27	25	0.072	0.081	0.112	3175	34.3	0.153	0.173	0.118
Campelo	2017	42.421	-8.685	SCA_17	Spain	30	30	0.073	0.082	0.115	4287	46.3	0.140	0.159	0.121
Moaña	2017	42.286	-8.730	SMO_17	Spain	20	19	0.070	0.077	0.088	2361	25.5	0.181	0.200	0.093
Baiona	2018	42.117	-8.822	SBI_18	Spain	17	17	0.075	0.082	0.092	3609	39.0	0.174	0.192	0.097

Table 2. Results of the redundancy analysis (RDA) on the SW British Isles region of *Cerastoderma edule*. Only variables included by the forward selection model are shown.

SW British Isles			Complete dataset		Neutral dataset		186 total outlier dataset	
Model	**Season**	**Variable**	**P-value**	**Adjusted R^2**	**P-value**	**Adjusted R^2**	**P-value**	**Adjusted R^2**
All seascape variables	Reproductive period	Latitude	-	0.102	-	0.098	0.005	0.414
		Longitude	0.001		0.001		0.001	
		SBS	-		–		0.051	
		BSS	0.004		0.001		-	
	Winter	Latitude	0.001	0.087	0.001	0.080	0.009	0.423
		Longitude	0.016		0.015		0.001	
		SBS	-		-		0.030	
	Summer	Latitude	-	0.102	-	0.098	0.012	0.410
		Longitude	0.002		0.003		0.001	
		SBS	-		-		0.055	
		BSS	0.001		0.001		-	
Only abiotic variables	Reproductive period	SST	-	0.053	-	0.053	0.013	0.319
		SBT	-		-		0.001	
		BSS	0.002		0.002		-	
		NPP	-		-		0.027	
	Winter	SST	0.003	0.067	-	0.069	-	0.202
		SSS	-		-		0.041	
		BSS	-		0.010		-	

		NPP	0.017		0.008		0.019	
	Summer	SST	0.011	0.086	0.014	0.083	0.001	0.355
		SBT	-		-		0.009	
		SBS	-		-		0.083	
		BSS	0.001		0.001		-	

Galicia			**Complete dataset**		**Neutral dataset**		**51 total outlier dataset**	
Model	**Season**	**Variable**	**P-value**	**Adjusted R^2**	**P-value**	**Adjusted R^2**	**P-value**	**Adjusted R^2**
All seascape variables	**Reproductive period**	Latitude	-	-	-	-	0.012	0.124
	Winter	Latitude	-	-	-	-	0.011	0.124
	Summer	Latitude	-	-	-	-	0.008	0.124
Only abiotic variables	**Reproductive period**	-	-	-	-	-	-	-
	Winter	BSS	-	-	-	-	0.045	0.083
	Summer	-	-	-	-	-	-	-

Adjusted R^2 and P-value associated to each variable of its selection stage. SST: Sea Surface Temperature; SBT: Sea Bottom Temperature; SSS: Sea Surface Salinity; SBS: Sea Bottom Salinity; BSS: Bottom Shear Stress; NPP: Net Primary Production.

Table 3. Distribution of divergent outliers and markers correlated with environmental variables in the SW British Isles and Galicia across the *Cerastoderma edule* genome (version 4.0).

		Outlier loci (divergent selection)			
Mega-scaffold (chromosome)	Chromosome length (bp)	British Isles	Galicia	Shared	Markers correlated envionmental variables*
C1	64,609,245	21	11	3	5 (3)
C2	56,319,168	14	2		7 (3)
C3	55,987,847	22	3	1	6 (5)
C4	52,087,795	18	5	2	7 (6)
C5	50,828,891	11	1	1	3 (2)
C6	40,237,005	13	3	2	4 (1)
C7	39,934,596	2	1		
C8	39,684,391	9			2 (1)
C9	39,070,162	11	3		2 (1)
C10	38,264,924	14	8	2	1
C11	38,197,540	2			1
C12	36,327,582	6	1		1 (1)
C13	35,955,507	10			5 (2)
C14	33,816,358	5			
C15	31,726,440	3	1	1	3 (1)
C16	31,510,408	10	8	1	2 (2)
C17	26,587,828	4			2 (1)
C18	22,603,465	1	1	1	
C19	21,711,631	4	1	1	1
Other scaffolds		6	2		2 (1)
Total		186	51	15	54 (30)

* Only detected in SW British Isles; in parentheses those markers also identified as outliers for divergent selection

