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1 Seascape genetic study on *Laminaria digitata* underscores the critical role of sampling schemes

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18 SHORT TITLE: Seascape genetic study on *Laminaria digitata*

21 **ABSTRACT:**

22 Understanding connectivity patterns in endangered species living in fragmented habitats is
23 fundamental to improve management and conservation actions. Such improvements can be
24 particularly pressing at trailing edges where populations are facing the greatest challenges of
25 climate change, and appear all the more crucial if the species is commercially harvested. Seascape
26 genetics have been increasingly used to meet these needs. In this study, we examined connectivity
27 patterns among 32 populations located at the southern range limit of the oarweed kelp *Laminaria*
28 *digitata*. Our populations were sampled in a roughly continuous manner, with the distance between
29 neighboring populations ranging from a few km to about a few hundreds. By genotyping 11
30 microsatellite markers, our aim was to (1) refine analyses of population structure, (2) test whether
31 on-shelf islands are genetically more differentiated compared to mainland populations, (3) evaluate
32 the relative importance of various abiotic conditions in shaping the genetic structure and (4)
33 evaluate if the relative importance of each environmental factor varied according to sampling
34 schemes. Our analyses revealed a positive relation between connectivity links and genetic
35 diversity: populations with high levels of connectivity were genetically enriched while isolated
36 populations showed signs of genetic erosion. The genetically impoverished populations
37 corresponded to the southernmost populations as well as populations along the northern coast of
38 Brittany (Locquirec, Saint-Malo Bay) and the northernmost population in Pas-de-Calais. By
39 performing db-RDA on various sampling schemes, geographic distance appeared as the dominant
40 factor influencing connectivity between populations separated by great distances, while
41 hydrodynamic processes were the main factor when analyzing continuously distributed
42 populations.

43
44 **KEYWORDS:** connectivity, seascape genetics, *Laminaria digitata*, microsatellite markers,
45 sampling scheme

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47

48 1. INTRODUCTION

49 Understanding connectivity patterns in endangered species living in fragmented habitats is
50 fundamental to assess their vulnerability to environmental changes and to define conservation
51 measures at appropriate scales (Manel et al. 2019, Benestan et al. 2023). Such knowledge is
52 particularly relevant at the trailing edge of species distribution, where the numerous effects of
53 global warming can interfere with the strong genetic and demographic drifts (Nadeau & Urban
54 2019). Investigating connectivity can additionally pinpoint populations that are isolated from gene
55 flow. Yet genetic isolation can, in some cases, impede adaptation and ultimately lead to extinction
56 (Lynch & Lande 1993). A deeper understanding of population connectivity can therefore advance
57 conservation action aiming to preserve species adaptive potential via measures that prevent the
58 loss of genetic diversity.

59 Most marine organisms disperse through planktonic propagules (*e.g.*, spores, eggs, larvae)
60 which are deemed unable to counter hydrodynamic forces (Alberto et al. 2010). The influence of
61 oceanographic processes on population genetic structure has therefore been repeatedly proven in
62 different marine taxa by means of biophysical models (*e.g.*, Gilg & Hilbish 2003, Treml et al.
63 2008, Mitarai et al. 2009 and more recently by Xuereb et al. 2018, Benestan et al. 2021, Reynes et
64 al. 2021). For instance, hydrodynamic processes have been associated with larval retention and
65 asymmetrical gene flow (Gaylord & Gaines 2000), both of which inevitably affect metapopulation
66 dynamics. White et al. (2010) have additionally demonstrated that ocean currents enable exchanges
67 between coastal islands - defined as the ones located on the continental shelf - and mainland
68 populations. Although coastal islands have limited evolutionary and ecological interests compared
69 to more remote oceanic islands (Dawson 2016), understanding their connectivity patterns could
70 still have significant implications for conservation. Yet, to this date, a formal comparison of the
71 connectivity between on-shelf island and coastal populations is still lacking for marine species in
72 comparison to terrestrial ones (Bell 2008). Although oceanic currents are fundamental in shaping
73 the genetic structure of marine species, their effects on their own are insufficient to explain entire
74 connectivity patterns (Hu et al. 2020). Species' life history traits and larval behavior appear to

75 influence dispersal kernels to a certain extent (Sanford & Kelly 2011), as illustrated by the
76 differences in phylogeographic breaks among marine taxa, albeit historical patterns and/or habitat
77 availability being also at play (Teske et al. 2011, 2017, Martins et al. 2022). When considering
78 heterogeneous environments, local adaptation can constrain gene flow (or the rate of effective
79 migration, Aeschbacher et al. 2017) even in the absence of physical barriers to dispersal, a
80 phenomenon that has been termed “isolation by adaptation” (Nosil et al. 2009, Schoville et al.
81 2012). In such scenarios, contrasted patterns of genetic structure can be observed at neutral and
82 putatively selected loci (see Grummer et al. 2019 for review and Sandoval-Castillo et al. 2018,
83 Van Oppen & Coleman 2022).

84 Seascape genetics aims to investigate which and how marine environmental features
85 influence the spatial distribution of genetic variation at neutral or putatively adaptive loci (Xuereb
86 et al. 2019, Boussarie et al. 2022). Among the tested features, water depth (*e.g.*, Engel et al. 2004,
87 Hickey et al. 2009, Krueger-Hadfield et al. 2013), habitat discontinuity (*e.g.*, Alberto et al. 2010,
88 2011, D’Aloia et al. 2014, Durrant et al. 2018), sea surface temperature (“SST”, *e.g.*, Johansson
89 et al. 2015, Benestan et al. 2016, Guzinski et al. 2020) and salinity (*e.g.*, Gaggiotti et al. 2009,
90 Sjöqvist et al. 2015) have been shown to explain, separately or jointly, a large part of the variation
91 in genetic structure. However, most of these studies have relied on linear regressions and Mantel
92 tests to show the influence of environmental factors (see Benestan et al. 2016 for references),
93 although these statistical frameworks suffer from high false positive rates (Graves et al. 2013).
94 This problem has been significantly reduced by the use of variance partitioning methods
95 (Capblancq & Forester 2021), such as distance-based redundancy analysis (db-RDA; Legendre &
96 Anderson 1999). In addition to the statistical advances, the improvement of hydrodynamic models
97 and the developments of Moran’s and asymmetric eigenvector maps (Dray et al. 2006, Blanchet
98 et al. 2008b) allowed a better apportioning of the contribution of geographic distance and
99 oceanographic features (*e.g.*, Benestan et al. 2016, 2021, Xuereb et al. 2018, Reynes et al. 2021).
100 Yet some of the oceanographic processes have very localized effects (Legendre & Demers 1984),
101 and other abiotic factors influencing genetic structure (*e.g.*, SST) can similarly vary at a fine

102 geographical scale (see for example Gallon et al. 2014). Their relative influence on genetic
103 structure is therefore expected to vary according to geographical extents (Jombart et al. 2009,
104 Dalongeville et al. 2018), which underlines how sampling design can itself influence the
105 conclusions.

106 Kelp forests are a dominant feature along many temperate to boreal rocky shores and play a
107 foundation role for numerous species by providing them substrate, shelter or food (Teagle et al.
108 2017, Jayathilake & Costello 2020, Coleman & Veenhof 2021). The decline they have shown in
109 some North-East Atlantic biogeographic regions has justified their recent inclusion in the OSPAR
110 list of threatened and declining habitats (de Bettignies et al. 2021). SST is considered as the major
111 abiotic factor shaping kelp species' distribution as denoted by the cold-water niches they tend to
112 associate with (Lüning 1990, Bartsch et al. 2008). Over the past decade, various studies have
113 shown the harmful consequences of rising SST on kelp forests, notably as a result of ever more
114 frequent and intense marine heatwaves , which especially affect warm-edge populations
115 (Fernández 2011, Starko et al. 2019, Arafeh-Dalmau et al. 2019, Filbee-Dexter et al. 2020, but see
116 Klingbeil et al. 2022). In this context, clarifying connectivity in the warm distribution edge might
117 be particularly valuable to gauge the resilience of marginal populations. For instance, detecting
118 effective dispersal from the range center towards the margin could indicate the possibility of an
119 evolutionary rescue. Yet, an evolutionary rescue will be possible only if marginal and core
120 populations are adapted to similar environmental conditions (Bridle et al. 2009, DuBois et al.
121 2022).

122 *Laminaria digitata* (Hudson) J.V. Lamouroux is a boreal kelp species with an amphi-Atlantic
123 distribution. Its geographic range in the northeast Atlantic extends from temperate southern
124 Brittany (47°N, France) to the arctic Spitsbergen archipelago (79°N, Norway) (Kain 1979, Lüning
125 1990, Araújo et al. 2016). Along the shorelines, *L. digitata* generally occurs within a narrow band
126 spanning the lower intertidal and upper subtidal zones (Robuchon et al. 2014). This species thus
127 presents an interesting case to test the effect of coastal oceanographic currents on genetic structure,
128 especially along the rugged coast of Brittany, where hydrodynamics is highly complex due to

129 numerous mesoscale features (*e.g.*, fronts, upwellings, river plumes, low salinity lenses) and
130 macrotidal ranges (Salomon & Breton 1993, Ayata et al. 2010, Nicolle et al. 2017). This species
131 has been historically harvested in Brittany, where an adaptation of the ongoing exploitation is
132 currently under discussion (Garineaud 2021). Additionally, annual mean SST varies at a fine scale
133 across Brittany, with the western and north-western sectors being cooler and currently less affected
134 by climate change than Southern and North-Eastern Brittany (Gallon et al. 2014). As suggested by
135 Liesner et al. (2020), this mosaic of SST conditions might have driven the distinct thermal
136 adaptations observed between populations from northern and southern Brittany. Finally, by using
137 a hierarchical sampling scheme, previous analyses of population structure at the scale of Brittany
138 have revealed significant genetic differentiation at both small (< 1 km) and large scales (> 10-50
139 km) relative to the region (Billot et al. 2003, Robuchon et al. 2014).

140 In this study, we extended the geographical sampling of previous microsatellite analyses
141 (Billot et al. 2003, Valero et al. 2011, Couceiro et al. 2013, Robuchon et al. 2014) by using a
142 dataset built from 32 populations ranging from the southern range limit of *L. digitata* to the
143 northernmost population found on the French coast, situated in the Strait of Dover. Using this
144 dataset, we explored the respective and combined effects of sampling year, hydrodynamic
145 processes, habitat discontinuity, spatial distance and SST on the genetic structure. We specifically
146 aimed to (1) refine the previous analyses of population structure for this species and identify
147 isolated populations, (2) test whether on-shelf island populations are genetically more
148 differentiated compared to mainland populations and thus show signs of genetic erosion, (3)
149 evaluate the relative importance of each environmental factor in shaping the genetic structure using
150 a db-RDA and finally (4) evaluate if their relative importance varies according to the sampling
151 scheme.

152 2. MATERIAL AND METHODS

153 2.1. Study area

154 Brittany is the northwestern-most region of mainland France (NE Atlantic, Figure 1). Its 2,860
155 km-length coastline encompasses a major biogeographical transition zone between cold- and

156 warm-temperate waters (Spalding et al. 2007). The northern shores, which border the English
157 Channel, are characterized by well-mixed waters produced by a macrotidal regime that intensifies
158 eastwards. Contrastingly, waters in southern Brittany are seasonally to permanently stratified and
159 show larger temperature fluctuations throughout the year (Gallon et al. 2014, Blauw et al. 2019).
160 Brittany's western-most sector is subject to both the macrotidal regime and the full impact of
161 Atlantic storms, which collectively maintain well-mixed conditions throughout the year and curb
162 seasonal temperature fluctuations (Gallon et al. 2014). Various boreal-affinity species benefit from
163 this nutrient-rich and thermally-buffered environment, including various kelp species that form
164 some of Europe's most important marine forests along Brittany's rocky shores.

165 2.2. Samples

166 Populations of *Laminaria digitata* were sampled between 2003 and 2015 in 32 sites ranging from
167 the southern limit of its NE Atlantic distribution (47°N) up to the Strait of Dover, at the entrance
168 of the North Sea (50°N, Table 1, Figure 1). The population at the Strait of Dover (S32) is known
169 to be geographically isolated, with the closest population along the French coast being in Étretat,
170 at *circa* 200 km to the southwest (see Figure 2C of Araújo et al. 2016) and for which we did not
171 have any sample. Among our populations, 10 were located around islands while 22 were on the
172 mainland coast (Table 1, Figure 1). In our study, we have defined *island* populations as those
173 situated on the continental shelf (*i.e.*, above 200 m depth, Dawson 2016). All of them were part of
174 the mainland during the Last Glacial Maximum when the ocean level was approximately 120 m
175 lower than present (Figure 1, Frenzel et al. 1992, Lambeck 1997). Some of these populations were
176 sampled and genotyped for previous studies as indicated in Table 1. At each site, blade tissue was
177 collected from 30 to 50 randomly selected sporophytes. Tissue samples were then wiped, cleaned
178 from epiphytes and stored in silica-gel crystals until DNA extraction.

179 2.3. Microsatellite genotyping

180 2.3.1. DNA extraction

181 DNA was extracted from 8–12 mg of dried tissue using the NucleoSpin 96 Plant II kit (Macherey-
182 Nagel GmbH & Co. KG) following manufacturer's instructions. The lysis, microsatellite

183 amplification and scoring were performed for 12 polymorphic loci following Robuchon et al.
184 (2014). Multiplex PCRs were modified using 5X GoTaq Flexi colorless reaction buffer (Promega
185 Corp., Madison, USA) instead of 1X and performed using a T100™ Thermal Cycler (Bio-Rad
186 Laboratories Inc.).

187 2.3.2. Microsatellite amplification, scoring

188 Among the markers used for this study, six were developed for *L. digitata* (Ld148, Ld158, Ld167,
189 Ld371, Ld531, and Ld704; Billot et al. 1998) and five for *L. ochroleuca* (Lo4-24, Lo454-17,
190 Lo454-23, Lo454-24, and Lo454-28; Coelho et al. 2014). Alleles were sized using the SM594 size
191 standard (Mauger et al. 2012) and scored manually using GeneMapper 4.0 (Applied Biosystems).
192 Individuals for which more than one locus did not amplify were removed from the dataset.

193 2.4. Preliminary analyses

194 Prior to genetic analyses, a Principal Component Analysis (PCA) was run using the “adegenet”
195 package (Jombart 2008) in R (R Core Team 2017) to check for the presence of other species. The
196 identity of the individuals was additionally confirmed based on allelic size at markers Ld148,
197 Ld158, Ld704, Lo4-24 and Lo454-23 following Mauger et al. (2021). In order to test the
198 independence of each marker, genotypic linkage disequilibrium was calculated for all pairs of
199 markers within and across populations using Genepop 4.7.5 (Rousset 2008). We used 1,000
200 dememorization, 100 batches and 1,000 iterations per batch for the Markov chain parameters. The
201 presence of null alleles was tested using MICROCHECKER (Van Oosterhout et al. 2004) and
202 genotypes were corrected according to the Van Oosterhout method. Difference between the
203 uncorrected and corrected F_{ST} matrices (pairwise estimates of genetic differentiation, see section
204 below) was checked using a Mantel test available in the “vegan” package (Oksanen et al. 2013).
205 Given the non-independence of the two datasets (corrected and uncorrected), differences in genetic
206 diversity parameters were checked using a Wilcoxon test available in the “stats” R package.

