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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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38

39   **Abstract**

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

## 61    **Introduction**

62    Knowledge of genetic diversity distribution is crucial for the sustainable management  
63    and conservation of natural resources (Leary et al. 2009; Sa-Pinto et al. 2012). This  
64    distribution is affected by larval connectivity, demographic parameters and selective  
65    processes operating on species populations. Scarcity of physical barriers in marine  
66    environments is expected to promote higher connectivity among populations in  
67    comparison to terrestrial species (Waples 1998). Moreover, marine species usually  
68    show large population sizes, which along with pelagic larval stages, often lasting  
69    several weeks, facilitate population genetic homogenization across wide regions (Sa-  
70    Pinto et al. 2012; do Prado et al. 2018). Despite these general features, genetic studies  
71    on marine organisms have frequently detected genetic differentiation, even at local  
72    scales (i.e., below the geographic scale of effective dispersal of the species studied,  
73    known as chaotic genetic patchiness (CGP); see Eldon et al. 2016), which can be  
74    explained by historical and reproductive/demographic factors (e.g. high fecundity and  
75    high mortality in early life stages, sweepstakes reproductive success; see Parrondo et al.  
76    2022), natural selection associated with environmental conditions (Vilas et al. 2015; do  
77    Prado et al. 2018; Vera et al. 2019) and oceanic features such as residual currents,  
78    bathymetry, coastline shape, upwelling, fronts, gyres and eddies (Vera et al. 2016;  
79    Coscia et al. 2020; Handal et al. 2020; Fisher et al. 2022; Vera et al. 2022).

80    Different types of ocean fronts have been described across the Northeast Atlantic  
81    region, encompassing tidal mixing fronts, shelf break fronts, and freshwater fronts  
82    separating estuarine freshwater and higher salinity coastal waters (Sharples and  
83    Simpson 2019). Examples of these frontal systems on the NW European Shelf include  
84    the Celtic Sea Front (NE Celtic Sea), the Irish Sea Front (NW Irish Sea), the Alderney  
85    Race (with one of the strongest current in Europe) and the Ushant Front (W English

86 Channel) (Suberg et al. 2019). These fronts may influence genetic structure acting as  
87 barriers to cross-front planktonic dispersal and as conduits through along-front dispersal  
88 by frontal jets, with important influences on the pelagic distribution of larvae of marine  
89 species (Galarza et al. 2009). Biogeographical barriers can also limit dispersal in marine  
90 environments. In the Northeast Atlantic region, Cape Finisterre, the Cornwall  
91 Peninsula, the tip of Brittany, the Llyn Peninsula, and the Alderney race along Cotentin  
92 Peninsula have been identified as potential barriers to the connectivity of marine  
93 organisms due to their oceanographic features, including fish (Abaunza et al. 2008;  
94 Larmuseau et al. 2009) and molluscs (Dupont et al. 2007; Piñeira et al. 2008; Martinez  
95 et al. 2015; Handal et al. 2020; Vera et al. 2022).

96 The common cockle, *Cerastoderma edule*, is a bivalve mollusc naturally distributed  
97 throughout the Northeast Atlantic coast, from Senegal, West Africa, to Norway,  
98 northern Europe, where it inhabits on intertidal and shallow subtidal soft sediments  
99 (Hayward and Ryland 1995). The species is commercially exploited and provides a  
100 wealth of services to coastal communities mainly in Ireland, United Kingdom, France,  
101 Spain and Portugal, where it is harvested (Flach and de Bruin 1994; Carss et al. 2020;  
102 Jackson-Bue et al. 2022). Cockle harvest has been reduced since the 1980s (> 100,000  
103 tonnes) to nowadays (~ 25,000 tonnes in 2019) due to changes in fisheries policies,  
104 overfishing, variable recruitment and mass mortalities produced by pollution, climate  
105 events and parasites (Villalba et al. 2014; Mahony et al. 2020; Pampin et al. 2023).

106 Furthermore, cockles are considered keystone for ecosystem due to their role as reef  
107 engineers, agents of carbon sequestration and their linking between primary producers  
108 and higher trophic levels (Norris et al. 1998; Carss et al. 2020). The species is dioecious  
109 and can live up to 10 years displaying fast sexual maturation (reached in the first year of  
110 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,

136 characterised by putative habitat fragmentation due to tidal mixing fronts and  
137 biogeographical barriers; and (2) the Northwest coast of Spain (Galicia), representing a  
138 quite homogeneous region according to previous information on other mollusc species  
139 (Diz and Presa 2009; Vera et al. 2016). The results confirmed the significant  
140 differentiation of cockles' populations at microgeographic scale, but also the power of  
141 larval dispersal to homogenize rather wide coastal areas, thus providing essential  
142 information for proper management of this valuable resource.

143

## 144 **Material and methods**

### 145 *Sample area and oceanography*

146 Two geographic areas along the Northeast Atlantic coast were investigated (Fig. 1).  
147 The first was focused on the British Isles and English Channel (hereafter called the SW  
148 British Isles region), where previous, though incomplete information, supported  
149 significant genetic sub-structuring (e.g. Coscia et al. 2020; Vera et al. 2022). The  
150 second area was Galicia (Northwest Spain), which may be genetically homogeneous  
151 according to information in other mollusc species (Diz and Presa 2009; Vera et al.  
152 2016).

153 Over the cockle reproductive season (May to September; Mahony et al. 2020), the  
154 coastline of Galicia is characterised by wind-driven upwelling of cold waters resulting  
155 in sea surface temperatures (SSTs) that are several degrees colder than off-shore SSTs  
156 (Supplementary Fig. 1b). Also driven by the predominantly northerly winds in the  
157 summer months, the Portugal coastal current transports waters southwards along the  
158 coastline of Iberia (Teles-Machado et al. 2016) with residual current strengths along the  
159 Galician coastline exceeding 0.15 m/s (Supplementary Fig. 1d). The SW British Isles  
160 region is divided into distinct oceanographic regions (the English Channel, the Celtic



161 Deep, the Celtic Sea and the Irish Sea) by diverging current or seasonal frontal systems  
162 (Galparsoro et al. 2014). Several tidal mixing fronts separate seasonally stratified and  
163 mixed waters (Supplementary Fig. 1a): the Ushant Front (Group “Grepma”, 1988), the  
164 Celtic Sea Front, and the Irish Sea Front (Simpson and Pingree, 1978). The Celtic Sea  
165 is characterised by northward flow along the western coast of Cornwall which merges  
166 into the Celtic Sea Front jet and links into the Irish Coastal Current which transports  
167 water clockwise along the south and west coast of Ireland (Supplementary Fig. 1c;  
168 Brown et al. 2003; Fernand et al. 2006). Northward currents along the Ushant Front  
169 link the American Shelf with the Celtic Sea. The southern English Channel coast is  
170 dominated by northeastward flow, with the strongest currents occurring around the  
171 Cotentin Peninsula.