Fig.1

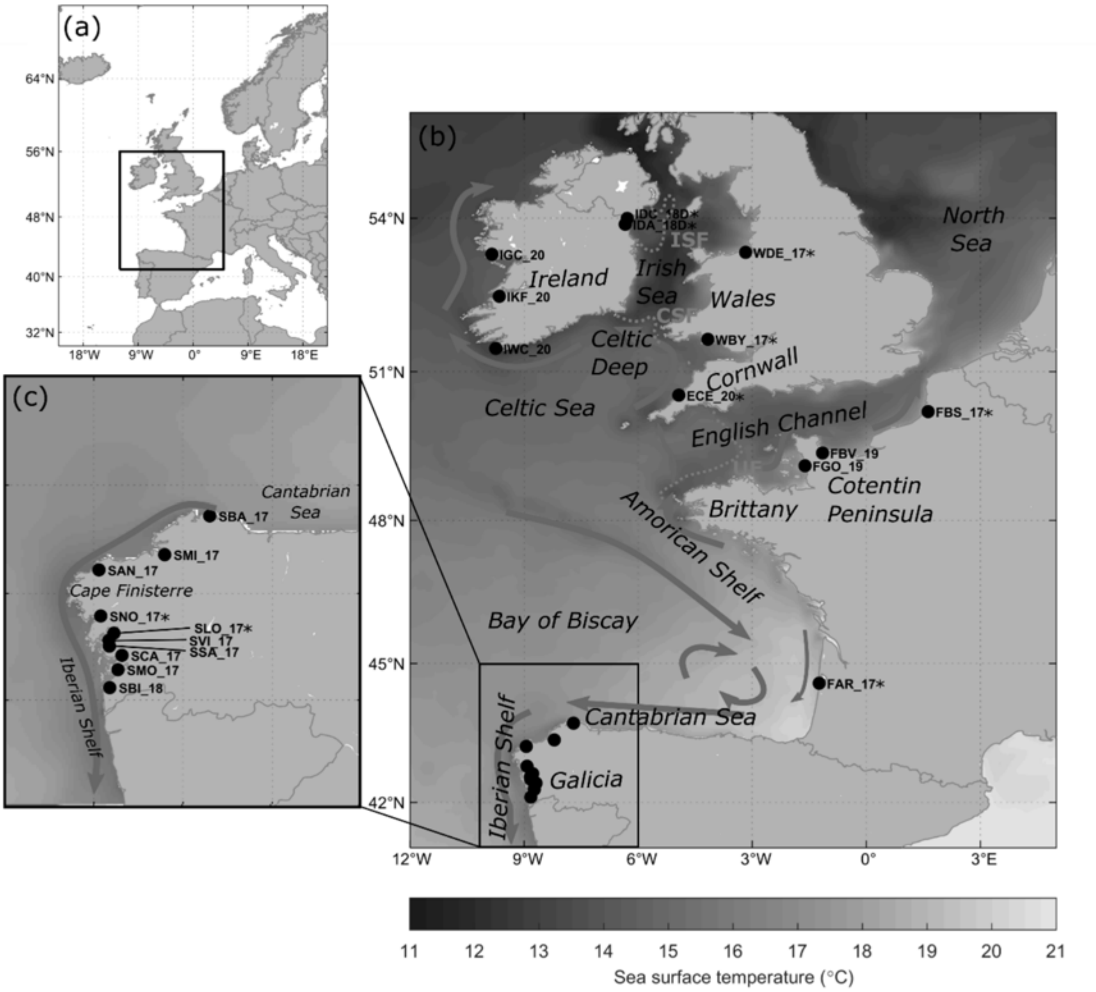