207 2.5. Population structure

208 Population structure was first assessed with two multivariate methods: a Principal Coordinate
209 Analysis (PCoA) available in the “ape” package (Paradis & Schliep 2019) and STRUCTURE

210 v2.3.4 (Pritchard et al. 2000). The PCoA was run as it represents the first step of the distance-based
211 redundancy analysis (db-RDA). STRUCTURE was run with the admixture model without prior
212 population information and 10 independent replicate runs were performed from $K = 1$ to 20 rather
213 than 32 to reduce computation time. For each replicate, the burn-in was set to 100,000 and the
214 Markov chain Monte Carlo iterations to 500,000 following guidance from Gilbert et al. (2012).
215 The most likely value of K was determined using both Evanno ΔK (Evanno et al. 2005) and \log
216 $\Pr(X|K)$ methods (Pritchard & Wen 2003) in structureHarvester (Earl & VonHoldt 2012). Based
217 on the recommendations of Janes et al. (2017), the number of genetic clusters was assessed by
218 comparing these two methods. Finally, CLUMPAK (Kopelman et al. 2015) was used to summarize
219 and visualize STRUCTURE outputs. Population structure was additionally investigated with
220 pairwise estimates of F_{ST} (Weir & Cockerham 1984) and confidence intervals were obtained with
221 95% confidence level and 1,000 resampling procedure using the “hierfstat” package (Goudet
222 2005). A Wilcoxon test was performed to test the null hypothesis that the average F_{ST} associated
223 with divergent (*i.e.*, populations associated with the highest F_{ST} values) and the rest of the
224 populations did not significantly differ. The same test was used to test the effect of the location
225 (*i.e.*, island or mainland) on F_{ST} values, this test was performed on the continuous dataset (S1 to
226 S24), as no islands were sampled from S25 to S32 (Figure 1 and Table 1).

227 2.6. Genetic diversity

228 Single and multilocus estimates of genetic diversity were calculated for each population as the
229 expected heterozygosity (H_e , *sensu* Nei 1978), observed heterozygosity (H_o) and the mean number
230 of private alleles ($\overline{P_a}$) using GenAlEx 6.5 (Peakall & Smouse 2006). In addition, standardized
231 allelic richness (A_r) was computed using the rarefaction method in “hierfstat”. Departure from
232 Hardy Weinberg equilibrium (F_{IS}) was calculated according to the method of Weir & Cockerham
233 (1984) in GENETIX 4.02 (Belkhir et al. 2004) as well as the 1,000 permutations computed to test
234 for their statistical significance. Wilcoxon tests were used to assess the effect of the type (*i.e.*,
235 divergent or not) and the location (island or mainland) on each estimator of genetic diversity and
236 F_{IS} . As previously stated, the effect of the location was performed on the continuous dataset.

237 2.7. Connectivity model

238 2.7.1. Hydrodynamic modeling

239 Flow fields were provided by a 3D regional configuration (MANGA2500) of the MARS3D
240 hydrodynamic model (Petton et al. 2023). The model domain ranges from 41°N to 55°N in latitude,
241 and 18°W to 9°30'E in longitude, encompassing all studied populations from southern Brittany to
242 the Strait of Dover. The domain is resolved horizontally by a regular 2.5 km grid and vertically by
243 40 sigma levels. The model was forced by meteorological conditions obtained from the ARPEGE
244 and AROME models (Yessad 2015) for the nested zooms with spatial and temporal resolutions of
245 2.5 km and 1 h, respectively. At the boundaries of the global 3D domain, tidal forcing was provided
246 by a larger 2D model covering the northwest Atlantic, driven by 14 tidal constituents (Lyard et al.
247 2006).

248 2.7.2. Lagrangian Modeling

249 The Lagrangian trajectory of the particles (meiospores or fertile parts of the thallus) was simulated
250 using ICHTHYOP v.3.3.6 (Lett et al. 2008), which employed the hourly 3D flow fields as input
251 data. Particles were released within circles with a radius of 2 km and were allowed to drift for 15
252 days to account for dispersal by fertile thallus and by meiospores while reducing the duration of
253 the simulations. The computational time step of the Lagrangian model was set to 300 s and the
254 position of the particle was recorded every 20 min. For each simulation, 5,000 particles were
255 released every two hours. This configuration was applied for each location, repeated for eight days
256 per month from June to October (corresponding to *L. digitata*'s highest peak of fertility, Bartsch
257 et al. 2008), using the hydrodynamic outputs of years 2014 and 2015. The eight days were chosen
258 by randomly selecting two days per week in order to account for tidal variation occurring over a
259 month while reducing computational time. A total of 960 dispersal events were hence simulated
260 over two years for each site. Pairwise oceanographic connectivity (P_{ij}) was estimated following
261 Reynes et al. (2021) and is defined as: $P_{ij} = N_{i-j}/N_i$, with N_i corresponding to the total number of
262 released particles from site i and N_{i-j} the total number of released particles from i arriving at j within
263 15 days of dispersal. P_{ij} was then averaged over the full period of the simulation to obtain the mean

264 connectivity matrix. The level of self-recruitment (P_{ii}) was estimated with the same method as P_{ij}
265 but using a threshold of 48 h to distinguish emitted particles (from the release area) from those
266 returning to the release area after 48 h. A Wilcoxon test was performed to assess the effect of the
267 type (*i.e.*, divergent or not) or the pair of populations (continuous dataset) on the rate of self-
268 recruitment.

269 2.8. Geographic distance and habitat discontinuity

270 The bathymetric contour was extracted from a 0.001°-resolution digital terrain model (or DTM,
271 data.shom.fr) using ArcGIS 10. In order to standardize the calculation of pairwise distances
272 between coastal populations around the peninsula, distances were calculated following the 5 m
273 isobath. However, when at least one of the populations was situated on an island, the straight-line
274 distance across the sea was considered. A 0.009°-resolution raster layer representing the
275 distribution of rocky seabed in the English Channel and around Brittany was prepared from the
276 best available substrate information available at Ifremer in May 2019. Information regarding the
277 spatial distribution of bedrock comes from the combination of several sources: (1) maps of coastal
278 habitats produced as part of the Rebent project, with the scales varying from 1/2,000 to 1/10,000;
279 (2) maps of existing habitat produced as part of the MESH project (Bajjouk 2005), with the scales
280 varying from 1/50,000 to 1/10,0000 and (3) from the local extraction of the information on the
281 presence of rock from topo-bathymetric Lidar data (DTM of 5 m resolution) (Gorman et al. 2013,
282 Bajjouk et al. 2015). This layer was subsequently used to compute the continuity of rocky substrata
283 between pairs of sites. Only the rock extents situated above 5 m depth (corresponding to 5 m below
284 the lowest astronomical tide, Figure 1) were considered in this calculation given that *L. digitata* is
285 considered unable to colonize areas below this depth (Robuchon et al. 2014). The proportion of
286 the geographic distance unoccupied by rocky substrata was considered for subsequent analyses.

287 2.9. Temperature data

288 Sea-surface temperature (SST) was generated using E.U. Copernicus Marine Service Information,
289 with 0.05°x0.05° resolution (product with DOI 10.48670/moi-00169 and see Merchant et al. 2019
290 and Good et al. 2020 for product details). To account for the fact that populations are still trying

291 to catch up the effect of past temperature variations, we considered SST data obtained for a period
292 of 10 years preceding each sampling year (*i.e.*, from 1995 to 2004 for a population sampled in
293 2005). While the annual mean and range of annual SST were averaged across the period, the
294 minimum (resp. maximum) was chosen as being the minimum (resp. maximum) SST observed
295 across these 10 years as we can imagine that extreme thermal episodes can represent a strong
296 selection.

297 2.10. Linking environmental variables to genetic structure

298 Global (resp. partial) db-RDA (Legendre & Anderson 1999) were conducted to investigate the
299 joint (resp. individual) effect of geographic distance, ocean currents, sampling years, SST
300 (minimum, maximum, mean and range) and habitat discontinuity on the total explained genetic
301 variation. The first two axes of the PCoA performed on the F_{ST} matrix were used as the response
302 variables representing the core of the genetic structure in the db-RDA. The analyses were repeated
303 on three datasets to assess *if* and *how* the contribution of each predictor varied according to the
304 sampling scheme. The *overall* dataset corresponded to the whole dataset (*i.e.*, 32 populations), the
305 *regional* dataset accounted for the 29 populations from Brittany (S1 to S29) and the *continuous*
306 dataset solely included the populations that were continuously sampled along the coast (S1 to S24,
307 Figure 1).

308 Sampling years were taken into account to assess whether variation in sampling year across
309 samples influenced the contemporary genetic differentiation. The environmental explanatory
310 variables accounting for geographic distance and ocean currents were respectively transformed
311 into distance-based Moran's eigenvector maps (dbMEM, Dray et al. 2006) and Asymmetric
312 Eigenvector Maps (AEM, Blanchet et al. 2008b). dbMEM eigenvectors were computed from the
313 matrix of geographic distance with the "adespatial" package using the default settings for
314 truncations, while only retaining positive eigenvalues as we did not expect any negative
315 autocorrelation between sampling positions (Dray et al. 2006). For the construction of AEMs, the
316 oceanographic connectivity matrix was transformed into a nodes-to-edges matrix and the edges
317 were weighted by the probability of dispersal before calculating AEM eigenvectors with the

318 “adespatial” package. Calculations of dbMEM and AEM eigenvectors were iterated for each
319 dataset following the aforementioned method. It is worth noting that the first eigenvectors in both
320 dbMEMs and AEMs (*e.g.*, AEM1, dbMEM1) are associated with broad-scale patterns while the
321 highest (*e.g.*, dbMEM5, AEM25) highlight finer patterns. To test for correlation between dbMEMs
322 and SST variables, a Spearman correlation was measured using the “stats” package.

323 Prior to each global db-RDA, an elastic net regularized regression was performed using the
324 “glmnet” package (Friedman et al. 2010) with the elastic net mixing parameter α fixed at 0.08 in
325 order to decrease the number of explanatory variables (Ogutu et al. 2012). We considered all
326 independent predictors with Variance Inflation Factor (VIF) below 10 to avoid multicollinearity
327 effects using the `vif_func` function available on `walterxie/ComMA`. The remaining variables were
328 then selected via a stepwise forward procedure using the `ordiR2step` function from the “vegan”
329 package. This function selects variables to build the *optimal* model, defined as the model
330 maximizing the adjusted coefficient of determination (R^2_{adj}), while minimizing the *p*-value
331 (Blanchet et al. 2008a). For partial db-RDAs, the variables were directly selected using the
332 `ordiR2step` function as the number of explanatory variables were already lower than the sample
333 size. Finally, ANOVAs (1,000 permutations) were performed to assess the significance of each
334 model (global and partial db-RDA), axes and retained variables.

335 3. RESULTS

336 3.1. Preliminary analyses

337 The PCA ran on the whole dataset allowed to identify 12 *Laminaria hyperborea* individuals
338 (Figure S1, Table S1), a sister species with overlapping range distribution (Robuchon et al. 2014).
339 These individuals were sampled in S6 (2 ind.), S9 (1 ind.), S21 (3 ind.), S22 (3 ind.), S25 (1 ind.),
340 S28 (1 ind.) and S30 (1 ind.) and were removed from our dataset, giving a total of 896 individuals
341 of *L. digitata*. No significant genotypic linkage disequilibrium was obtained, neither within nor
342 across populations (Table S2). Null alleles were present at locus Ld158 in five populations (S1,
343 S2, S7, S10 and S19, Table S3) and several homozygous genotypes were corrected by adding an
344 allele which was initially absent from the whole dataset (allelic size 246, Table S4). The same

345 analyses were rerun on the corrected dataset (detection of MLG, F_{ST} , parameters of genetic
346 diversity, db-RDA etc.), which brought us to the decision to keep our original dataset given: (1)
347 the high correlation between genetic diversity parameters (whichever the parameter, p -value of the
348 Wilcoxon tests were always higher than 0.6) and F_{ST} matrices (Tables S5 and S6, Mantel statistic
349 based on Pearson's product-moment correlation $r = 0.9993$), (2) the acquisition of the same db-
350 RDA results, (3) the correlation between the number of alleles and the number of genotypes with
351 missing data (p -value = 0.462) suggesting a negligible presence of null alleles and finally (4) the
352 impossibility to rerun multilocus analyses such as STRUCTURE or linkage disequilibrium
353 analyses due to the fact that MICROCHECKER modifies the original sample numbers.

354 3.2. Population Structure

355 According to both ΔK and $\ln \Pr(X|K)$ methods, $K = 2$ appeared as the optimal number of genetic
356 clusters (Figure S2). The barplot for $K = 2$ illustrated a general North-South differentiation, with
357 southern Brittany (S1-S4, referred to as “SB” hereafter) and Saint-Malo Bay (S26-S29, referred to
358 as “SMB” hereafter) being particularly well separated (Figure 2A). ΔK method suggested $K = 3$ to
359 be the next optimal value, followed by $K = 12$, while the $\ln \Pr(X|K)$ method first indicated $K = 12$
360 and then $K = 3$ (Figure S2). The barplot for $K = 3$ separated SB in another cluster (Figure 2B), and
361 the one for $K = 12$ additionally separated southwest Brittany (S5-S9), S21 (Locquirec), S25
362 (Roche-Douvres), SMB, Normandy (S30-S31) and S32 (Wissant), while western and northern
363 populations (S10-S20, S22-S24) remained highly admixed (Figure 2C). From these results, eight
364 major genetic groups can be defined: SB, southwest Brittany (S5-S9), S21, populations from
365 western and northern Brittany (S10-S20, S22-S24), S25, SMB, Normandy and S32 (Figure 3).
366 Among these genetic groups, populations from SB, S21, SMB and S32 were associated with
367 significantly higher mean F_{ST} values (Table 2, and Table S5 for pairwise F_{ST} values and their
368 significance; p -value < 0.0001) and will be referred to as *divergent* populations from here onwards.
369 The high mean F_{ST} obtained for S32 can be interpreted from allele frequencies spectra, in particular
370 at loci Ld148, Ld371, Lo454-17 and Lo454-28 (Figure S3). However, allelic spectra were less
371 informative for the remaining divergent populations. STRUCTURE results suggested that island

372 populations are generally well admixed with coastline populations with the exception of S25
373 (Figure 2C). This result is supported by the fact that the average values of F_{ST} did not significantly
374 differ between coastline and island populations (p -value = 0.379).

375 3.3. Genetic diversity

376 Estimates of genetic diversity averaged over the 11 markers are provided in Table 3. The lowest
377 value was always associated to S32 and the highest to populations at the western tip (S8-S14).
378 Variation in genetic diversity across populations was the highest for A_r , with values ranging from
379 2.542 (S32) to 6.151 (S12, Figure 3). Values of F_{IS} showed a significant deficit of heterozygotes
380 for several populations in the raw dataset. The correction for null alleles did not significantly
381 change the values (F_{IS} = -0.04; 0.02; 0.016; 0.068 and 0.067 after correction for respectively S1,
382 S2, S7, S10 and S19. Wilcoxon test, p -value = 0.421 when only accounting for the five
383 populations) as well as the significance of the departure from Hardy-Weinberg (HW) equilibrium,
384 except for S7 for which the F_{IS} was not significantly different from 0 after correction. One
385 multilocus genotype shared by two individuals was detected in S4 and S28 but was not correlated
386 with any significant deviation from HW equilibrium (Table 3).

387 The 10 divergent populations were associated with the lowest level of genetic diversity (p -
388 value < 0.001 for H_e , H_o and A_r , see Figure 3) although the same tendency was not observed for
389 $\overline{P_a}$ (p -value: 0.283). These populations also appeared to have significantly lower F_{IS} values
390 compared to the rest of the populations (p -value = 0.023). In contrast, while genetic diversity
391 estimates were always higher in coastal than island populations, differences were not significant
392 based on Wilcoxon tests (p -value for H_e : 0.347, H_o : 0.263, A_r : 0.174 and $\overline{P_a}$: 0.165). Similarly,
393 higher F_{IS} values were observed in islands but the difference was, again, not significant (p -value:
394 0.905).