172

### 173 *Sample collection*

174 A total of 374 cockles from 14 wild natural beds were collected across the  
175 aforementioned two regions in the period 2017-2020 and stored in 100% ethanol for  
176 analyses (Table 1). Additionally, 231 cockles from eight beds previously analysed  
177 (Vera et al. 2022: identified as IDA\_18, IDC\_18, WDE\_17, WBY\_17, FBS\_17,  
178 FAR\_17, SNO\_17 and SLO\_17, where 17 and 18 in the codes represent 2017 and  
179 2018, respectively) were included in the analysis to achieve a comprehensive picture of  
180 the areas studied, thus providing an overall total of 605 cockles. To avoid generation  
181 overlapping, all samples belonged to the 0+ year age class of their sampling year. No  
182 temporal replicates were included considering the temporal genetic stability previously  
183 reported by Vera et al. (2022).

184

### 185 *Single Nucleotide Polymorphism (SNP) genotyping*

186 Total DNA was extracted from gills using the E.Z.N.A. E-96 mollusc DNA kit  
 187 (OMEGA Bio-tek), following manufacturer recommendations. 2b-RAD libraries (~ 90  
 188 cockles per run) were constructed using the Alfl Iib restriction enzyme and sequenced  
 189 in an Illumina NextSeq 500 platform following Maroso et al. (2018; 2019). Bowtie  
 190 1.1.2 (Langmead et al. 2009) was used to align reads to the cockle's genome (Bruzos et  
 191 al. 2022) allowing a maximum of three mismatches and a unique valid alignment (-v 3 -  
 192 m 1). The reference-based mode with default parameters in the gstacks module of  
 193 STACKS 2.0 (Catchen et al. 2013) was used for SNP calling. For genotyping, SNPs  
 194 were filtered following Vera et al. (2022): *i*) SNPs genotyped in > 60% individuals; *ii*)  
 195 MAC (minimum allele count)  $\geq 3$ ; *iii*) conformance to Hardy-Weinberg expectations  
 196 (i.e. SNPs with significant  $F_{IS}$  values ( $P < 0.05$ ) in at least 25% of the populations were  
 197 removed); and *iv*) the most polymorphic SNP within each RAD-tag was retained.  
 198 Individuals with less than 250,000 reads were discarded.

199

#### 200 *Genetic diversity and population structure*

201 Estimates of genetic diversity (i.e. mean number of alleles per locus ( $N_a$ ), observed  
 202 ( $H_o$ ) and expected ( $H_e$ ) heterozygosity, proportion of polymorphic loci), departure  
 203 from Hardy–Weinberg equilibrium (HWE) and inbreeding coefficients ( $F_{IS}$ ) were  
 204 estimated using GENEPOP v4.0 (Rousset 2008) and ARLEQUIN v3.5 (Excoffier and  
 205 Lischer 2010). Because a minimum allele frequency (MAF) filtering was not applied,  
 206 ARLEQUIN was also used to estimate  $H_o$ ,  $H_e$  and  $F_{IS}$  exclusively with polymorphic  
 207 loci (Minimum Allele Frequency (MAF) > 0.017 according to sample size) for  
 208 comparison with previous studies.  
 209 Global and pairwise coefficients of population differentiation ( $F_{ST}$ ) between cockle  
 210 beds were calculated with ARLEQUIN v3.5 using 10,000 permutations to test for

211 significance. The variational Bayesian clustering method implemented in the package  
212 fastSTRUCTURE v2.3.4 (Raj et al. 2014) was used to estimate the number of genetic  
213 population units (K) in the whole studied area and in each region testing from K = 1 to  
214 K = number of beds + 1, with an admixture ancestry model, convergence criterion of  $1 \times 10^{-8}$ , five cross-validated sets and the simple prior (flat-beta prior). The most likely  
215 number of K was estimated using the “chooseK.py” program included in the  
216 fastSTRUCTURE which gives the best K value and the K corresponding with weak  
217 population structure in the data using heuristic scores. Summarised outputs were carried  
218 out using the software POPHELPER (Francis 2017). Discriminant analyses of principal  
219 components (DAPC) were run in ADEGENET package (Jombart et al. 2010; Jombart  
220 and Ahmed 2011) for the R platform (R Development Core Team, 2014; [http://www.r-](http://www.r-project.org)  
221 [project.org](http://www.r-project.org)) with the whole dataset and for each region. Data were transformed using  
222 PCA (Principal Component Analysis) and the optimal number of principal components  
223 (PC) was calculated using the `optim.a.score()` command (see Miller et al. 2020).  
224 Isolation by distance (IBD) was checked by the correlation between geographical  
225 (measured as the shortest oceanic distance between two beds in Km) and genetic  
226 distance (measured as  $F_{ST}/1-F_{ST}$ ; Rousset 1997) matrices using a Mantel test with  
227 10,000 permutations using NTSYS v.2.1 (Rohlf 1993).

229

### 230 *Outlier tests*

231 The Bayesian  $F_{ST}$  –based method implemented in BAYESCAN v2.1 (Foll and  
232 Gaggiotti 2008) was used to identify outlier loci subjected to selection. BAYESCAN  
233 was run using default parameters (i.e. 20 pilot runs; prior odds value of 10; 100,000  
234 iterations; burn-in of 50,000 iterations and a sample size of 5,000, hereafter “BY10”),  
235 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, °C); sea bottom temperature (SBT, °C); sea surface salinity (SSS, psu); sea bottom salinity (SBS, psu); bottom shear stress (BSS, N·m<sup>-2</sup>); net primary productivity (NPP, mg·m<sup>-3</sup>·day<sup>-1</sup>); 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](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](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

286 Galicia, respectively. First, analyses were performed with 100,000 iterations across five  
287 independent runs to obtain the average covariance matrix for each subset. Secondly, the  
288 correlation between each SNP and the different variables was calculated using 100,000  
289 iterations to obtain Bayes factors (BF). As in the previous step, five independent runs  
290 were used. Only SNPs with a BF > 10 and Spearman's coefficient ( $\rho$ ,  $\rho$ ) thresholds >  
291 1% for any variable in all runs were considered as a well-supported environment-  
292 associated SNPs. Finally, significantly correlated SNPs were compared with the outliers  
293 identified in the BAYESCAN and PCADAPT analyses.