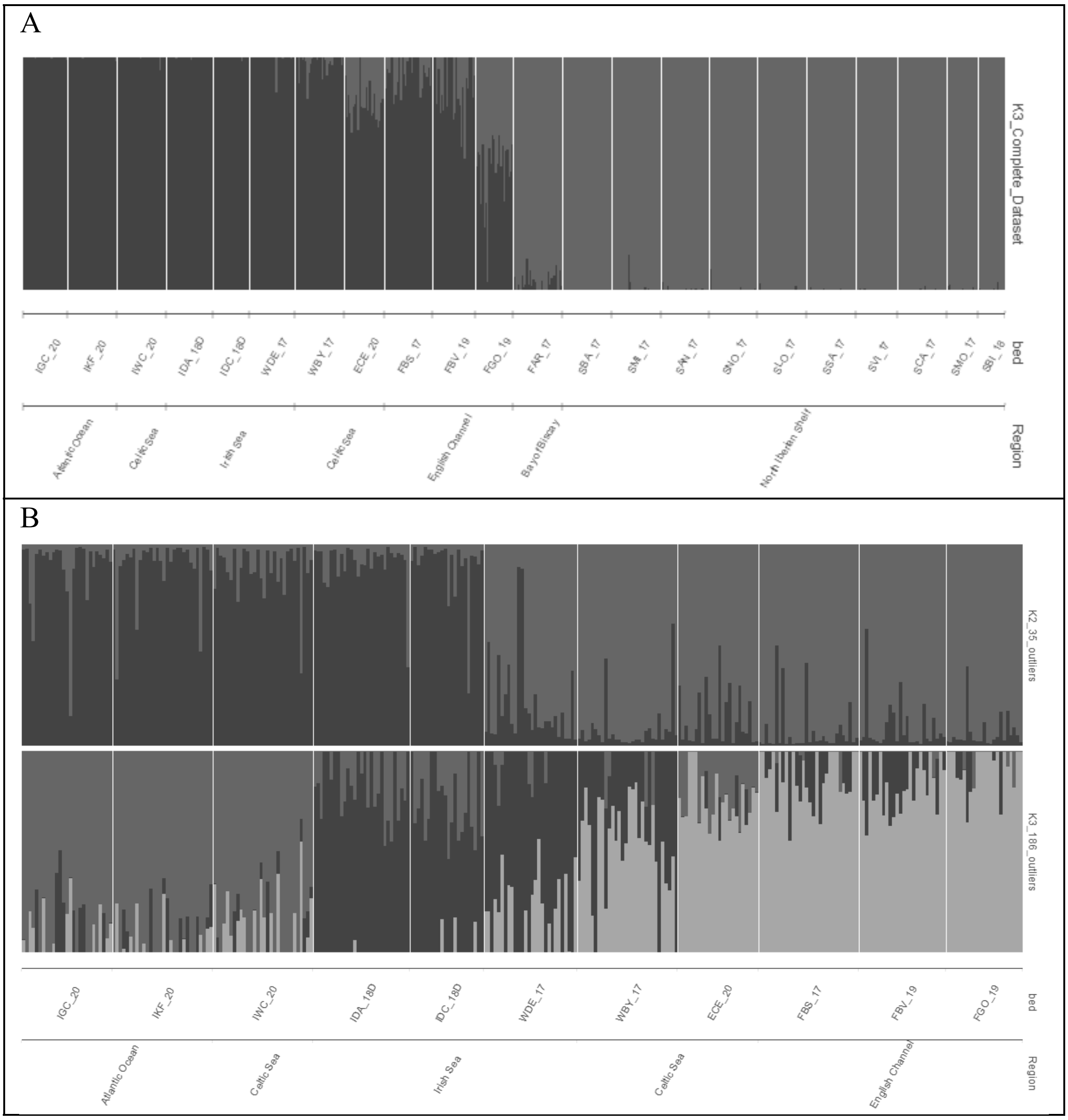
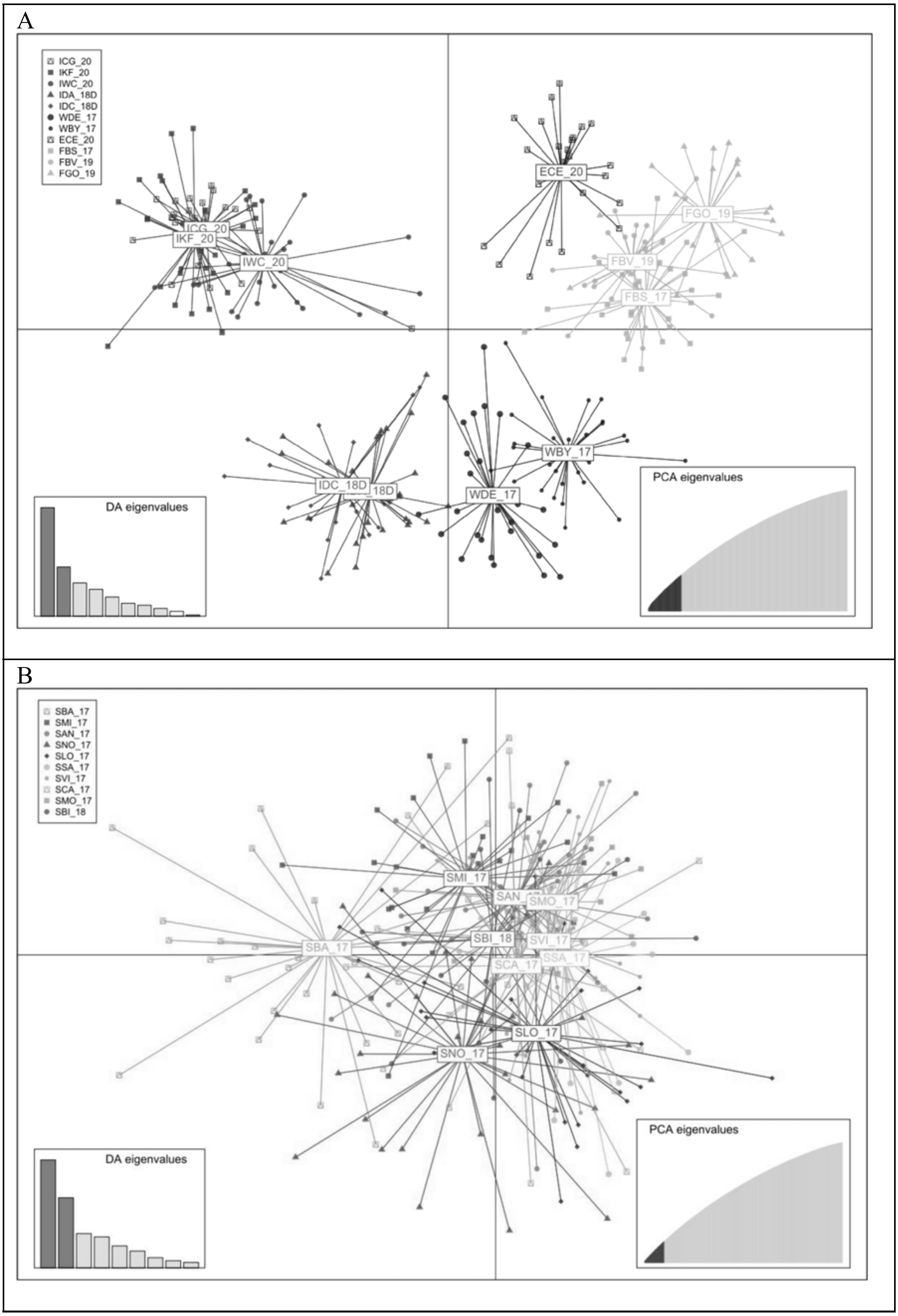