395 3.4. Habitat discontinuity

396 The proportion of habitat discontinuity shown in Table S7 suggested a patchy pattern with several
397 populations appearing particularly isolated. As illustrated by Figure 1, island populations appeared
398 naturally isolated by the absence of continuous favorable substrate (*i.e.*, rocky substrata above 5

399 m depth) connecting them to the nearest mainland or island populations thus revealing high
400 fragmentation. At the same time, the expanse of rocky habitat appeared continuous along northern
401 Brittany (S15-S29) as shown by the small proportion of geographic distance which was
402 unoccupied by rocky substrata. The increase in habitat discontinuity between southern ($< S11$) and
403 northern populations ($> S11$) was mainly driven by the topography of the Rade of Brest and its
404 lack of rocky substrata at the 5 m isobath, and even above, as suggested by our dataset on rocky
405 substrata.

406 3.5. Oceanographic connectivity

407 Connectivity probabilities resulting from Lagrangian simulations are shown in Figure 4 and Table
408 S8. In most cases, the highest probabilities of connectivity were associated with neighboring
409 populations. Contrastingly, groups of populations such as SB, SMB and Normandy appeared
410 highly connected to each other, but isolated from other populations (Figure 4). The probability of
411 connectivity of S32 with any other population was null, highlighting its strong isolation. In the
412 case of S21, while a particle released from this population attained neighboring populations, this
413 was not true for the other way around, as suggested by the low probabilities that particles released
414 from neighboring populations recruited in S21. The difference between divergent and non-
415 divergent populations was noticeable when comparing the number of connectivity links, defined
416 as the mean number of populations with which the probability of connectivity is different from 0
417 (Table S8). Indeed, spores released from divergent populations reached on average 5.2 populations
418 compared to 7.9 for non-divergent populations. Similarly, spores recruiting in divergent
419 populations originated on average from 4.9 populations, compared to 9.1 for non-divergent ones.
420 The difference in connectivity was less pronounced between island and coastal populations: spores
421 released from islands reached on average 8.5 populations, compared to 6.6 for coastal populations;
422 and spores recruiting in islands originated from an average of 9.2 populations, compared to 6.5 for
423 coastal populations.

424 In terms of directionality, dispersal appeared to have a north-western direction in the south of the
425 Peninsula (S1-S7) and a north-eastern direction when considering north-western and northern

426 populations (S10-S25, Figure 4). For instance, a spore released from S10 reached S11 to S14 with
427 a higher probability than in the opposite direction (Figure 4, Table S8). The pattern became less
428 clear from SMB. However, as previously stated, these populations tended to be highly connected
429 within each genetic group (SMB, Normandy) but not with populations beyond them, making
430 directionality analyses less relevant.

431 Finally, self-recruitment probability varied from 0.005 (S8) to 0.476 (S25, Table S8). The
432 probability did not significantly differ between island and coastline populations (0.211 and 0.189,
433 respectively, p -value = 0.077), nor between divergent and non-divergent populations (0.255 and
434 0.169, respectively, p -value = 0.64).

435 3.6. Hierarchical effects of environmental factors on genetic structure

436 Whichever the geographical scale, habitat discontinuity and sampling years were not retained in
437 the global nor partial db-RDA (Table 4). Therefore, for the sake of parsimony, these two variables
438 will not be mentioned in the following results.

439 3.6.1. Overall dataset

440 The model and the two first axes associated with the global db-RDA were significant (p -value <
441 0.001) with an adjusted coefficient of determination (R^2_{adj}) of 0.604 (Table 4). Five variables were
442 selected by the ordiR2step function which were related to geographic distance (dbMEM1, 3 and
443 5) and oceanographic connectivity (AEM1 and 3, Table 4, Figure 5B). The first axis, accounting
444 for 71.6% of the variance, showed a clear differentiation between southern and northern Brittany
445 which appeared to be driven by geographic distance (dbMEM1, Figure 5B) and by oceanographic
446 processes to a lesser extent (AEM1 and 3, Figure 5B and S4). The second axis, accounting for
447 18.1% of the variance and mostly driven by geographic distance (dbMEM3), isolated S32 whilst
448 populations from Normandy remained poorly differentiated (Figure 5B). When partitioning the
449 respective effects of oceanographic connectivity, geographical distance and SST using partial db-
450 RDA, each predictor appeared significant. Geographic distance explained the greatest amount of
451 variance with $R^2_{\text{adj}} = 0.475$, against 0.165 for SST (minimum and mean) and 0.115 for
452 oceanographic connectivity (Table 4).

453 3.6.2. Regional dataset

454 To investigate the relative contribution of each environmental factor at a regional scale,
455 populations S30, S31 and S32 were excluded because of their high geographic isolation (*ca.* 600
456 km from the rest of the populations). The model and the two first axes associated with the global
457 db-RDA were again significant (p -value < 0.001) with $R^2_{\text{adj}} = 0.614$ (Table 4). Six variables were
458 retained by the ordiR2step selection process: two accounted for geographic distance (dbMEM2
459 and 3, Table 4) and four for oceanographic connectivity (AEM1, 2, 23 and 25, Table 4). The first
460 axis (84.9% of the variance) was driven by geographic distance (dbMEM2, Figure 5C), while
461 oceanographic processes appeared important for finer genetic structure (Figure S4). The first axis
462 again clearly separated populations according to their latitude and SMB appeared isolated due to
463 geographic distance. The second axis (10.3%) was driven by AEM25 and isolated S21, suggesting
464 the role of oceanographic currents on its genetic isolation (Figure 5C). When partitioning the
465 respective effects of oceanographic connectivity, geographical distance and SST, each predictor
466 appeared significant. With this dataset, oceanographic connectivity explained a slightly higher
467 amount of variance compared to geographic distance ($R^2_{\text{adj}} = 0.549$ and 0.485 , respectively) while
468 $R^2_{\text{adj}} = 0.221$ for SST (mean, Table 4).

469 3.6.3. Continuous dataset

470 The third analysis accounting for the 24 continuously sampled populations (S1-S24) was
471 performed by additionally excluding SMB and S25. At this scale, the highest distance between
472 two neighboring populations is reduced to *ca.* 160 km (between S11 and S12 when following
473 coastline) without any major gap in connectivity (Figure 4). The model and the three first axes
474 were significant (p -value < 0.001 for the model and the first axis, p -value < 0.05 for the remaining
475 two axes) with $R^2_{\text{adj}} = 0.777$ (Table 4). Eight variables remained after the two selection processes:
476 seven associated to oceanographic currents (AEM1, 2, 3, 5, 10, 16 and 19) and one to geographic
477 distance (dbMEM3, Table 4, Figure 5D). This first axis was mostly explained by AEM1, denoting
478 a gradual north-wise differentiation (Figure 5D), whilst higher order AEMs mostly revealed the
479 strong density of connectivity links amongst northern (S10-S25) or southern populations (S1-S7,

480 Figure S4). The second axis was mostly driven by AEM5, which again isolated S21. With this
481 dataset, oceanographic connectivity explained a greater amount of variance than geographic
482 distance ($R^2_{\text{adj}} = 0.794$ and 0.513 , respectively) denoting the fact that genetic differentiation
483 between populations was widely explained by oceanographic processes, while SST explained
484 21.0% of the variance (maximum SST).

485 Finally, whichever the dataset, SST was never retained in global db-RDAs, which is most likely
486 due to the correlation between some of the SST-related variables and dbMEMs observed
487 whichever the datasets (Table S9).

488 4. DISCUSSION

489 Our study builds on previous microsatellite research (Billot et al. 2003, Valero et al. 2011,
490 Couceiro et al. 2013, Robuchon et al. 2014) to refine our understanding of *Laminaria digitata*'s
491 population structure in the southern edge of its East Atlantic distribution. We specifically aimed at
492 deepening our knowledge of connectivity patterns among the studied populations which comprised
493 22 coastline and 10 on-shelf island populations. To do this, we combined inference and analyses
494 of genetic structure, genetic diversity and dispersal probabilities resulting from Lagrangian
495 simulations. This enabled us to identify divergent populations, defined as those associated with
496 high genetic differentiation and poor diversity, surrounded by highly connected populations
497 associated with high genetic diversity. This pattern is consistent with the ecological and
498 demographic status of *L. digitata* forest which has been described as highly contrasted in the
499 studied area, ranging from a “no decline reported” status in north-western Brittany to a “local
500 decline” status in South Brittany and Saint-Malo Bay (de Bettignies et al. 2021). We additionally
501 compared connectivity patterns between coastal and island populations and found that island
502 populations are generally well connected to other islands or coastal populations. A distance-based
503 redundancy analysis (db-RDA) was applied to disentangle the contribution of various
504 environmental factors which are thought to influence connectivity and thus genetic structure,
505 namely: habitat discontinuity, geographical distance, hydrodynamic processes, sea surface
506 temperature (SST) and sampling year. This analysis was repeated for three datasets corresponding

507 to varying sampling schemes, as we expect the presence of rocky substrata, hydrodynamic features
508 and SST to vary at relatively small spatial scales. Overall, our analyses have shown that the amount
509 of variation explained by seascape features increased as the sampling gap between sampled
510 populations was reduced. Our study therefore shows how the conclusions heavily depend on the
511 presence and extent of sampling gaps. Given that seascape genetics tools are nowadays being more
512 and more used, we call for greater attention in the conclusions that are drawn.

513 Analyses of population structure have shown a discrepancy between southern and northern
514 Brittany, which can be related to oceanic currents according to the db-RDA run on the dataset with
515 continuously distributed populations. This discrepancy is in line with the fact that this region
516 corresponds to an oceanographic boundary: while the main ocean current in the southern coast of
517 Brittany corresponds to the shelf residual current which has a northwest-ward direction, northern
518 Brittany is dominated by the English Channel residual circulation which has a northeast-ward
519 direction (Pingree & Le Cann 1989). This genetic divergence was also reported for other species
520 (Roman & Palumbi 2004, Jolly et al. 2006, Nunes et al. 2021) and could also correspond to the
521 limit between the northern European Sea and the Lusitanian biogeographical provinces which was
522 pointed out to explain the biogeographic breaks observed in various marine taxa (Spalding et al.
523 2007). The directionality observed in the Lagrangian simulations is consistent with the direction
524 of these two major currents, albeit the variation in directionality due to tides and winds (Ayata et
525 al. 2010).

526 Previous results on *L. digitata* have shown significant population differentiation from 1 to
527 10 km (Billot et al. 2003, Valero et al. 2011, Robuchon et al. 2014), a fine-scale genetic structure
528 supported by the commonly reported short dispersal distance in kelps (Dayton 1985, Norton 1992).
529 Contrastingly, our results suggest that genetic differentiation was not significant between several
530 pairs of populations separated by more than 50 km, particularly for populations located in western
531 and north-western Brittany. Low genetic differentiation at large geographic distances was
532 particularly clear for island populations which were separated by more than 100 km from the coast
533 and despite the absence of continuous favorable substrate (*i.e.*, rocky substrata above 5 m depth)

534 connecting them to the nearest mainland or island populations. In fact, the number of connectivity
535 links (defined as the mean number of populations with which the probability of connectivity is non
536 null), as well as values of genetic differentiation and of genetic diversity revealed that islands are
537 generally well connected. Nonetheless, this conclusion might be affected by species' means of
538 dispersal and should not be taken as a general rule. In addition, we have only considered on-shelf
539 coastal populations which were connected to the mainland at the Last Glacial Maximum when the
540 sea level was 100 to 120 m below present (Frenzel et al. 1992, Lambeck 1997). These islands
541 therefore share the same evolutionary history as populations found along the coastline, and this
542 historical pattern is expected to influence the observed low genetic differentiation of island
543 populations.

544 In contrast to the low genetic differentiation observed for island populations, our analyses
545 have revealed genetically divergent populations, associated with high genetic differentiation and
546 significantly lower values of genetic diversity. Amongst these divergent populations, the ones from
547 southern Brittany and Saint-Malo Bay appeared to be particularly differentiated. Results from
548 Lagrangian simulations have shown that populations within these two genetic clusters are highly
549 connected but largely unrelated to other populations. Nonetheless, results from db-RDA revealed
550 that Saint-Malo Bay was genetically isolated due to geographic distance rather than by the
551 occurrence of tidal gyres, as previously suggested by Billot et al. (2003) and Robuchon et al.
552 (2014). However, geographic distance might appear as the causal factor for the divergence of
553 Saint-Malo Bay due to gaps in the sampling. Indeed, by repeating the db-RDA on three datasets,
554 we have demonstrated how sampling schemes can greatly influence the conclusions that can be
555 drawn. In particular, we have shown that as the extent of the sampling gaps decreased, the relative
556 importance of ocean currents (mainly in relation to geographic distance) increased. Therefore, our
557 dataset does not allow us to properly infer the origin of the genetic isolation of Saint-Malo Bay.

558 In addition to South Brittany and Saint-Malo Bay, two other divergent populations were
559 identified: Locquirec, which also appeared highly differentiated from surrounding populations at
560 small spatial scale (< 20 km), and the geographically isolated population of Wissant. All of these

561 divergent populations (populations from South Brittany, Saint-Malo Bay, Locquirec and Wissant)
562 were associated with lower genetic diversity, with Wissant being particularly impoverished.
563 Unlike what has been previously suggested by Billot et al. (2003), the results of the db-RDA as
564 well as the ones from Lagrangian simulations suggest that Locquirec is isolated due to oceanic
565 currents. This result is supported by the description of eddies at the entrance of Lannion Bay and
566 a slow residual current within the Bay (Beslier et al. 1980, Garreau 1993). This confirms that ocean
567 currents not only affect long-distance dispersal (*e.g.*, between islands and coastline) but also have
568 localized effects as reported for *L. digitata* in Strangford Narrows (Brennan et al. 2014) and for
569 other species of seaweed characterized by low dispersal abilities (Buonomo et al. 2017, Reynes et
570 al. 2021). Nonetheless, habitat appeared highly discontinuous between Locquirec and its
571 surrounding populations (> 90% of the total distance is devoid of rocky substrata above 5 m depth),
572 which could intensify the genetic isolation of this population. As opposed to Locquirec, geographic
573 distance appears as the main cause for the isolation of Wissant. In this case, a finer sampling
574 scheme along the French coast might not change the results given the absence of nearby
575 populations (Araújo et al. 2016). The low genetic diversity measured on neutral markers reflects a
576 low effective population size and thus higher strength of genetic drift (compared to selection),
577 which ultimately leads to an increase in the probability of going extinct. Careful attention and
578 appropriate conservation measures should therefore be taken in order to prevent this end.

579 The stepwise variable selection procedure applied prior to each global db-RDA has never
580 selected variables associated with sampling year, SST or habitat discontinuity. Although
581 parameters associated to SST were significant in partial db-RDA, habitat discontinuity was never
582 significant despite the findings on other kelp species (Alberto et al. 2010, 2011, Selkoe et al. 2010,
583 Johansson et al. 2015). This discrepancy could stem from the fact that our rock layer was built by
584 combining various data with different precisions, or from the fact that the calculation of habitat
585 discontinuity was constrained by the 5 m bathymetric contour. Another argument is that Alberto
586 et al. (2010, 2011) and Selkoe et al. (2010) have measured habitat continuity by looking at kelp
587 coverage rather than proportion of rocky substrata *per se*. Yet, evidence from other kelp species

588 suggests that sporophyte recruitment largely depends on meiospore density ensuring sperm-egg
589 encountering (Reed 1990). By considering kelp coverage rather than rocky substrata, Alberto et
590 al. (2010, 2011) and Selkoe et al. (2010) might have incorporated the effect of meiospores dilution
591 into habitat discontinuity, which was not our case. Nonetheless, the use of other methods (e.g.,
592 resistance matrix, Wilcox et al. 2023) could have led to other conclusions.