294

#### 295 *Gene mining and functional enrichment*

296 RAD-tags including divergent outlier SNPs were mapped in the *C. edule* genome (Bruzos  
297 et al. 2022) and their position compared with the consistent genomic windows under  
298 divergent selection previously reported by Vera et al. (2022) in the Northeast Atlantic  
299 Ocean. The very low genetic differentiation with neutral markers in the studied areas  
300 precluded the detection of consistent genomic regions under stabilizing selection. Thus,  
301 we could verify in more restricted geographical scenarios (SW British Isles and Galicia)  
302 the consistency of the genomic regions under divergent selection previously detected.  
303 Additionally, we looked for new regions under selection considering the singularity of  
304 the new sample collections of this study following a similar methodology to that proposed  
305 by Vera et al. (2022). Briefly, we defined a consistent window when  $\geq 2$  consecutive  
306 outliers were detected; then, we expanded the region  $\pm 250$  kb from the external outliers  
307 of the seed to define a genomic window for mining. Genes included in those genomic  
308 windows were identified using the cockle's transcriptome assembled and annotated by  
309 Pardo et al. (2022), which was used as reference to detect Gene Ontology (GO) functional  
310 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 ( $\pm$  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 ( $H_o$ ) and expected ( $H_e$ ) heterozygosities ranged respectively from 0.070 (SMO\_17, Spain) to 0.080 (IWC\_20, IGC\_20 and IKF\_20, Ireland; mean  $\pm$  SD = 0.075  $\pm$  0.003) and from 0.076 (WDE\_17, Wales) to 0.087 (SNO\_17, Spain and IKF\_20, Ireland; mean  $\pm$  SD = 0.082  $\pm$  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

336 (Spain) (mean  $\pm$  SD =  $41.3 \pm 7.2\%$ ). When only polymorphic loci within each bed were  
 337 considered,  $H_o$  ranged from 0.137 in SLO\_17 (Spain) to 0.181 in SMO\_17 (Spain)  
 338 (mean  $\pm$  SD =  $0.155 \pm 0.014$ ), showing these two beds also the lowest (0.156) and  
 339 highest (0.200)  $H_e$  (mean  $\pm$  SD =  $0.171 \pm 0.012$ ). No differences in genetic diversity  
 340 were found between the SW British Isles and Galician regions (Mann-Whitney U tests  
 341  $P > 0.250$  for  $H_o$ ,  $H_e$  with all loci and with polymorphic loci). Genetic diversity was in  
 342 the range of previous values reported by Vera et al. (2022) for the whole Atlantic area  
 343 using the same methodology.

344 Global  $F_{ST}$  for all beds was 0.02118 ( $P < 0.001$ ), pairwise  $F_{ST}$  ranged from 0 (non-  
 345 significant  $\neq 0$ ) for many bed pairs up to a maximum of 0.05040 ( $P < 0.001$ ) between  
 346 IDC\_18 and SVI\_17 (Supplementary Table 2). Most pairwise comparisons were  
 347 significant excluding those from Galicia. Average pairwise  $F_{ST}$  between the SW British  
 348 Isles and Galicia was 0.03400 ( $P < 0.001$ ), while 0.01374 ( $P < 0.001$ ) within the SW  
 349 British Isles and -0.00529 ( $P = 1.000$ ) within Galicia. The two beds from the Cotentin  
 350 Peninsula (FBV\_19 and FGO\_19, SW British Isles region), separated by 190  
 351 kilometres, showed significant genetic differentiation ( $F_{ST} = 0.01207$ ,  $P < 0.001$ ). The  
 352 most likely K values inferred by fastSTRUCTURE were 1 and 3. When K = 3 was  
 353 plotted, two main groups were identified differentiating the SW British Isles (IGC\_20,  
 354 IKF\_20, IWC\_20, IDA\_18, IDC\_18, WDE\_17, WBY\_17, ECE\_20, FBS\_17, FBV\_19  
 355 and FGO\_19) from Galicia (plus Arcachon) (FAR\_17, SBA\_17, SMI\_17, SAN\_17,  
 356 SNO\_17, SLO\_17, SSA\_17, SVI\_17, SCA\_17, SMO\_17, SBI\_18) (Fig. 2A). FGO\_19  
 357 (France, Cotentin Peninsula) showed a high component of the southern group, also  
 358 detectable in all samples from the English Channel (ECE\_20, FBS\_17 and FBV\_18),  
 359 suggesting some introgression between the two groups. The DAPC representation on  
 360 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. 4A).

#### *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

386 (IKF\_20 – WDE\_17) to 0.02366 (IGC\_20 – FGO\_19 pair) for neutral markers; from  
 387 0.00061 (IDA\_18 – IDC\_18 pair) to 0.17142 (IDA\_18 – FGO\_19 pair) for the 186 total  
 388 outliers; and from -0.00345 (IDA\_18 – IDC\_18 pair) to 0.27313 (IKF\_20 – FBS\_17  
 389 pair) for the 35 shared outliers (Supplementary Table 4). IBD was significant with the  
 390 shared and total outlier datasets ( $r = 0.63169$  and  $0.55136$ , respectively;  $P < 0.001$ ), but  
 391 not with the neutral dataset ( $r = 0.08578$ ,  $P = 0.330$ ). These results suggest that  
 392 correlations could be a by-product of the unequal spatial distribution of the  
 393 environmental factors responsible of selective forces shaping the cockle's genome,  
 394 since IBD patterns should be reflected by the balance between drift and migration on  
 395 neutral markers. The fastSTRUCTURE analyses identified  $K = 1$ ,  $K = 2$  and  $K = 3$  as  
 396 the most likely values for the neutral, 35 shared outlier and 186 total outlier datasets,  
 397 respectively (Fig. 2B), which consistently differentiated the Celtic Sea and the North-  
 398 west Irish cluster (IGC\_20, IKF\_20 and IWC\_20), not studied to date, and the English  
 399 Channel cluster (ECE\_20, FBS\_17, FBV\_19, FGO\_19). In contrast, the Irish Sea  
 400 appeared as a rather differentiated group with the 186 outliers, which was split into two  
 401 clusters, the Irish side (IDA\_18 and IDC\_18) most closely associated with the Celtic  
 402 and Atlantic Ocean cluster, and the Welsh side (WDE\_17 and WBY\_17), most closely  
 403 linked with the English Channel cluster, when using the 35 outlier loci. The  
 404 differentiation of the Irish Sea from the other samples, and the contrast between the  
 405 Welsh and Irish (east and west, respectively) samples of the Irish Sea, was shown when  
 406 exploring a scenario with a larger  $K$  value, with both datasets displaying a very similar  
 407 structure with  $K = 4$  (Supplementary Figures 2 and 3). The DAPC analysis with neutral  
 408 markers showed a very similar picture to that described with the whole SNP dataset  
 409 (Fig. 3B), however, the 186 and 35 outlier datasets displayed a very distinct picture,  
 410 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) (Figs. 3C and 3D). 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 (Figs. 4A and B). 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. 4) and only suggested with DAPC (Fig. 4C).