(a)
(b)
(c)
Ireland
Irish Sea
Wales
North Sea
Celtic Deep
Celtic Sea
Cornwall
English Channel
Brittany
Cotentin Peninsula
American Shelf
Bay of Biscay
Cantabrian Sea
Galicia
Iberian Shelf
Cape Finisterre
ISF
CSF
IDL_18D*
IDA_18D*
IGC_20
IKF_20
IWC_20
WDE_17*
WBY_17*
ECE_20*
FBS_17*
FBV_19
FGO_19
FAR_17*
SBA_17
SMI_17
SAN_17
SNO_17*
SLO_17*
SVI_17
SSA_17
SCA_17
SMO_17
SBI_18
Sea surface temperature (°C)

Fig.2



A
K3_Complete_Dataset
IGC_20
IKF_20
IWC_20
IDA_18D
IDC_18D
WDE_17
WBY_17
ECE_20
FBS_17
FBV_19
FGO_19
FAR_17
SBA_17
SMI_17
SMO_17
SLO_17
SSA_17
SVI_17
SCA_17
SMO_17
SBI_18
bed
Atlantic Ocean
Celtic Sea
Irish Sea
Celtic Sea
English Channel
Bay of Biscay
North Iberian Shelf
Region
B
K2_35_outliers
K3_186_outliers
IGC_20
IKF_20
IWC_20
IDA_18D
IDC_18D
WDE_17
WBY_17
ECE_20
FBS_17
FBV_19
FGO_19
bed
Atlantic Ocean
Celtic Sea
Irish Sea
Celtic Sea
English Channel
Region

Fig.3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IWC_20
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IDC_18D
WDE_17
WBY_17
ECE_20
FBS_17
FBV_19
FGO_19
ECE_20
FGO_19
ICG_20
IKF_20
IWC_20
FBV_19
FBS_17
WBY_17
IDC_18D
18D
WDE_17
DA eigenvalues
PCA eigenvalues
B
SBA_17
SMI_17
SAN_17
SNO_17
SLO_17
SSA_17
SVI_17
SCA_17
SMO_17
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SMI_17
SAN
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SBI_18
SVI_17
SCA_17
SSA_17
SLO_17
SNO_17
DA eigenvalues
PCA eigenvalues