593 The fact that SST variables were never retained in global db-RDA could stem from the
594 limitation to the use of dbMEMs which may underestimate the importance of other environmental
595 variables that show some correlations with one of these Moran's eigenvector decomposition
596 (Dalongeville et al. 2018). To overcome this limitation, one could consider hourly temperature
597 data (e.g., from *in situ* dataloggers) which, in addition to its relevance for intertidal species, could
598 decrease the correlation with dbMEMs. Despite these results, partial db-RDA accounting for SST
599 were significant whichever the datasets, therefore pointing out its relevance in explaining genetic
600 structure. This could be particularly true for this kelp species as sporulation has been shown to be
601 severely impacted at temperatures above 17°C (Bartsch et al. 2013), yet SST in southern Brittany
602 reaches 21°C in summer (Gallon et al. 2014). Although mechanisms linked to sporulation could
603 be adapted to higher temperature, Oppliger et al. (2014) have shown that the mean number of
604 released meiospores is significantly lower in Quiberon (corresponding to S4) compared to a
605 population in northern Brittany. Yet a decreased amount of released meiospores should lead to a
606 decreased connectivity and thus higher genetic differentiation. This underlines the fact that SST
607 could have various consequences on life history traits in *L. digitata* which should be apparent on
608 data obtained using neutral markers through the phenomenon of isolation by adaptation (Nosil et
609 al. 2009, Schoville et al. 2012). Similarly, the sharp genetic break observed between southwestern
610 populations (S5-S9) and southern Brittany could have also been attributed to the difference in SST
611 between these two regions.

612

613 Conclusion

614 Our study revealed a mosaic of connectivity patterns with well-connected populations surrounded
615 by populations that appeared less connected and less diverse, with the population of Wissant being
616 particularly impoverished. This pattern is consistent with the ecological and demographic status of
617 *Laminaria digitata* forest which has been described as highly contrasted in the studied area.
618 Various db-RDA were conducted to deepen our understanding of the observed genetic variation.
619 Unlike previous studies carried out on *L. digitata* as well as on other kelp species, our results
620 indicated a limited effect of habitat fragmentation compared to ocean currents and geographic
621 distance. Moreover, the relative effect of these two latter environmental variables varied according
622 to sampling schemes: while geographic distance was particularly relevant in our overall dataset,
623 which included sampling gaps of more than 600 km, oceanographic processes appeared as the
624 main drivers at finer spatial resolution.
625

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639

640 **Competing interests**

641 The authors declare no competing interests.

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- 645 Aeschbacher S, Selby JP, Willis JH, Coop G (2017) Population-genomic inference of the strength
646 and timing of selection against gene flow. *Proc Natl Acad Sci* 114:7061–7066.
- 647 Alberto F, Raimondi PT, Reed DC, Coelho NC, Leblois R, Whitmer A, Serrão EA (2010) Habitat
648 continuity and geographic distance predict population genetic differentiation in giant kelp.
649 *Ecology* 91:49–56.
- 650 Alberto F, Raimondi PT, Reed DC, Watson JR, Siegel DA, Mitarai S, Coelho N, Serrão EA
651 (2011) Isolation by oceanographic distance explains genetic structure for *Macrocystis*
652 *pyrifera* in the Santa Barbara Channel. *Mol Ecol* 20:2543–2554.
- 653 Arafteh-Dalmau N, Montaña-Moctezuma G, Martínez JA, Beas-Luna R, Schoeman DS, Torres-
654 Moye G (2019) Extreme marine heatwaves alter kelp forest community near its
655 equatorward distribution limit. *Front Mar Sci* 6.
- 656 Araújo RM, Assis J, Aguillar R, Airolidi L, Bárbara I, Bartsch I, Bekkby T, Christie H, Davoult
657 D, Derrien-Courtel S, Fernandez C, Fredriksen S, Gevaert F, Gundersen H, Le Gal A,
658 Lévêque L, Mieszkowska N, Norderhaug KM, Oliveira P, Puente A, Rico JM, Rinde E,
659 Schubert H, Strain EM, Valero M, Viard F, Sousa-Pinto I (2016) Status, trends and drivers
660 of kelp forests in Europe: An expert assessment. *Biodivers Conserv* 25:1319–1348.
- 661 Ayata SD, Lazure P, Thiébaud É (2010) How does the connectivity between populations mediate
662 range limits of marine invertebrates? A case study of larval dispersal between the Bay of
663 Biscay and the English Channel (North-East Atlantic). *Prog Oceanogr* 87:18–36.
- 664 Bajjouk T (2005) Traitement et structuration des données en zones côtières. Projet MESH.
665 Contrat Ifremer-Capgemini N° 04/2 210 934. 29p.
- 666 Bajjouk T, Rochette S, Laurans M, Ehrhold A, Hamdi A, Le Niliot P (2015) Multi-approach
667 mapping to help spatial planning and management of the kelp species *Laminaria digitata*
668 and *Laminaria hyperborea*: Case study of the Molène Archipelago, Brittany. *J Sea Res*
669 100:2–21.
- 670 Bartsch I, Vogt J, Pehlke C, Hanelt D (2013) Prevailing sea surface temperatures inhibit summer
671 reproduction of the kelp *Laminaria digitata* at Helgoland (North Sea). *J Phycol* 49:1061–
672 1073.
- 673 Bartsch I, Wiencke C, Bischof K, Buchholz CM, Buck BH, Eggert A, Feuerpfeil P, Hanelt D,
674 Jacobsen S, Karez R, Karsten U, Molis M, Roleda MY, Schubert H, Schumann R, Valentin
675 K, Weinberger F, Wiese J (2008) The genus *Laminaria* sensu lato: Recent insights and
676 developments. *Eur J Phycol* 43:1–86.
- 677 Belkhir K, Borsa P, Chikhi L, Raufaste N, Bonhomme F (2004) GENETIX 4.05, logiciel sous
678 Windows pour la génétique des populations. Laboratoire Génome, Populations,
679 Interactions, CNRS UMR 5000, Université de Montpellier II, Montpellier.
- 680 Bell PR (2008) Connectivity between island Marine Protected Areas and the mainland. *Biol*
681 *Conserv* 141:2807–2820.
- 682 Benestan L, Loiseau N, Guérin P, Pérez-Ruzafa A, Forcada A, Arcas E, Lenfant P, Mallol S,
683 Goñi R, Velez L, Mouillot D, Puebla O, Manel S (2023) Contrasting influence of seascape,
684 space and marine reserves on genomic variation in multiple species. *Ecography* 2023.
- 685 Benestan L, Quinn BK, Maaroufi H, Laporte M, Clark FK, Greenwood SJ, Rochette R,
686 Bernatchez L (2016) Seascape genomics provides evidence for thermal adaptation and
687 current-mediated population structure in American lobster (*Homarus americanus*). *Mol*
688 *Ecol* 25:5073–5092.
- 689 Benestan LM, Rougemont Q, Senay C, Normandeau E, Parent E, Rideout R, Bernatchez L,
690 Lambert Y, Audet C, Parent GJ (2021) Population genomics and history of speciation
691 reveal fishery management gaps in two related redfish species (*Sebastes mentella* and
692 *Sebastes fasciatus*). *Evol Appl* 14:588–606.
- 693 Beslier A, Birrien JL, Cabioch L, Larssonneur C, Borgne L (1980) La pollution des Baies de
694 Morlaix et de Lannion par les hydrocarbures de l' "Amoco Cadiz": Répartition sur les fonds
695 et évolution. *Helgoländer Meeresunters* 33:209–224.
- 696 de Bettignies T, Hébert C, Assis J, Bartsch I, Bekkby T, Christie H, Dahl K, Derrien-Courtel S,

697 Edwards H, Filbee-Dexter K, Franco J, Gillham K, Harrald M, Hennicke J, Hernández S,
698 Le Gall L, Martinez B, Mieszkowska N, Moore P, Moy F, Mueller M, Norderhaug KM,
699 Parry M, Ramsay K, Robuchon M, Russel T, Serrão E, Smale D, Steen H, Street M,
700 Tempera F, Valero M, Werner T, La Rivière M (2021) Case Report for kelp forests habitat.
701 OSPAR 787/2021.

702 Billot C, Engel CR, Rousvoal S, Kloareg B, Valero M (2003) Current patterns, habitat
703 discontinuities and population genetic structure: The case of the kelp *Laminaria digitata* in
704 the English Channel. *Mar Ecol Prog Ser* 253:111–121.

705 Billot C, Rousvoal S, Estoup A, Epplen JT, Saumitou-Laprade P, Valero M, Kloareg B (1998)
706 Isolation and characterization of microsatellite markers in the nuclear genome of the brown
707 alga *Laminaria digitata* (Phaeophyceae). *Mol Ecol* 7:1778–1780.

708 Blanchet FG, Legendre P, Borcard D (2008a) Forward selection of explanatory variables.
709 *Ecology* 89:2623–2632.

710 Blanchet FG, Legendre P, Borcard D (2008b) Modelling directional spatial processes in
711 ecological data. *Ecol Model* 215:325–336.

712 Blauw A, Eleveld M, Prins T, Zijl F, Groenenboom J (2019) Coherence in assessment framework
713 of chlorophyll a and nutrients as part of the EU project ‘Joint monitoring programme of the
714 eutrophication of the North Sea with satellite data’.

715 Boussarie G, Momigliano P, Robbins WD, Bonnin L, Cornu J, Fauvelot C, Kiszka JJ, Manel S,
716 Mouillot D, Vigliola L (2022) Identifying barriers to gene flow and hierarchical
717 conservation units from seascape genomics: a modelling framework applied to a marine
718 predator. *Ecography* 2022.

719 Brennan G, Kregting L, Beatty GE, Cole C, Elsässer B, Savidge G, Provan J (2014)
720 Understanding macroalgal dispersal in a complex hydrodynamic environment: A combined
721 population genetic and physical modelling approach. *J R Soc Interface* 11:1–12.

722 Bridle JR, Gavaz S, Kennington WJ (2009) Testing limits to adaptation along altitudinal
723 gradients in rainforest *Drosophila*. *Proc R Soc B Biol Sci* 276:1507–1515.

724 Buonomo R, Assis J, Fernandes F, Engelen AH, Airoidi L, Serrão EA (2017) Habitat continuity
725 and stepping-stone oceanographic distances explain population genetic connectivity of the
726 brown alga *Cystoseira amentacea*. *Mol Ecol* 26:766–780.

727 Capblancq T, Forester BR (2021) Redundancy analysis: A Swiss Army Knife for landscape
728 genomics. *Methods Ecol Evol* 12:2298–2309.

729 Cavanaugh KC, Reed DC, Bell TW, Castorani MCN, Beas-Luna R (2019) Spatial variability in
730 the resistance and resilience of giant kelp in Southern and Baja California to a multiyear
731 heatwave. *Front Mar Sci* 6.

732 Coelho NC, Serrão EA, Alberto F (2014) Characterization of fifteen microsatellite markers for
733 the kelp *Laminaria ochroleuca* and cross species amplification within the genus. *Conserv*
734 *Genet Resour* 6:949–950.

735 Coleman MA, Minne AJP, Vranken S, Wernberg T (2020) Genetic tropicalisation following a
736 marine heatwave. *Sci Rep* 10:1–11.

737 Coleman MA, Veenhof RJ (2021) Reproductive versatility of kelps in changing oceans. *J Phycol*
738 57:708–710.

739 Couceiro L, Robuchon M, Destombe C, Valero M (2013) Management and conservation of the
740 kelp species *Laminaria digitata*: Using genetic tools to explore the potential exporting role
741 of the MPA “Parc naturel marin d’Iroise.” *Aquat Living Resour* 26:197–205.

742 D’Aloia CC, Bogdanowicz SM, Harrison RG, Buston PM (2014) Seascape continuity plays an
743 important role in determining patterns of spatial genetic structure in a coral reef fish. *Mol*
744 *Ecol* 23:2902–2913.

745 Dalongeville A, Andrello M, Mouillot D, Lobreaux S, Fortin M-J, Lasram F, Belmaker J, Rocklin
746 D, Manel S (2018) Geographic isolation and larval dispersal shape seascape genetic
747 patterns differently according to spatial scale. *Evol Appl* 11:1437–1447.

748 Dawson MN (2016) Island and island-like marine environments. *Glob Ecol Biogeogr* 25:831–
749 846.

- 750 Dayton PK (1985) Ecology of kelp communities. *Annu Rev Ecol Syst* Vol 16:215–245.
- 751 Dray S, Legendre P, Peres-Neto PR (2006) Spatial modelling: a comprehensive framework for
752 principal coordinate analysis of neighbour matrices (PCNM). *Ecol Model* 196:483–493.
- 753 DuBois K, Pollard KN, Kauffman BJ, Williams SL, Stachowicz JJ (2022) Local adaptation in a
754 marine foundation species: Implications for resilience to future global change. *Glob*
755 *Change Biol* 28:2596–2610.
- 756 Durrant H, Barrett N, Edgar G, Coleman M, Burridge C (2018) Seascape habitat patchiness and
757 hydrodynamics explain genetic structuring of kelp populations. *Mar Ecol Prog Ser* 587:81–
758 92.
- 759 Earl DA, VonHoldt BM (2012) STRUCTURE HARVESTER: a website and program for
760 visualizing STRUCTURE output and implementing the Evanno method. *Conserv Genet*
761 *Resour* 4:359–361.
- 762 Engel CR, Destombe C, Valero M (2004) Mating system and gene flow in the red seaweed
763 *Gracilaria gracilis*: Effect of haploid-diploid life history and intertidal rocky shore
764 landscape on fine-scale genetic structure. *Heredity* 92:289–298.
- 765 Evanno G, Regnaut S, Goudet J (2005) Detecting the number of clusters of individuals using the
766 software STRUCTURE: A simulation study. *Mol Ecol* 14:2611–2620.
- 767 Fernández C (2011) The retreat of large brown seaweeds on the north coast of Spain: the case of
768 *Saccorhiza polyschides*. *Eur J Phycol* 46:352–360.
- 769 Filbee-Dexter K, Feehan C, Scheibling R (2016) Large-scale degradation of a kelp ecosystem in
770 an ocean warming hotspot. *Mar Ecol Prog Ser* 543:141–152.
- 771 Filbee-Dexter K, Wernberg T, Grace SP, Thormar J, Fredriksen S, Narvaez CN, Feehan CJ,
772 Norderhaug KM (2020) Marine heatwaves and the collapse of marginal North Atlantic kelp
773 forests. *Sci Rep* 10:1–11.
- 774 Frenzel B, Beug H-J, Brunnacker K, Busche D, Frankenberg P, Fritz P, Geyh MA, Hagedorn H,
775 Hövermann J, Kessler A, Königswald W v., Krumsiek K, Lauer W, Mensching H, Moser
776 H, Münnich K-O, Sonntag Chr, Vinken R (1992) Climates during the Last Glacial
777 Maximum. In: *Atlas of paleoclimates and paleoenvironments of the Northern Hemisphere*.
778 Frenzel B, Pécsi M, Velichko AA (eds) Geographical Research Institute, Hungarian
779 Academy of Sciences, Budapest; Gustav Fischer Verlag, Stuttgart; Jena; New York
- 780 Friedman J, Hastie T, Tibshirani R (2010) Regularization paths for generalized linear models via
781 coordinate descent. *J Stat Softw* 33:1–20.
- 782 Gaggiotti OE, Bekkevold D, Jørgensen HBH, Foll M, Carvalho GR, Andre C, Ruzzante DE
783 (2009) Disentangling the effects of evolutionary, demographic and environmental factors
784 influencing genetic structure of natural populations: Atlantic herring as a case study.
785 *Evolution* 63:2939–2951.
- 786 Gallon RK, Robuchon M, Leroy B, Le Gall L, Valero M, Feunteun E (2014) Twenty years of
787 observed and predicted changes in subtidal red seaweed assemblages along a
788 biogeographical transition zone: Inferring potential causes from environmental data. *J*
789 *Biogeogr* 41:2293–2306.
- 790 Garineaud C (2021) Appréhender et s'adapter. *Rev D'ethnoécologie*:0–25.
- 791 Garreau P (1993) Hydrodynamics of the North Brittany coast: a synoptic study. *Oceanol Acta*
792 16:469–477.
- 793 Gaylord B, Gaines SD (2000) Temperature or transport? Range limits in marine species mediated
794 solely by flow. *Am Nat* 155:769–789.
- 795 Gilbert KJ, Andrew RL, Bock DG, Franklin MT, Kane NC, Moore JS, Moyers BT, Renaut S,
796 Rennison DJ, Veen T, Vines TH (2012) Recommendations for utilizing and reporting
797 population genetic analyses: The reproducibility of genetic clustering using the program
798 structure. *Mol Ecol* 21:4925–4930.
- 799 Gilg MR, Hilbish TJ (2003) The geography of marine larval dispersal: coupling genetics with
800 fine-scale physical oceanography. *Ecology* 84:2989–2998.
- 801 Good S, Fiedler E, Mao C, Martin MJ, Maycock A, Reid R, Roberts-Jones J, Searle T, Waters J,
802 While J, Worsfold M (2020) The current configuration of the OSTIA system for

803 operational production of foundation sea surface temperature and ice concentration
804 analyses. *Remote Sens* 12:720.