#### *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

436 seasons, respectively. Net primary production (NPP) was suggested for all datasets in  
437 the winter season and for the 186 outlier dataset for the reproductive season. Finally,  
438 BSS was suggested in all seasons for the neutral dataset and in the reproductive and  
439 summer seasons for the complete dataset. In Galician region, no associations were  
440 found, except for latitude in all periods analysed using the 51 outliers, and for BSS  
441 during winter when latitude and longitude were removed (Table 2). However, VIF  
442 values were usually high ( $> 10$ ), suggesting that results should be taken with caution  
443 due to the high collinearity among the variables in many cases.

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

451

#### 452 *Gene mining around outliers and environmental correlated markers*

453 Genetic markers associated with divergent selection or correlated with environmental  
454 variables were mapped in the common cockle genome to look for functional  
455 interpretation (Supplementary Tables 3 and 6). Outliers identified in the SW British  
456 Isles area were scattered across all chromosomes, between one in C18 and 22 in C3,  
457 while five chromosomes (C8, C11, C13, C14, C17) did not bear any outlier in Galicia,  
458 the maximum being detected in C1 (11 outliers) (Table 3). The 51 outliers detected in  
459 Galicia only identified a single consistent genomic region (window) under selection  
460 according to our criteria and other five outliers were distributed across four confident

461 genomic windows previously reported by Vera et al. (2022) (Supplementary Tables 7  
 462 and 8). However, among the 186 outliers detected in the SW British Isles, 14 defined  
 463 five new consistent genomic windows under divergent selection and other 45 mapped  
 464 on genomic windows previously reported by Vera et al. (2022) (Supplementary Tables  
 465 7 and 8). Most outliers detected in Galicia were specific to this region, while an  
 466 important number of outliers from the SW British Isles were shared with the Northern  
 467 region previously analysed by Vera et al. (2022) (Supplementary Fig. 5). Still, a notable  
 468 proportion of outliers in the North were specific of each study (North-Vera et al.  
 469 (2022): 137 vs SW British Isles: 101) suggesting specific evolutionary factors related to  
 470 each scenario. Among the genes annotated in the five new windows, several related to  
 471 oxidative stress, hypoxia and immunity were identified in a 200 kb region in C2 and in  
 472 a 340 kb region in C3 (Supplementary Table 9) (Gerdol and Venier 2015; Grandi et al.  
 473 2016; Sokolov et al. 2019). Also, in a 480 kb region in C5, some genes involved in  
 474 signalling and detoxification (Wang et al. 2018; Kron 2022; Thoma et al. 2022) were  
 475 identified. Finally, a gene associated with ocean acidification (Lim et al. 2021) was  
 476 identified in C19. Despite the low number of genes handled, a significantly enriched  
 477 GO Molecular Function was detected (protein serine/threonine phosphatase activity;  
 478 GO:0004722) taking as background the common cockle transcriptome reported by  
 479 Pardo et al. (2022).

480 Markers correlated with environmental variables were scattered across most  
 481 chromosomes, excluding C7, C14 and C18, and the higher number (seven markers)  
 482 were detected in two big chromosomes (C2 and C4) (Table 3). An important number of  
 483 correlated markers were also identified as outliers for divergent selection (55.6 %),  
 484 some of them associated with consistent genomic windows (Supplementary Table 8).  
 485 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 °C in the Cantabrian coast compared with the 18.5 °C 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 °C) than in the southern ones (mean = 16.47 °C) 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



561 relevant genes related to oxidative stress and immunity that would deserve further  
562 studies as candidates to explain the association observed with environmental factors.  
563 Despite biotic factors, such as pathogens, could not be contemplated in our study, their  
564 diversity and distribution (influenced by abiotic factors) are important drivers shaping  
565 the genome and distribution of species (Theodosopoulos et al. 2019) and specifically in  
566 cockles (Vera et al. 2022; Pampin et al. 2023). Furthermore, we also deepened into the  
567 correlation of specific SNPs with environmental factors and could identify, by mining  
568 in the cockle genome several genes related to nervous transmission and immunity,  
569 arranged in clusters or scattered in different chromosomes, that had been previously  
570 reported in other mollusc associated with temperature or oxidative stress (Woo et al.  
571 2011; Barbosa et al. 2022; Chen et al. 2022).

572 The population structure observed in the SW British Isles region may be in part  
573 explained by the residual ocean currents and ocean fronts that characterise this area, but  
574 also by selective factors such as salinity gradients, variable bottom shear stress (due to  
575 large tidal variability) and sea temperature gradients (driven by ocean currents,  
576 stratification and mixing, and latitudinal gradients); however, spatial seascape results  
577 should be taken with caution due to the collinearity detected among variables. Both  
578 outlier datasets could identify four genetic clusters following two main west-east and  
579 north-south axes, which could explain the correlation observed between genetic and  
580 geographic distances for outlier loci, but also the identification of longitude and latitude  
581 as two main drivers in the seascape analysis. According to the outlier information, the  
582 new sampled beds from Western Ireland (IGC\_20, IKF\_20 and IWC\_20) (Northeast  
583 Atlantic) would constitute a new cluster. These sites are connected by the Irish coastal  
584 current (Brown et al. 2003; Fernand et al. 2006) and larval dispersal modelling (see Fig.  
585 7 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 fornicata* (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.

606

#### 607 *Management implications*

608 The present study represents a refined analysis of the population structure of *C. edule* in  
609 two geographic areas of small-medium size representing differentiated models that could  
610 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.

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638

#### 639 **Author Contributions**

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

647

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652

#### 653 **Conflict of interest**

654 The authors declare no conflict of interest.

655

#### 656 **Data archiving**

657 Data for this study are available at Dryad Digital Repository (<http://to be completed after>  
658 *manuscript is accepted for publication*) and Supplementary material.

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978

979 **Figure legends:**

980 Figure 1. Geographical distribution of the *Cerastoderma edule* beds analysed in the  
981 present study. Ocean bathymetry is shaded in blue. Summer sea surface ocean currents  
982 are schematically depicted with magenta coloured arrows. Tidal mixing fronts are  
983 indicated with purple dashed lines. 'UF' stands for Ushant Front, 'CSF' for Celtic Sea  
984 Front, and 'ISF' for Irish Sea Front. Location codes are shown in Table 1. Beds  
985 previously analysed by Vera et al. (2022) are marked with asterisks.