805 Gorman D, Bajjouk T, Populus J, Vasquez M, Ehrhold A (2013) Modeling kelp forest
806 distribution and biomass along temperate rocky coastlines. *Mar Biol* 160:309–325.

807 Goudet J (2005) HIERFSTAT, a package for R to compute and test hierarchical F-statistics. *Mol*
808 *Ecol Notes* 5:184–186.

809 Graves TA, Beier P, Royle JA (2013) Current approaches using genetic distances produce poor
810 estimates of landscape resistance to interindividual dispersal. *Mol Ecol* 22:3888–3903.

811 Grummer JA, Beheregaray LB, Bernatchez L, Hand BK, Luikart G, Narum SR, Taylor EB
812 (2019) Aquatic Landscape Genomics and Environmental Effects on Genetic Variation.
813 *Trends Ecol Evol* 34:641–654.

814 Guzinski J, Ruggeri P, Ballenghien M, Mauger S, Jacquemin B, Jollivet C, Coudret J, Jaugeon
815 L, Destombe C, Valero M (2020) Seascape genomics of the sugar kelp *Saccharina*
816 *latissima* along the North Eastern Atlantic latitudinal gradient. *Genes* 11:1503.

817 Hickey AJR, Lavery SD, Hannan DA, Baker CS, Clements KD (2009) New Zealand triplefin
818 fishes (family Tripterygiidae): contrasting population structure and mtDNA diversity
819 within a marine species flock. *Mol Ecol* 18:680–696.

820 Hu ZM, Zhong KL, Weinberger F, Duan DL, Draisma SGA, Serrão EA (2020) Linking ecology
821 to genetics to better understand adaptation and evolution: A review in marine macrophytes.
822 *Front Mar Sci* 7:1–12.

823 Janes JK, Miller JM, Dupuis JR, Malenfant RM, Gorrell JC, Cullingham CI, Andrew RL (2017)
824 The K = 2 conundrum. *Mol Ecol* 26:3594–3602.

825 Jayathilake DRM, Costello MJ (2020) A modelled global distribution of the kelp biome. *Biol*
826 *Conserv* 252:1–10.

827 Johansson ML, Alberto F, Reed DC, Raimondi PT, Coelho NC, Young MA, Drake PT, Edwards
828 CA, Cavanaugh K, Assis J, Ladah LB, Bell TW, Coyer JA, Siegel DA, Serrão EA (2015)
829 Seascape drivers of *Macrocystis pyrifera* population genetic structure in the northeast
830 Pacific. *Mol Ecol* 24:4866–4885.

831 Jolly MT, Viard F, Gentil F, Thiébaud E, Jollivet D (2006) Comparative phylogeography of two
832 coastal polychaete tubeworms in the Northeast Atlantic supports shared history and
833 vicariant events. *Mol Ecol* 15:1841–1855.

834 Jombart T (2008) ADEGENET: a R package for the multivariate analysis of genetic markers.
835 *Bioinformatics* 24:1403–1405.

836 Jombart T, Dray S, Dufour AB (2009) Finding essential scales of spatial variation in ecological
837 data: A multivariate approach. *Ecography* 32:161–168.

838 Kain JM (1979) A view of the genus *Laminaria*. *Oceanogr Mar Biol Annu Rev* 17:101–161.

839 Klingbeil WH, Montecinos GJ, Alberto F (2022) Giant kelp genetic monitoring before and after
840 disturbance reveals stable genetic diversity in Southern California. *Front Mar Sci* 9:1–16.

841 Kopelman NM, Mayzel J, Jakobsson M, Rosenberg NA, Mayrose I (2015) Clumpak: a program
842 for identifying clustering modes and packaging population structure inferences across K.
843 *Mol Ecol Resour* 15:1179–1191.

844 Krueger-Hadfield SA, Roze D, Mauger S, Valero M (2013) Intergametophytic selfing and
845 microgeographic genetic structure shape populations of the intertidal red seaweed
846 *Chondrus crispus*. *Mol Ecol* 22:3242–3260.

847 Lambeck K (1997) Sea-level change along the French Atlantic and Channel coasts since the time
848 of the Last Glacial Maximum. *Palaeogeogr Palaeoclimatol Palaeoecol* 129:1–22.

849 Legendre L, Demers S (1984) Towards Dynamic Biological Oceanography and Limnology. *Can*
850 *J Fish Aquat Sci* 41:2–19.

851 Legendre P, Anderson MJ (1999) Distance-based redundancy analysis: Testing multispecies
852 responses in multifactorial ecological experiments. *Ecol Monogr* 69:1–24.

853 Lett C, Verley P, Mullon C, Parada C, Brochier T, Penven P, Blanke B (2008) A Lagrangian tool
854 for modelling ichthyoplankton dynamics. *Environ Model Softw* 23:1210–1214.

855 Liesner D, Fouqueau L, Valero M, Roleda MY, Pearson GA, Bischof K, Valentin K, Bartsch I

856 (2020) Heat stress responses and population genetics of the kelp *Laminaria digitata*
857 (Phaeophyceae) across latitudes reveal differentiation among North Atlantic populations.
858 Ecol Evol:1–34.

859 Lüning K (1990) Seaweeds: Their Environment, biogeography, and ecophysiology. Wiley &
860 Sons, New York, USA.

861 Lyard F, Lefevre F, Letellier T, Francis O (2006) Modelling the global ocean tides: modern
862 insights from FES2004. Ocean Dyn 56:394–415.

863 Lynch M, Lande R (1993) Evolution and extinction in response to environmental change. In:
864 *Biotic interactions and global change*. Kareiva PM, Kingsolver JG, Huey RB (eds) Sinauer
865 Associates: Sunderland, MA, p 234–250

866 Manel S, Loiseau N, Puebla O (2019) Long-distance marine connectivity: Poorly understood but
867 potentially important. Trends Ecol Evol 34:688–689.

868 Martins NT, Macagnan LB, Cassano V, Gurgel CFD (2022) Brazilian marine phylogeography:
869 A literature synthesis and analysis of barriers. Mol Ecol 31:5423–5439.

870 Mauger S, Couceiro L, Valero M (2012) A simple and cost-effective method to synthesize an
871 internal size standard amenable to use with a 5-dye system. Prime Res Biotechnol 2:2315–
872 5299.

873 Mauger S, Fouqueau L, Avia K, Reynes L, Serrao EA, Neiva J, Valero M (2021) Development
874 of tools to rapidly identify cryptic species and characterize their genetic diversity in
875 different European kelp species. J Appl Phycol 33:4169–4186.

876 Merchant CJ, Embury O, Bulgin CE, Block T, Corlett GK, Fiedler E, Good SA, Mittaz J, Rayner
877 NA, Berry D, Eastwood S, Taylor M, Tsushima Y, Waterfall A, Wilson R, Donlon C
878 (2019) Satellite-based time-series of sea-surface temperature since 1981 for climate
879 applications. Sci Data 6:223.

880 Mitarai S, Siegel DA, Watson JR, Dong C, McWilliams JC (2009) Quantifying connectivity in
881 the coastal ocean with application to the Southern California Bight. J Geophys Res
882 114:C10026.

883 Nadeau CP, Urban MC (2019) Eco-evolution on the edge during climate change. Ecography
884 42:1280–1297.

885 Nei M (1978) Estimation of average heterozygosity and genetic distance from a small number of
886 individuals. Genetics 89:583–590.

887 Nicolle A, Moitié R, Ogor J, Dumas F, Foveau A, Foucher E, Thiébaud E (2017) Modelling larval
888 dispersal of *Pecten maximus* in the English Channel: A tool for the spatial management of
889 the stocks. ICES J Mar Sci 74:1812–1825.

890 Norton TA (1992) Dispersal by macroalgae. Br Phycol J 27:293–301.

891 Nosil P, Funk DJ, Ortiz-Barrientos D (2009) Divergent selection and heterogeneous genomic
892 divergence. Mol Ecol 18:375–402.

893 Nunes FLD, Rigal F, Dubois SF, Viard F (2021) Looking for diversity in all the right places?
894 Genetic diversity is highest in peripheral populations of the reef-building polychaete
895 *Sabellaria alveolata*. Mar Biol 168:63.

896 Ogutu JO, Schulz-Streeck T, Piepho H-P (2012) Genomic selection using regularized linear
897 regression models: ridge regression, lasso, elastic net and their extensions. BMC Proc
898 6:S10.

899 Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O’Hara
900 RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2013) Package ‘vegan’,
901 version 2.5-7. 1–298.

902 Oppliger LV, Von Dassow P, Bouchemousse S, Robuchon M, Valero M, Correa JA, Mauger S,
903 Destombe C (2014) Alteration of sexual reproduction and genetic diversity in the kelp
904 species *Laminaria digitata* at the southern limit of its range. PLoS ONE 9.

905 Paradis E, Schliep K (2019) Ape 5.0: An environment for modern phylogenetics and evolutionary
906 analyses in R. Bioinformatics 35:526–528.

907 Peakall R, Smouse PE (2006) GENALEX 6: Genetic analysis in Excel. Population genetic
908 software for teaching and research. Mol Ecol Notes 6:288–295.

909 Petton S, Garnier V, Caillaud M, Debreu L, Dumas F (2023) Using the two-way nesting
910 technique AGRIF with MARS3D V11.2 to improve hydrodynamics and estimate
911 environmental indicators. *Geosci Model Dev* 16:1191–1211.

912 Pingree RD, Le Cann B (1989) Celtic and Armorican slope and shelf residual currents. *Prog*
913 *Oceanogr* 23:303–338.

914 Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus
915 genotype data. *Genetics* 155:945–959.

916 Pritchard JK, Wen W (2003) Documentation for STRUCTURE Software: Version 2.

917 R Core Team (2017) R: A language and environment for statistical computing.

918 Reed DC (1990) The effects of variable settlement and early competition on patterns of kelp
919 recruitment. *Ecology* 71:776–787.

920 Reynes L, Aurelle D, Chevalier C, Pinazo C, Valero M, Mauger S, Sartoretto S, Blanfuné A,
921 Ruitton S, Boudouresque CF, Verlaque M, Thibaut T (2021) Population genomics and
922 Lagrangian modeling shed light on dispersal events in the Mediterranean endemic *Ericaria*
923 *zosteroides* (= *Cystoseira zosteroides*) (Fucales). *Front Mar Sci* 8:1–18.

924 Robuchon M, Le Gall L, Mauger S, Valero M (2014) Contrasting genetic diversity patterns in
925 two sister kelp species co-distributed along the coast of Brittany, France. *Mol Ecol*
926 23:2669–2685.

927 Rogers-Bennett L, Catton CA (2019) Marine heat wave and multiple stressors tip bull kelp forest
928 to sea urchin barrens. *Sci Rep* 9:15050.

929 Roman J, Palumbi SR (2004) A global invader at home: population structure of the green crab,
930 *Carcinus maenas*, in Europe. *Mol Ecol* 13:2891–2898.

931 Rousset F (2008) GENEPOP'007: a complete re-implementation of the genepop software for
932 Windows and Linux. *Mol Ecol Resour* 8:103–106.

933 Salomon JC, Breton M (1993) An atlas of long-term currents in the Channel. *Oceanol Acta*
934 16:439–448.

935 Sandoval-Castillo J, Robinson NA, Hart AM, Strain LWS, Beheregaray LB (2018) Seascape
936 genomics reveals adaptive divergence in a connected and commercially important mollusc,
937 the greenlip abalone (*Haliotis laevigata*), along a longitudinal environmental gradient. *Mol*
938 *Ecol* 27:1603–1620.

939 Sanford E, Kelly MW (2011) Local adaptation in marine invertebrates. *Annu Rev Mar Sci* 3:509–
940 535.

941 Schoville SD, Bonin A, François O, Lobreaux S, Melodelima C, Manel S (2012) Adaptive
942 genetic variation on the landscape: Methods and cases. *Annu Rev Ecol Evol Syst* 43:23–
943 43.

944 Selkoe KA, Watson JR, White C, Horin TB, Iacchei M, Mitarai S, Siegel DA, Gaines SD, Toonen
945 RJ (2010) Taking the chaos out of genetic patchiness: seascape genetics reveals ecological
946 and oceanographic drivers of genetic patterns in three temperate reef species. *Mol Ecol*
947 19:3708–3726.

948 Sjöqvist C, Godhe A, Jonsson PR, Sundqvist L, Kremp A (2015) Local adaptation and
949 oceanographic connectivity patterns explain genetic differentiation of a marine diatom
950 across the North Sea–Baltic Sea salinity gradient. *Mol Ecol* 24:2871–2885.

951 Spalding MD, Fox HE, Allen GR, Davidson N, Ferdaña ZA, Finlayson M, Halpern BS, Jorge
952 MA, Lombana A, Lourie SA, Martin KD, McManus E, Molnar J, Recchia CA, Robertson
953 J (2007) Marine ecoregions of the world: A bioregionalization of coastal and shelf areas.
954 *BioScience* 57:573–583.

955 Starko S, Bailey LA, Creviston E, James KA, Warren A, Brophy MK, Danasel A, Fass MP,
956 Townsend JA, Neufeld CJ (2019) Environmental heterogeneity mediates scale-dependent
957 declines in kelp diversity on intertidal rocky shores. *PLoS ONE* 14:e0213191.

958 Teagle H, Hawkins SJ, Moore PJ, Smale DA (2017) The role of kelp species as biogenic habitat
959 formers in coastal marine ecosystems. *J Exp Mar Biol Ecol* 492:81–98.

960 Teske PR, Sandoval-Castillo J, Waters J, Beheregaray LB (2017) An overview of Australia's
961 temperate marine phylogeography, with new evidence from high-dispersal gastropods. *J*

962 Biogeogr 44:217–229.

963 Teske PR, Von Der Heyden S, McQuaid CD, Barker NP (2011) A review of marine
964 phylogeography in southern Africa. *South Afr J Sci* 107:43–53.

965 Trembl EA, Halpin PN, Urban DL, Pratson LF (2008) Modeling population connectivity by ocean
966 currents, a graph-theoretic approach for marine conservation. *Landsc Ecol* 23:19–36.

967 Valero M, Destombe C, Mauger S, Ribout C, Engel CR, Daguin-Thiebaut C, Tellier F (2011)
968 Using genetic tools for sustainable management of kelps: A literature review and the
969 example of *Laminaria digitata*. *Cah Biol Mar* 52:467–483.

970 Van Oosterhout C, Hutchinson WF, Wills DPM, Shipley P (2004) MICRO-CHECKER: software
971 for identifying and correcting genotyping errors in microsatellite data. *Mol Ecol Notes*
972 4:535–538.

973 Van Oppen MJH, Coleman MA (2022) Advancing the protection of marine life through
974 genomics. *PLOS Biol* 20:e3001801.

975 Weir BS, Cockerham CC (1984) Estimating *F*-Statistics for the analysis of population structure.
976 *Evolution* 38:1358.

977 Wernberg T, Bennett S, Babcock RC, de Bettignies T, Cure K, Depczynski M, Dufois F, Fromont
978 J, Fulton CJ, Hovey RK, Harvey ES, Holmes TH, Kendrick GA, Radford B, Santana-
979 Garçon J, Saunders BJ, Smale DA, Thomsen MS, Tuckett CA, Tuya F, Vanderklift MA,
980 Wilson S (2016) Climate-driven regime shift of a temperate marine ecosystem. *Science*
981 353:169–172.

982 White C, Selkoe KA, Watson J, Siegel DA, Zacherl DC, Toonen RJ (2010) Ocean currents help
983 explain population genetic structure. *Proc R Soc B Biol Sci* 277:1685–1694.

984 Wilcox MA, Jeffery NW, DiBacco C, Bradbury IR, Lowen B, Wang Z, Beiko RG, Stanley RRE
985 (2023) Integrating seascape resistances and gene flow to produce area-based metrics of
986 functional connectivity for marine conservation planning. *Landsc Ecol* 38:2189–2205.

987 Xuereb A, Benestan L, Normandeau É, Daigle RM, Curtis JMR, Bernatchez L, Fortin M-J (2018)
988 Asymmetric oceanographic processes mediate connectivity and population genetic
989 structure, as revealed by RADseq, in a highly dispersive marine invertebrate
990 (*Parastichopus californicus*). *Mol Ecol* 27:2347–2364.

991 Xuereb A, D’Aloia CC, Daigle RM, Andrello M, Dalongeville A, Manel S, Mouillot D, Guichard
992 F, Côté IM, Curtis JMR, Bernatchez L, Fortin M-J (2019) Marine Conservation and Marine
993 Protected Areas. In: *Population Genomics: Marine Organisms*. Oleksiak MF, Rajora OP
994 (eds) Springer, Cham., p 423–446

995 Yessad K (2015) Basics about ARPEGE/IFS, ALADIN and AROME in the cycle 42 of
996 ARPEGE/IFS. Research report. Météo-France/CNRM/GMAP/ALGO.

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Table 1. Information on the sampled populations: population codes as indicated in Figure 1; geographic locations (Latitude, Longitude); locality; year of sampling; position relative to the coastline; number of genotyped individuals and source of the data.

N°	Lat.	Long.	Locality	Year	Position	Nb.	Source
S1	47.339	-2.892	Hoedic	2011	Island	30	Robuchon et al. (2014)
S2	47.394	-2.958	Houat	2011	Island	30	Robuchon et al. (2014)
S3	47.328	-3.124	Belle-île	2006	Island	30	This study
S4	47.470	-3.091	Quiberon	2008	Coastline	28	This study
S5	47.762	-3.549	Lorient	2006	Coastline	24	Valero et al. (2011)
S6	47.791	-3.761	Pont Aven	2006	Coastline	28	Valero et al. (2011)
S7	47.700	-3.983	Glénan	2008	Island	30	This study
S8	47.786	-4.152	Loctudy	2008	Coastline	20	This study
S9	47.799	-4.383	Penmarc'h	2006	Coastline	29	Valero et al. (2011)
S10	48.032	-4.835	Ile de Sein	2009	Island	24	This study
S11	48.284	-4.601	Crozon	2011	Coastline	30	This study
S12	48.326	-4.764	Le Conquet	2011	Coastline	30	Robuchon et al. (2014)
S13	48.381	-4.919	Le Conquet	2011	Island	30	Robuchon et al. (2014)
S14	48.519	-4.779	Porspoder	2003	Coastline	25	Robuchon et al. (2014)
S15	48.673	-4.216	Plouescat	2005	Coastline	30	Valero et al. (2011)
S16	48.700	-4.152	Téven-Meur	2011	Coastline	30	Robuchon et al. (2014)
S17	48.711	-4.060	Ile de Sieck	2005	Coastline	30	Valero et al. (2011)
S18	48.725	-3.919	Roscoff	2011	Coastline	30	Robuchon et al. (2014)
S19	48.721	-3.803	Plougasnou	2011	Coastline	30	Robuchon et al. (2014)
S20	48.775	-3.777	Plateau de la Méloine	2015	Island	26	This study
S21	48.687	-3.613	Locquirec	2006	Coastline	27	Valero et al. (2011)
S22	48.871	-3.643	Triagoz	2012	Island	27	This study
S23	48.878	-3.513	Trégastel	2006	Island	27	This study
S24	48.881	-3.099	Tréguier	2006	Coastline	20	This study
S25	49.118	-2.821	Roche Douvres	2012	Island	26	This study

S26	48.688	-2.325	Plévenon	2011	Coastline	30	Robuchon et al. (2014)
S27	48.651	-2.118	Saint-Lunaire	2011	Coastline	30	Robuchon et al. (2014)
S28	48.694	-1.984	Saint-Malo	2011	Coastline	29	Robuchon et al. (2014)
S29	48.697	-1.919	Saint-Malo	2006	Coastline	27	This study
S30	49.729	-1.919	Omonville	2006	Coastline	29	This study
S31	49.653	-1.234	Barfleur	2006	Coastline	30	This study
S32	50.912	1.677	Wissant	2006	Coastline	30	This study

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Table 2. F_{ST} values averaged across all pairwise comparisons ($\overline{F_{ST}}$) for the samples or the group of samples mentioned in the first column. When the first column indicates a group of samples (which correspond to a genetic cluster, see Figure 2), the F_{ST} was additionally averaged across the populations belonging to that group. The populations or groups of populations from the southernmost populations (S1-S4); Locquirec (S21); populations from Saint-Malo Bay (S26-S29) and Dover Strait (S32) appeared to be particularly differentiated, as shown by higher $\overline{F_{ST}}$ compared to the rest of the populations (last line, “Others”). Minimum and maximum $\overline{F_{ST}}$ values are also indicated. The full pairwise F_{ST} matrix can be found in Table S5.

Samples or group of samples	$\overline{F_{ST}}$	F_{ST} min	F_{ST} max
S1-S4	0.183	0.024	0.395
S21	0.168	0.107	0.317
S26-S29	0.144	0.019	0.395
S32	0.227	0.159	0.356
Others	0.08	0.01	0.23

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Table 3. Estimates of genetic diversity associated to each population using *Ho*: observed heterozygosity, *He*: expected heterozygosity, *Ar*: allelic richness (calculated with minimum 19 diploid individuals), $\overline{P_a}$: mean private alleles and deviation from Hardy-Weinberg Equilibrium estimated using *F_{IS}*, * when the deviation is significant (*p*-value < 0.001, based on 1,000 permutations using GENETIX).

Nº	Position	<i>Ho</i>	<i>He</i>	<i>Ar</i>	$\overline{P_a}$	<i>F_{IS}</i>
S1	Island	0.552 ± 0.065	0.541 ± 0.055	3.724 ± 0.406	0 ± 0	-0.002
S2	Island	0.49 ± 0.051	0.51 ± 0.051	3.543 ± 0.304	0 ± 0	0.057
S3	Island	0.43 ± 0.068	0.425 ± 0.067	3.595 ± 0.31	0.091 ± 0.091	0.003
S4	Coastline	0.432 ± 0.072	0.426 ± 0.063	3.733 ± 0.452	0.091 ± 0.091	0.003
S5	Coastline	0.547 ± 0.066	0.555 ± 0.053	5.05 ± 0.684	0 ± 0	0.035
S6	Coastline	0.551 ± 0.066	0.539 ± 0.05	4.67 ± 0.584	0.091 ± 0.091	-0.004
S7	Island	0.539 ± 0.062	0.565 ± 0.051	5.22 ± 0.68	0.091 ± 0.091	0.063 *
S8	Coastline	0.586 ± 0.052	0.579 ± 0.05	5.554 ± 1.014	0.182 ± 0.182	0.013
S9	Coastline	0.513 ± 0.055	0.549 ± 0.05	5.443 ± 0.769	0.182 ± 0.182	0.083 *
S10	Island	0.561 ± 0.054	0.596 ± 0.05	5.913 ± 0.854	0 ± 0	0.08 *
S11	Coastline	0.555 ± 0.067	0.62 ± 0.065	5.551 ± 0.995	0.091 ± 0.091	0.122 *
S12	Coastline	0.561 ± 0.051	0.609 ± 0.055	6.151 ± 0.87	0.455 ± 0.207	0.097 *
S13	Island	0.552 ± 0.06	0.576 ± 0.062	5.613 ± 0.859	0 ± 0	0.06 *
S14	Coastline	0.585 ± 0.063	0.582 ± 0.054	6.004 ± 0.812	0.182 ± 0.122	0.014
S15	Coastline	0.617 ± 0.063	0.584 ± 0.059	5.355 ± 0.989	0 ± 0	-0.038
S16	Coastline	0.526 ± 0.06	0.555 ± 0.062	5.404 ± 0.898	0 ± 0	0.07 *
S17	Coastline	0.561 ± 0.073	0.543 ± 0.07	5.476 ± 0.99	0.091 ± 0.091	-0.015
S18	Coastline	0.495 ± 0.073	0.508 ± 0.078	4.814 ± 0.809	0.091 ± 0.091	0.043
S19	Coastline	0.445 ± 0.081	0.488 ± 0.074	4.451 ± 0.699	0.091 ± 0.091	0.103 *
S20	Island	0.418 ± 0.077	0.426 ± 0.076	3.942 ± 0.734	0.091 ± 0.091	0.04
S21	Coastline	0.387 ± 0.072	0.376 ± 0.066	3.158 ± 0.456	0 ± 0	-0.01
S22	Island	0.461 ± 0.087	0.471 ± 0.09	4.482 ± 1.077	0 ± 0	0.04

S23	Island	0.465 ± 0.095	0.452 ± 0.09	4.483 ± 0.927	0.273 ± 0.141	-0.01
S24	Coastline	0.496 ± 0.086	0.486 ± 0.078	4.508 ± 0.832	0.182 ± 0.122	0.006
S25	Island	0.457 ± 0.08	0.485 ± 0.078	3.762 ± 0.626	0 ± 0	0.078 *
S26	Coastline	0.33 ± 0.083	0.347 ± 0.082	3.361 ± 0.679	0.091 ± 0.091	0.064
S27	Coastline	0.45 ± 0.08	0.403 ± 0.07	2.951 ± 0.532	0 ± 0	-0.1 *
S28	Coastline	0.426 ± 0.078	0.382 ± 0.062	3.22 ± 0.431	0.091 ± 0.091	-0.098 *
S29	Coastline	0.424 ± 0.078	0.423 ± 0.068	3.271 ± 0.58	0.091 ± 0.091	0.017
S30	Coastline	0.448 ± 0.086	0.454 ± 0.076	4.361 ± 0.846	0 ± 0	0.03
S31	Coastline	0.487 ± 0.091	0.477 ± 0.078	4.414 ± 0.812	0 ± 0	-0.003
S32	Coastline	0.308 ± 0.083	0.29 ± 0.073	2.542 ± 0.407	0 ± 0	-0.046

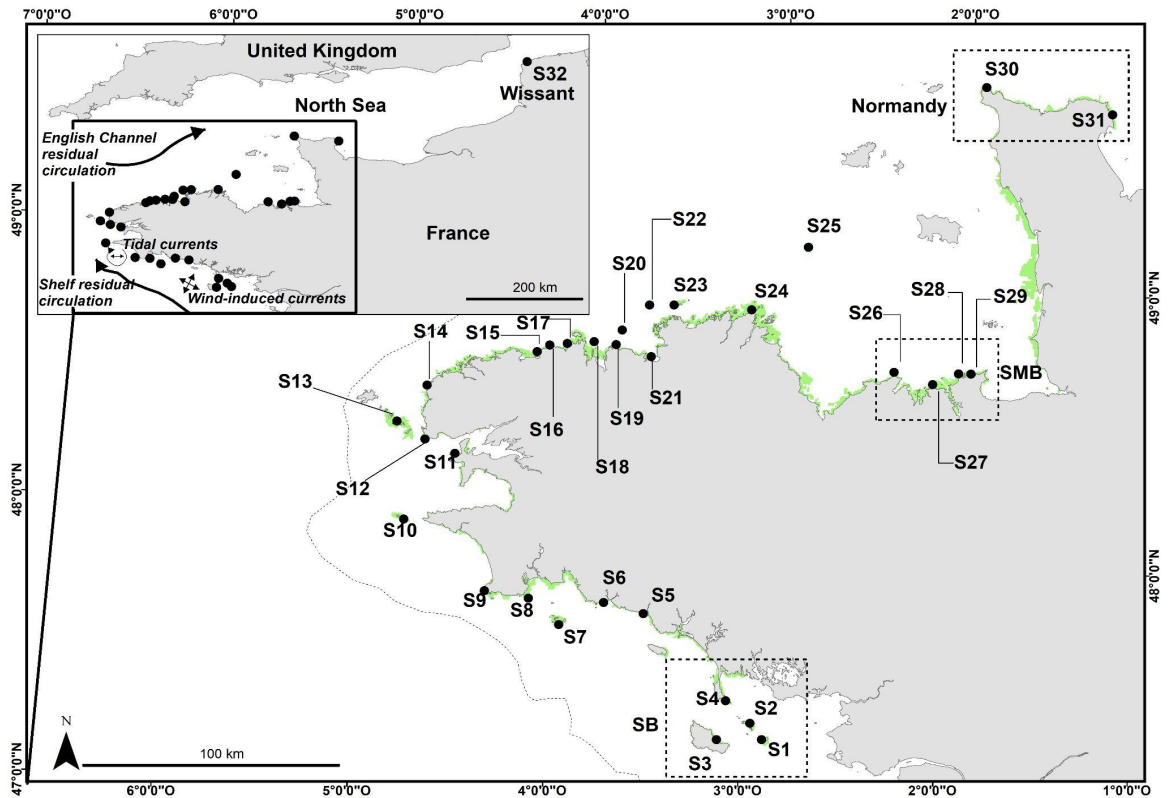
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Table 4. Results of the partial and global db-RDA for each dataset: overall (32 populations), regional (29 populations) and continuous datasets (24 populations). Environmental predictors selected by the stepwise forward selection (ordiR2step) are included in the db-RDA framework, the predictors highlighted in bold are significant at $p < 0.001$ according to the ANOVA. The adjusted coefficient of determination (R^2_{adj}) and the p -value of the model are reported. Habitat continuity and sampling year were not selected as a significant predictor in the global nor partial db-RDA and are therefore not represented in this table.