986 Figure 2. Population structure of *Cerastoderma edule* at different geographical scales  
987 using fastSTRUCTURE. Each vertical bar represents one individual, and the colour  
988 proportion of each bar represents the posterior probability of assignment of each  
989 individual to the different clusters (K) inferred by the program. The most likely K = 3  
990 using the whole dataset (A), and K = 2 using the 57 shared divergent outliers between  
991 methodologies and K = 3 using the total 186 divergent outliers (B) for the SW British  
992 Isles are represented. Codes are shown on Table 1. Plots for all the K values tested for  
993 the different datasets are shown in Supplementary Figures.

994 Figure 3. Discriminant Analysis of Principal Components (DAPC) plots of  
995 *Cerastoderma edule* beds belonging to the SW British Isles. The weight of retained  
996 discriminant analysis (DA) and principal components selected are shown on left bottom  
997 box and right bottom box, respectively. Results using the complete whole dataset (A),  
998 the neutral dataset (B), the 35 shared divergent outliers between methodologies (C) and  
999 the 186 divergent outliers (D) are represented. Codes are shown on Table 1.

1000 Figure 4. Discriminant Analysis of Principal Components (DAPC) plots of  
1001 *Cerastoderma edule* beds belonging to Galicia. The weight of retained discriminant  
1002 analysis (DA) and principal components selected are shown on left bottom box and

1003 right bottom box, respectively. Results using the complete dataset (A), neutral dataset  
1004 (B) and 51 divergent outliers (C) are represented. Codes are shown on Table 1.

1005 Table 1. *Cerastoderma edule* beds analysed in the present study. Location, sampling year, geographical coordinates, code, country, number of  
1006 individuals collected (N initial) and analysed after quality filtering (N), observed heterozygosity (Ho), expected heterozygosity (He), inbreeding  
1007 coefficient (F<sub>IS</sub>) for all dataset and for polymorphic loci are shown. Locations in italics were previously analysed by Vera et al. (2022).

Location	Year	Lat (deg N)	Lon (deg E)	Code	Country	N initial	All dataset				Polymorphic loci (MAF > 0.017)				
							N	Ho	He	F <sub>IS</sub>	Polymorphic loci	% Polymorphic loci	Ho	He	F <sub>IS</sub>
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
<i>Dundalk Bay-Annagassan</i>	<i>2018</i>	<i>53.884</i>	<i>-6.341</i>	<i>IDA_18</i>	<i>Ireland</i>	<i>29</i>	<i>29</i>	<i>0.074</i>	<i>0.080</i>	<i>0.082</i>	<i>2993</i>	<i>32.4</i>	<i>0.161</i>	<i>0.177</i>	<i>0.090</i>
<i>Dundalk Bay-Cooley</i>	<i>2018</i>	<i>53.996</i>	<i>-6.287</i>	<i>IDC_18</i>	<i>Ireland</i>	<i>22</i>	<i>22</i>	<i>0.077</i>	<i>0.083</i>	<i>0.081</i>	<i>3493</i>	<i>37.8</i>	<i>0.173</i>	<i>0.190</i>	<i>0.087</i>
<i>Dee Estuary</i>	<i>2017</i>	<i>53.343</i>	<i>-3.174</i>	<i>WDE_17</i>	<i>Wales</i>	<i>30</i>	<i>28</i>	<i>0.071</i>	<i>0.076</i>	<i>0.074</i>	<i>2561</i>	<i>27.7</i>	<i>0.167</i>	<i>0.182</i>	<i>0.084</i>
<i>Burry</i>	<i>2017</i>	<i>51.643</i>	<i>-4.166</i>	<i>WBY_17</i>	<i>Wales</i>	<i>30</i>	<i>30</i>	<i>0.073</i>	<i>0.080</i>	<i>0.091</i>	<i>3529</i>	<i>38.2</i>	<i>0.148</i>	<i>0.165</i>	<i>0.101</i>
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
<i>Somme Bay</i>	<i>2017</i>	<i>50.201</i>	<i>1.627</i>	<i>FBS_17</i>	<i>France</i>	<i>30</i>	<i>30</i>	<i>0.071</i>	<i>0.080</i>	<i>0.111</i>	<i>3438</i>	<i>37.2</i>	<i>0.147</i>	<i>0.167</i>	<i>0.119</i>
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
<i>Arcachon Bay</i>	<i>2017</i>	<i>44.580</i>	<i>-1.238</i>	<i>FAR_17</i>	<i>France</i>	<i>30</i>	<i>30</i>	<i>0.074</i>	<i>0.083</i>	<i>0.111</i>	<i>4335</i>	<i>46.9</i>	<i>0.140</i>	<i>0.159</i>	<i>0.120</i>
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
<i>Ría de Noia</i>	<i>2017</i>	<i>42.790</i>	<i>-8.923</i>	<i>SNO_17</i>	<i>Spain</i>	<i>30</i>	<i>30</i>	<i>0.078</i>	<i>0.087</i>	<i>0.099</i>	<i>4885</i>	<i>52.8</i>	<i>0.139</i>	<i>0.156</i>	<i>0.107</i>
<i>Lombos do Ulla</i>	<i>2017</i>	<i>42.629</i>	<i>-8.775</i>	<i>SLO_17</i>	<i>Spain</i>	<i>30</i>	<i>30</i>	<i>0.075</i>	<i>0.085</i>	<i>0.113</i>	<i>4602</i>	<i>49.8</i>	<i>0.137</i>	<i>0.156</i>	<i>0.120</i>
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

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1009 Table 2. Results of the redundancy analysis (RDA) on the SW British Isles region of *Cerastoderma edule*. Only variables included by the  
1010 forward selection model are shown.

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

1013

	NPP	0.017		0.008		0.019	1012
	SST	0.011		0.014		0.001	
<b>Summer</b>	SBT	-	0.086	-	0.083	0.009	0.355
	SBS	-		-		0.083	
	BSS	0.001		0.001		-	

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

Adjusted R<sup>2</sup> 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.

1017 Table 3. Distribution of divergent outliers and markers correlated with environmental  
 1018 variables in the SW British Isles and Galicia across the *Cerastoderma edule* genome  
 1019 (version 4.0).

Mega-scaffold (chromosome)	Chromosome length (bp)	Outlier loci (divergent selection)			Markers correlated environmental variables*
		British Isles	Galicia	Shared	
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)

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1021 \* Only detected in SW British Isles; in parentheses those markers also identified as  
 1022 outliers for divergent selection

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Fig.1

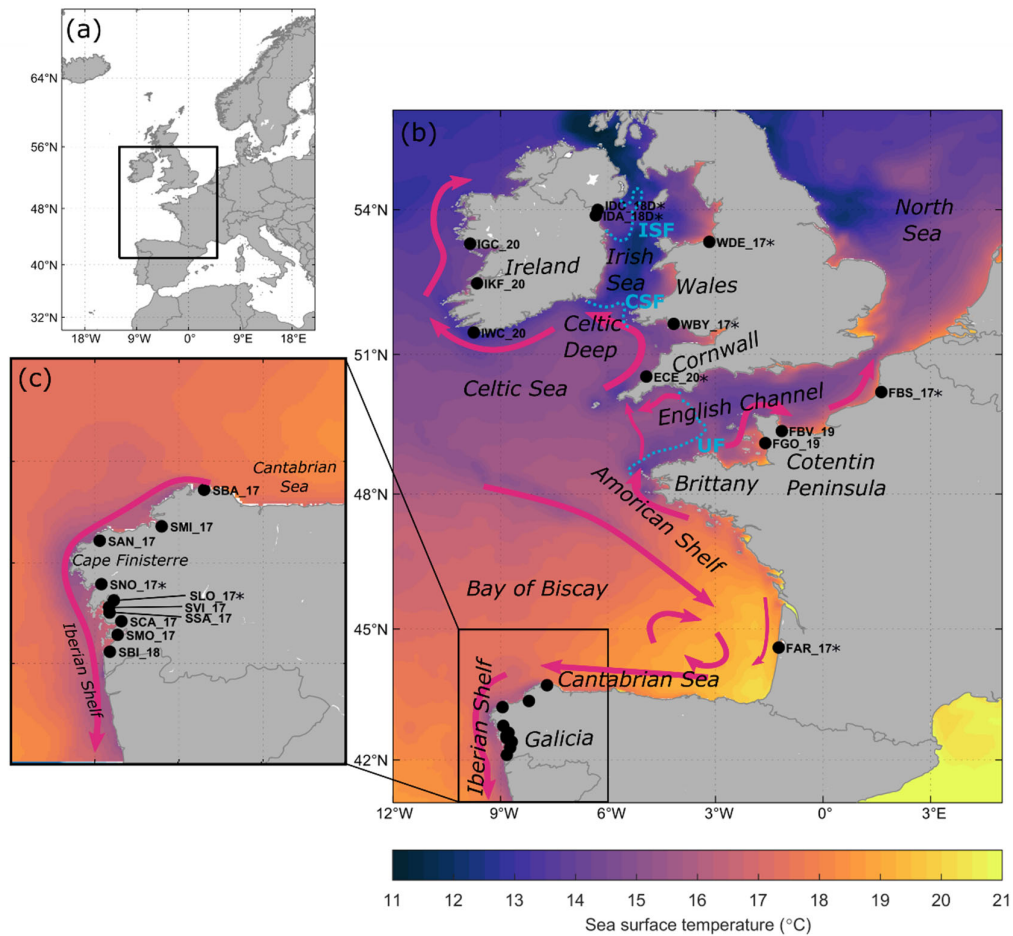


Fig.2

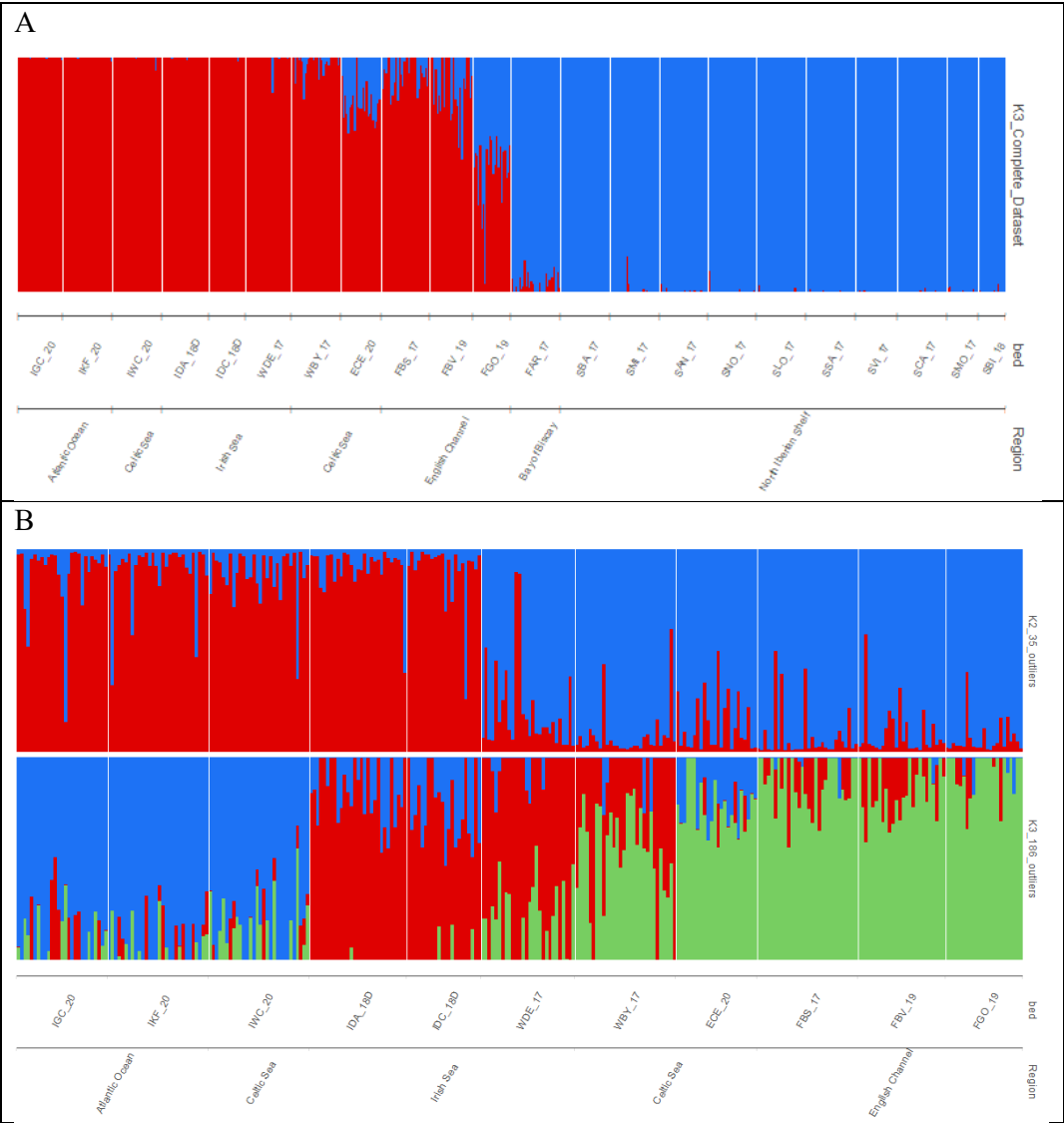
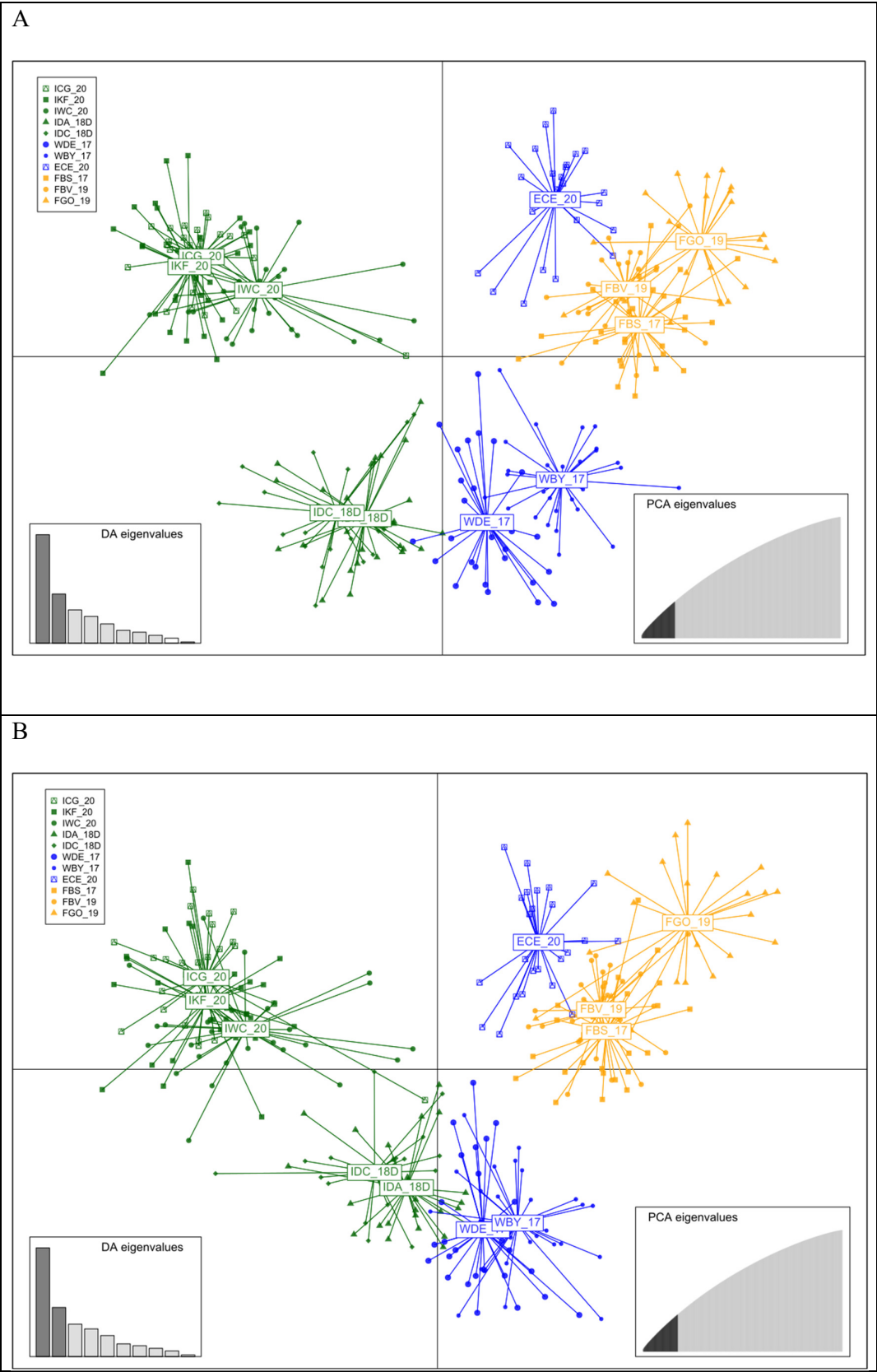
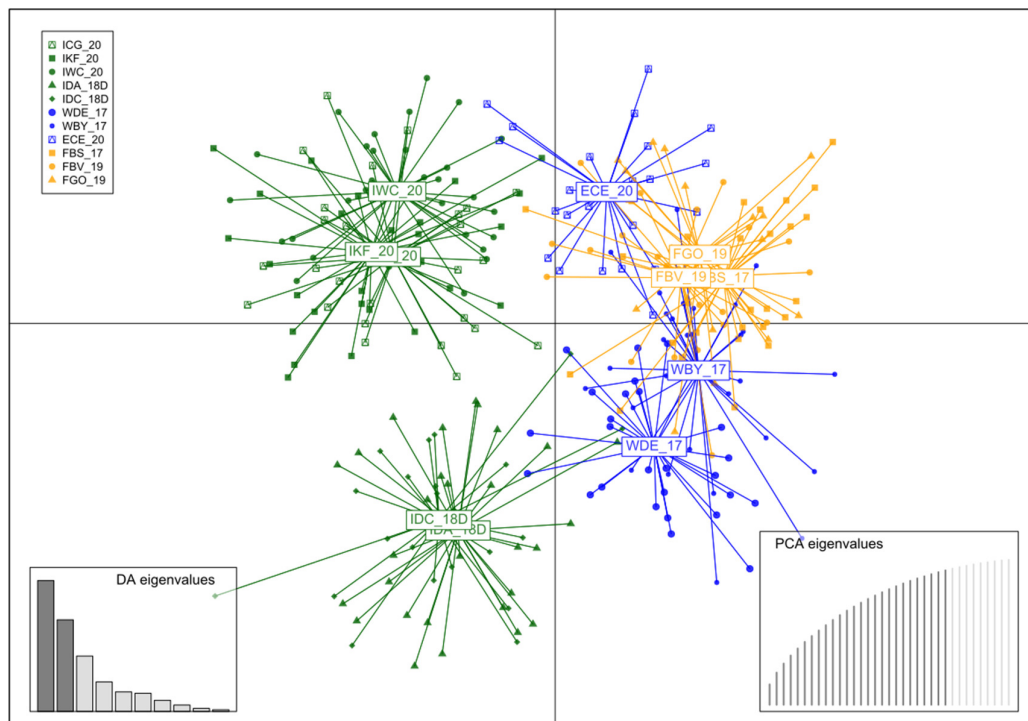