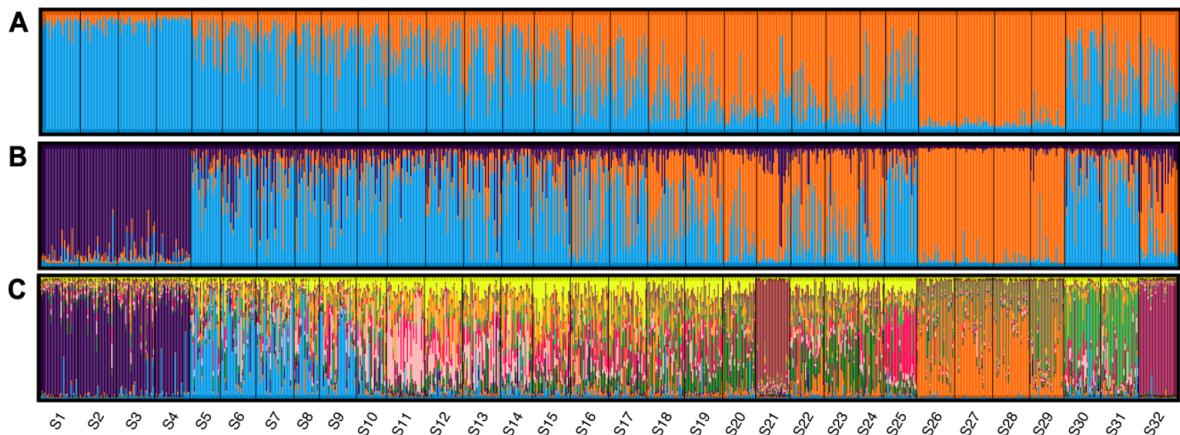
Overall	Oceanographic Connectivity	Geographic Position	Sea Surface Temperature	p -value	R^2_{adj}
Global db-RDA	AEM1, AEM3, AEM26, AEM2	dbMEM1, dbMEM3, dbMEM5		0.001	0.604
Partial db-RDA	AEM7, AEM6, AEM26			0.012	0.115
		dbMEM1, dbMEM3, dbMEM5		0.001	0.475
			Mean, Min	0.002	0.165
Regional					
Global db-RDA	AEM23, AEM2, AEM1, AEM25	dbMEM2, dbMEM3		0.001	0.614
Partial db-RDA	AEM2, AEM1, AEM23, AEM25, AEM7, AEM6, AEM9			0.001	0.549
		dbMEM2, dbMEM3, dbMEM1		0.001	0.485
			Mean, Min, Max, Range	0.001	0.221
Continuous					
Global db-RDA	AEM1, AEM2, AEM16, AEM10, AEM5, AEM19, AEM3	dbMEM3		0.001	0.748
Partial db-RDA	AEM1, AEM2, AEM16, AEM10, AEM5, AEM19, AEM3, AEM20, AEM9, AEM7			0.001	0.794
		dbMEM2, dbMEM3, dbMEM1		0.001	0.513
			Max	0.003	0.210

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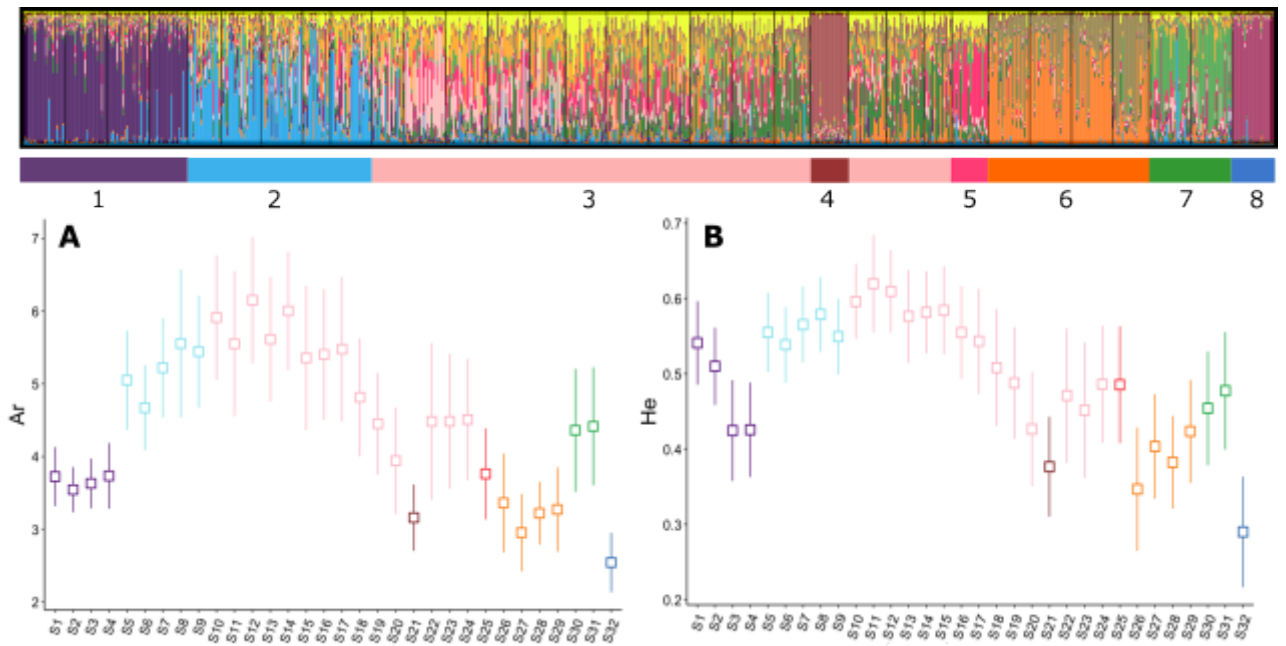
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Figure 1. Geographic position of the sampled populations, the Northernmost site (S32) is indicated in the inset. Population numbers correspond to the ones indicated in Table 1 and the area illustrated in green corresponds to rocky substrata above 5m depth obtained from IFREMER in May 2019. The information on the spatial distribution of bedrock comes from the combination of several sources as specified in the Material and Method section. The dotted line corresponds to the 120m isobath, which could correspond to the coastline at the Last Glacial Maximum. The inset illustrates the general circulation in the Bay of Biscay and in the English Channel, drawn according to Ayata et al. (2010).



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Figure 2. STRUCTURE barplot obtained for $K = 2$ (A), $K = 3$ (B) and $K = 12$ (C) which appeared the best number of clusters according to both ΔK and $\log \Pr(X|K)$ methods. Each vertical bar corresponds to one individual and the colors represent the individual's estimated proportion of ancestry in each of the K clusters. The numbers below correspond to the population code as indicated in Table and Figure 1.



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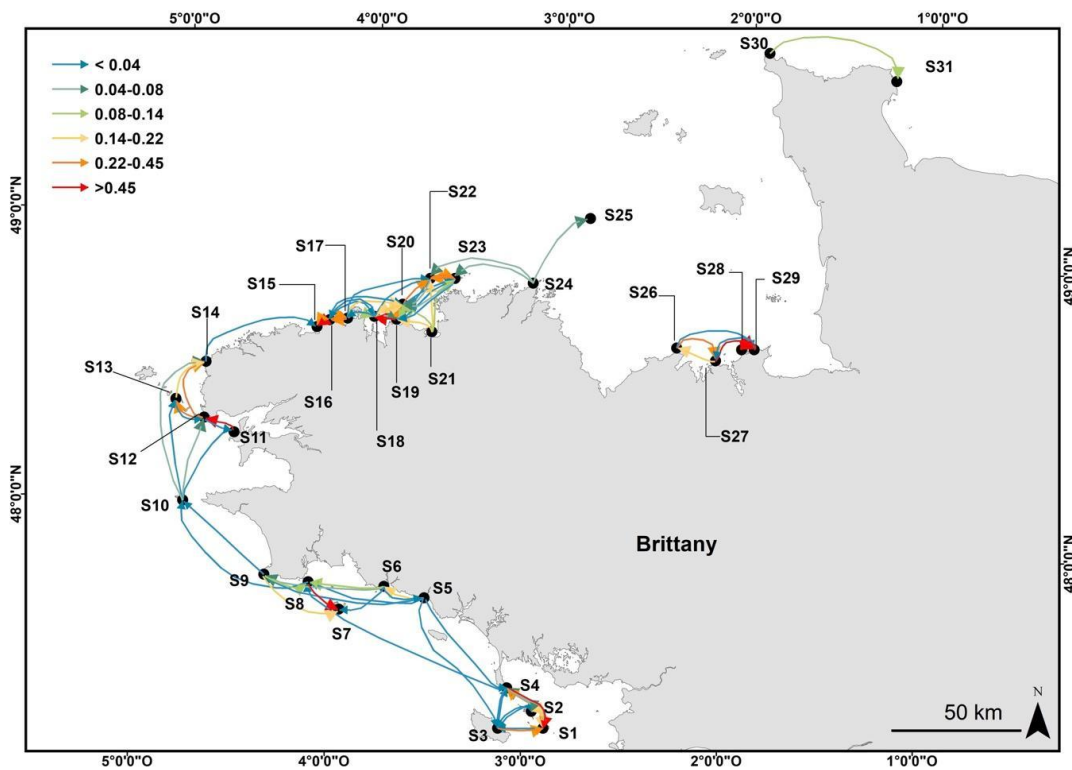
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Figure 3. **A.** Allelic richness (Ar) and **B.** Expected heterozygosity (He) observed among the 32 populations. The colors of the plots correspond to the eight genetic groups illustrated with the STRUCTURE barplot above. These figures illustrate the average and the standard deviation observed across markers.



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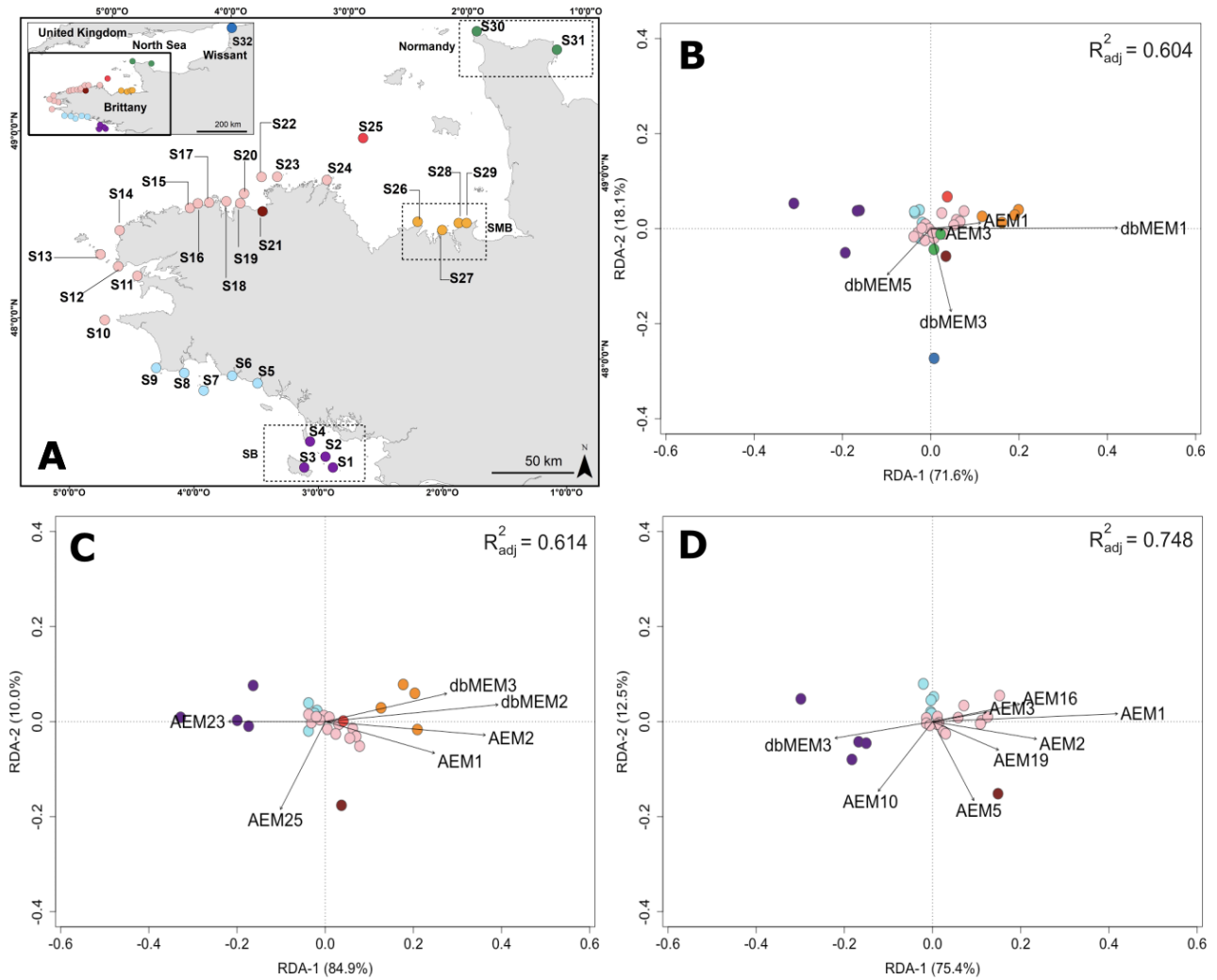
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Figure 4. Map illustrating the probability of connectivity obtained from the Lagrangian simulation model. The color gradient is located on the top left corner: cold color indicates low connectivity while warm color indicates high connectivity. For the clarity of the figure, values below 10^{-2} are not represented.



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Figure 5. Figure A. Geographic position of the sampled populations. The color used for each population corresponds to the genetic clusters illustrated in Figure 3. Figures B, C and D represent the results of the global db-RDA at the B. overall (32 populations), C. regional (29 populations) and D. continuous scale (24 populations). The numbers written in brackets on each axis correspond to the percentage of variance explained by each axis. The black arrows illustrate the relative contribution of the significant environmental factors according to the ANOVA and the stepwise forward selection (ordiR2step) process. The length of the arrows illustrates the relative contribution of each environmental predictor: as the length of the arrow increases, the contribution of the environmental predictor in explaining the neutral genetic variation increases. The adjusted coefficient of determination (R^2_{adj}) of each model is reported on the top right corner.

APPENDIX

Table S1. Genetic data of the 12 *Laminaria hyperborea* individuals that were found in our dataset and were then discarded.