Fig.3



C



D

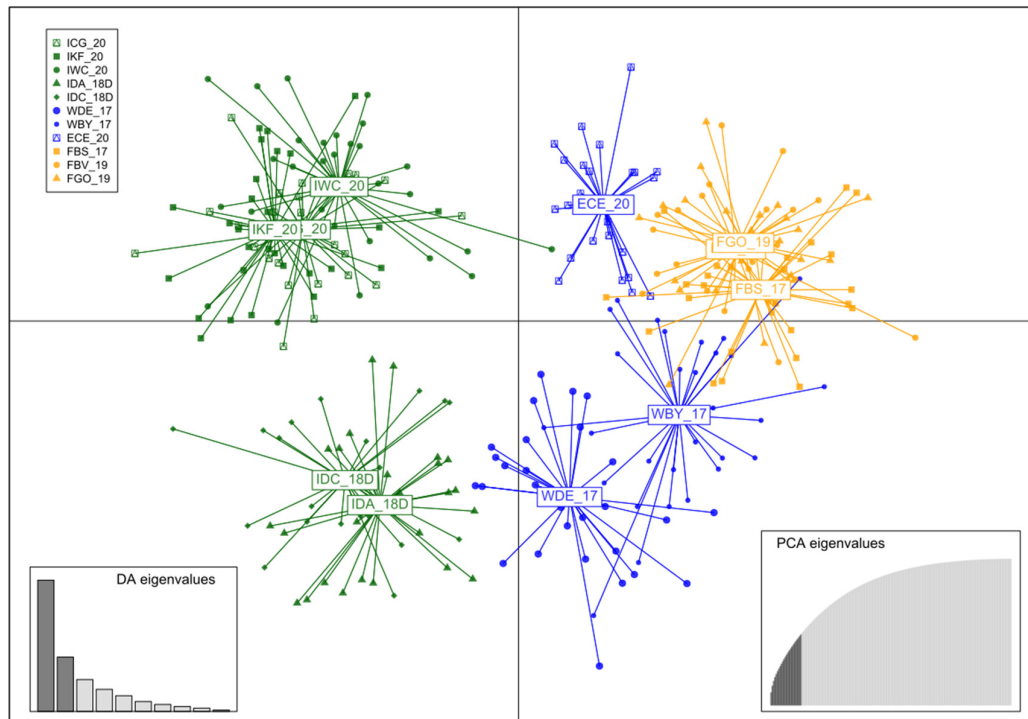
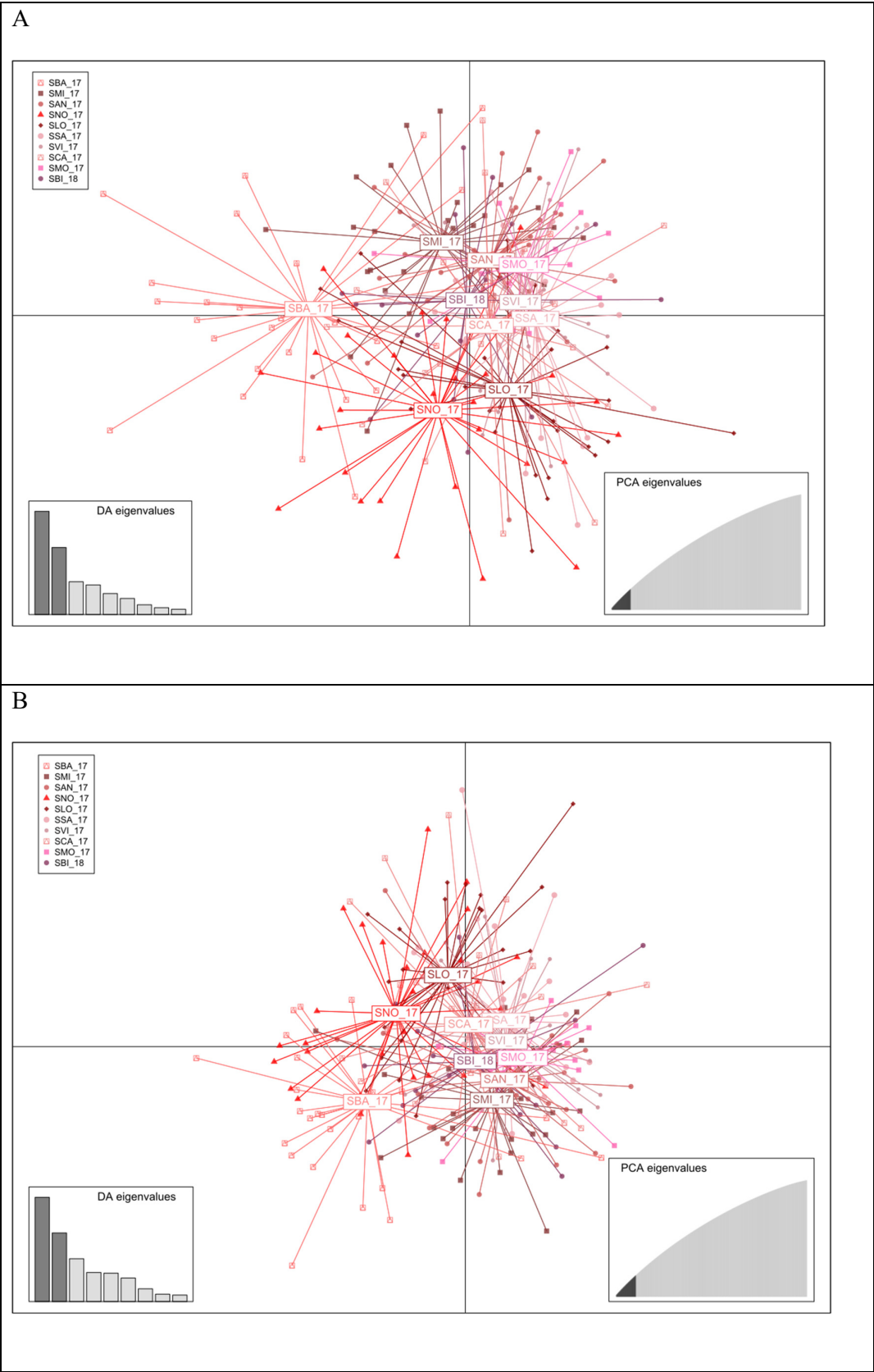


Fig. 4



C