Individual_code	Population	Ld148		Ld158		Ld167		Ld371		Ld531		Ld704		Lo454-23		Lo454-24		Lo454-17		Lo454-28		Lo4-24	
		Allele 1	Allele 2	Allele 1	Allele 2	Allele 1	Allele 2	Allele 1	Allele 2	Allele 1	Allele 2	Allele 1	Allele 2	Allele 1	Allele 2	Allele 1	Allele 2	Allele 1	Allele 2	Allele 1	Allele 2	Allele 1	Allele 2
LD_SB2_T2_03	S6	198	198	240	240	173	176	120	123	236	239	288	290	214	223	286	289	180	180	222	222	218	218
LD_SB2_T2_04	S6	198	198	238	240	173	173	123	126	233	245	288	292	223	226	280	289	165	165	222	222	218	218
LD_SB3_T2_20	S9	189	198	240	242	173	173	120	132	236	242	288	288	214	214	268	280	165	165	234	258	164	164
LD_NB48_T2_14	S21	195	195	240	242	176	176	120	123	242	242	286	288	199	211	268	268	180	180	234	234	216	216
LD_NB48_T2_18	S21	183	183	238	240	173	176	120	123	236	242	290	292	211	211	268	283	180	180	258	258	216	216
LD_NB48_T2_20	S21	186	198	240	240	176	176	123	132	236	242	288	292	211	211	268	280	180	180	234	258	216	216
LD_TRIA_12_09	S22	207	240	222	222	146	152	141	147	200	200	340	342	196	214	268	283	165	168	222	246	216	216
LD_TRIA_12_13	S22	240	249	222	222	152	158	147	153	200	200	0	0	214	214	268	289	165	165	234	246	164	216
LD_TRIA_12_14	S22	237	237	222	228	146	155	141	150	200	200	342	402	214	223	286	286	168	180	246	258	216	216
LD_RD_12_03	S25	207	240	222	222	155	155	117	150	200	200	348	350	214	214	268	289	165	165	222	258	216	216
LD_BIG_7	S28	198	198	238	240	170	170	120	144	304	316	233	242	316	316	304	316	180	180	206	206	224	224
LD_NO1_T2_15	S30	186	195	240	240	173	176	126	144	236	239	288	292	214	223	268	288	165	198	222	222	218	218

Table S2. Frequency of null alleles per marker and per population of *Laminaria digitata* obtained using FREENA (Chapuis & Estoup 2007) software. Significant values (>0.05) are highlighted in bold.

	1	2	3	4	5	6	7	8	9	10	11
S1	0.00000	0.14116	0.00000	0.00002	0.00003	0.00001	0.00000	0.01660	0.00000	0.00000	0.00003
S2	0.02774	0.14453	0.00914	0.01429	0.00176	0.00000	0.09697	0.00000	0.01186	0.00000	0.00001
S3	0.00000	0.00000	0.00000	0.04868	0.02706	0.00001	0.00000	0.00006	0.00027	0.00001	0.00001
S4	0.00003	0.00000	0.00001	0.00000	0.00001	0.03180	0.00000	0.00002	0.00001	0.02489	0.12131
S5	0.00000	0.00001	0.00000	0.00003	0.00001	0.00001	0.05281	0.12178	0.00000	0.00998	0.12604
S6	0.00001	0.01403	0.00000	0.02359	0.00000	0.00000	0.00000	0.06157	0.00010	0.06567	0.04787
S7	0.00002	0.22978	0.07437	0.00000	0.04443	0.01515	0.06585	0.00001	0.00000	0.00000	0.01234
S8	0.00000	0.10478	0.00000	0.01417	0.05713	0.00004	0.00001	0.00000	0.00001	0.00000	0.02857
S9	0.00000	0.02682	0.02117	0.01277	0.01499	0.07276	0.00001	0.03514	0.00000	0.08371	0.04428
S10	0.02275	0.10738	0.00000	0.00002	0.00669	0.01254	0.15491	0.00000	0.05791	0.00000	0.06169
S11	0.00000	0.01554	0.01249	0.03615	0.07386	0.07288	0.19612	0.00000	0.07836	0.06999	0.00001
S12	0.00000	0.05742	0.05824	0.05760	0.00000	0.09358	0.10696	0.00000	0.01317	0.05477	0.00000
S13	0.00003	0.01514	0.09196	0.00000	0.04064	0.00001	0.09185	0.00000	0.03628	0.00380	0.04258
S14	0.00000	0.00000	0.04776	0.00000	0.00000	0.00000	0.00001	0.00000	0.00001	0.14995	0.00000
S15	0.01337	0.05210	0.04766	0.00000	0.00000	0.00000	0.00000	0.00001	0.00000	0.00001	0.00001
S16	0.03932	0.03397	0.00001	0.01703	0.01464	0.00001	0.06292	0.05912	0.05874	0.00000	0.00001
S17	0.04793	0.00001	0.00001	0.00000	0.00000	0.00001	0.00000	0.00683	0.00001	0.04340	0.00001
S18	0.00000	0.00000	0.00377	0.03195	0.03602	0.00003	0.01581	0.00000	0.00000	0.05729	0.00006
S19	0.06208	0.11020	0.10713	0.00000	0.00000	0.00001	0.05086	0.00017	0.00000	0.14337	0.00003
S20	0.08324	0.06339	0.00000	0.00000	0.06476	0.00001	0.00000	0.00000	0.00002	0.00000	0.04129
S21	0.00000	0.00000	0.08722	0.00000	0.01225	0.00000	0.00001	0.00000	0.05202	0.00002	0.00100
S22	0.00918	0.04703	0.00001	0.00701	0.02473	0.00001	0.06987	0.00001	0.00001	0.00002	0.00100
S23	0.00000	0.00000	0.10286	0.00196	0.00001	0.00002	0.00000	0.00772	0.00002	0.00000	0.00005
S24	0.00000	0.00000	0.00000	0.00000	0.05630	0.00000	0.00000	0.00000	0.13000	0.00000	0.14934
S25	0.00000	0.05569	0.09105	0.06130	0.12111	0.00002	0.00000	0.00000	0.00000	0.10687	0.00005
S26	0.00000	0.07512	0.01105	0.05541	0.03104	0.11411	0.04832	0.00035	0.00100	0.00001	0.00100
S27	0.00000	0.00000	0.00012	0.00000	0.00002	0.00040	0.00000	0.00000	0.00100	0.00001	0.00006
S28	0.00000	0.00005	0.00000	0.00000	0.02300	0.05556	0.00000	0.00000	0.00003	0.02259	0.00100
S29	0.00014	0.00001	0.02214	0.00000	0.00587	0.00001	0.02941	0.07881	0.00142	0.11415	0.00100
S30	0.01765	0.00003	0.04487	0.00000	0.00001	0.00000	0.01796	0.06386	0.05004	0.00002	0.12557
S31	0.06137	0.00002	0.00000	0.00000	0.01193	0.00000	0.02918	0.09089	0.11065	0.00001	0.00100
S32	0.00000	0.01301	0.00001	0.00000	0.00000	0.06892	0.00001	0.00006	0.00100	0.00100	0.00100

Table S3. Test on linkage disequilibrium calculated across populations using Genepop 4.7.5 (Rousset 2008). The *p*-value was obtained using the log likelihood ratio statistic. The Markov chain parameters were: dememorization number 1,000, number of batches 100 and number of iterations per batch 1,000. The column df corresponds to the degrees of freedom. The same test has been performed at the individual-level, however, due to the size of the results (about 1680 rows) only the results obtained at the population-level are shown here.

Pair of locus	Chi2	df	<i>p</i> -value
Ld148 & Ld158	61.268593	64	0.573686
Ld148 & Ld167	42.493175	64	0.982484
Ld158 & Ld167	52.435867	64	0.848782
Ld148 & Ld371	54.364079	64	0.799238
Ld158 & Ld371	78.148001	64	0.109978
Ld167 & Ld371	50.098955	64	0.898109
Ld148 & Ld531	57.592577	64	0.700887
Ld158 & Ld531	61.404635	64	0.568834
Ld167 & Ld531	70.589502	64	0.266955
Ld371 & Ld531	39.414769	64	0.993362
Ld148 & Ld704	54.058741	64	0.807589
Ld158 & Ld704	61.528524	64	0.564413
Ld167 & Ld704	58.719018	64	0.663082
Ld371 & Ld704	77.932809	64	0.113144
Ld531 & Ld704	52.639406	64	0.843920
Ld148 & Lo454-23	47.407483	64	0.940200
Ld158 & Lo454-23	49.175046	64	0.914295
Ld167 & Lo454-23	38.753006	64	0.994736
Ld371 & Lo454-23	63.802023	64	0.483462
Ld531 & Lo454-23	58.601617	64	0.667085
Ld704 & Lo454-23	67.105332	64	0.371118
Ld148 & Lo454-24	46.519072	64	0.950850
Ld158 & Lo454-24	65.551027	64	0.422754
Ld167 & Lo454-24	69.728007	64	0.290998
Ld371 & Lo454-24	50.786090	64	0.884856
Ld531 & Lo454-24	62.019929	64	0.546860
Ld704 & Lo454-24	50.406460	64	0.892307
Lo454-23 & Lo454-24	68.470619	64	0.328181
Ld148 & Lo454-17	47.841024	58	0.826859
Ld158 & Lo454-17	74.338907	58	0.072860
Ld167 & Lo454-17	58.110128	58	0.471238
Ld371 & Lo454-17	37.051539	58	0.985433
Ld531 & Lo454-17	45.415862	58	0.885395
Ld704 & Lo454-17	42.039292	58	0.943114
Lo454-23 & Lo454-17	43.715190	58	0.917860
Lo454-24 & Lo454-17	45.470829	58	0.884227
Ld148 & Lo454-28	62.806792	62	0.447496
Ld158 & Lo454-28	53.613270	62	0.767138
Ld167 & Lo454-28	80.045575	62	0.061275
Ld371 & Lo454-28	77.249968	62	0.091798
Ld531 & Lo454-28	63.153229	62	0.435358
Ld704 & Lo454-28	48.081654	62	0.902663
Lo454-23 & Lo454-28	54.884311	62	0.727320
Lo454-24 & Lo454-28	33.594225	62	0.998792
Lo454-17 & Lo454-28	72.616313	58	0.093731
Ld148 & Lo4-24	26.784328	50	0.997090
Ld158 & Lo4-24	29.536432	50	0.990630
Ld167 & Lo4-24	53.755514	50	0.332557
Ld371 & Lo4-24	40.193247	50	0.837790
Ld531 & Lo4-24	33.543912	50	0.964280
Ld704 & Lo4-24	45.591302	50	0.650735
Lo454-23 & 4-24	43.829326	50	0.718035
Lo454-24 & 4-24	47.048043	50	0.592566
Lo454-17 & 4-24	39.936610	48	0.789608
Lo454-28 & 4-24	45.021258	50	0.672971

Table S4 Pairwise F_{ST} values calculated according to Weir & Cockerham (1984) using GENETIX (below the diagonal) and their significance calculated with 1,000 permutations using the same software (above the diagonal). The adjusted p -value obtained for multiple comparisons is: 0.0001. ** when p -value < 0.00001, * when p -value < 0.0001, NS when non-significant.

	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12	S13	S14	S15	S16	S17	S18	S19	S20	S21	S22	S23	S24	S25	S26	S27	S28	S29	S30	S31	S32					
S1		NS	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**				
S2	0.024		**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**			
S3	0.088	0.081		**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**		
S4	0.127	0.106	0.129		**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**		
S5	0.139	0.134	0.144	0.197		NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS		
S6	0.148	0.127	0.141	0.181	0.012		**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	
S7	0.141	0.136	0.133	0.182	0.017	0.023		NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	
S8	0.11	0.114	0.123	0.185	0.012	0.022	0.016		NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
S9	0.133	0.135	0.11	0.194	0.015	0.041	0.024	0.004		NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
S10	0.11	0.096	0.115	0.153	0.018	0.024	0.026	0.007	0.017		NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
S11	0.12	0.124	0.145	0.195	0.083	0.079	0.08	0.054	0.074	0.039		NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
S12	0.115	0.109	0.149	0.189	0.042	0.042	0.05	0.02	0.036	0.005	0.022		NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
S13	0.113	0.111	0.139	0.195	0.047	0.052	0.05	0.019	0.03	0.004	0.042	0.001		NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
S14	0.12	0.122	0.12	0.199	0.017	0.032	0.035	0.005	0.006	0.001	0.03	0.006	0.013		NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
S15	0.093	0.092	0.129	0.174	0.046	0.054	0.062	0.022	0.042	0.01	0.047	0.011	0.01	0.018		NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
S16	0.114	0.111	0.136	0.209	0.038	0.053	0.058	0.019	0.036	0.012	0.059	0.019	0.008	0.018	0.006		NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
S17	0.126	0.111	0.155	0.202	0.066	0.058	0.083	0.04	0.065	0.021	0.056	0.015	0.011	0.03	0.007	0.007		NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
S18	0.159	0.138	0.167	0.228	0.059	0.062	0.06	0.03	0.049	0.018	0.072	0.027	0.019	0.028	0.029	0.012	0.018		NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
S19	0.172	0.144	0.209	0.235	0.101	0.096	0.111	0.072	0.104	0.047	0.095	0.039	0.033	0.071	0.036	0.037	0.024	0.019		NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
S20	0.222	0.195	0.233	0.291	0.071	0.069	0.099	0.066	0.082	0.046	0.132	0.059	0.046	0.065	0.056	0.041	0.04	0.029	0.052		NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
S21	0.243	0.221	0.214	0.317	0.165	0.153	0.188	0.151	0.149	0.131	0.16	0.137	0.131	0.127	0.137	0.119	0.111	0.124	0.164	0.135		NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
S22	0.176	0.172	0.21	0.27	0.083	0.095	0.103	0.056	0.068	0.036	0.1	0.039	0.026	0.046	0.044	0.033	0.028	0.017	0.044	0.037	0.124		NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
S23	0.192	0.175	0.213	0.278	0.085	0.083	0.097	0.058	0.079	0.043	0.107	0.043	0.029	0.057	0.047	0.028	0.023	0.005	0.02	0.016	0.121	0.006		NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
S24	0.178	0.167	0.205	0.265	0.083	0.082	0.097	0.056	0.076	0.038	0.08	0.031	0.026	0.046	0.038	0.028	0.017	0.011	0.022	0.019	0.107	0.013	-0.005		NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
S25	0.187	0.167	0.211	0.268	0.068	0.069	0.085	0.042	0.081	0.048	0.086	0.035	0.044	0.047	0.041	0.045	0.046	0.035	0.045	0.056	0.185	0.06	0.05	0.055		NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	
S26	0.298	0.292	0.312	0.391	0.142	0.153	0.161	0.125	0.136	0.123	0.187	0.131	0.104	0.123	0.123	0.083	0.101	0.059	0.12	0.068	0.189	0.068	0.057	0.085	0.121		NS	NS	NS	NS	NS	NS	NS	NS	NS		
S27	0.239	0.272	0.284	0.387	0.164	0.181	0.168	0.125	0.133	0.132	0.157	0.113	0.093	0.117	0.123	0.082	0.106	0.096	0.155	0.135	0.211	0.084	0.103	0.104	0.154	0.086		NS	NS	NS	NS	NS	NS	NS	NS	NS	
S28	0.264	0.285	0.31	0.395	0.17	0.185	0.174	0.136	0.161	0.137	0.182	0.13	0.109	0.138	0.123	0.082	0.105	0.08	0.136	0.122	0.225	0.088	0.087	0.098	0.15	0.057	0.019		NS	NS	NS	NS	NS	NS	NS	NS	
S29	0.228	0.224	0.242	0.337	0.122	0.125	0.114	0.087	0.119	0.105	0.134	0.108	0.096	0.102	0.1	0.064	0.088	0.046	0.114	0.091	0.184	0.089	0.068	0.077	0.096	0.048	0.074	0.055		NS	NS	NS	NS	NS	NS	NS	
S30	0.203	0.177	0.21	0.261	0.066	0.067	0.083	0.056	0.071	0.037	0.084	0.045	0.052	0.036	0.075	0.054	0.062	0.04	0.066	0.087	0.189	0.076	0.072	0.073	0.06	0.147	0.184	0.182	0.137		NS	NS	NS	NS	NS		
S31	0.182	0.168	0.172	0.249	0.07	0.08	0.069	0.056	0.062	0.036	0.068	0.05	0.059	0.029	0.076	0.053	0.076	0.043	0.086	0.107	0.188	0.092	0.089	0.077	0.09	0.164	0.158	0.168	0.119	0.025		NS	NS	NS	NS	NS	
S32	0.284	0.278	0.229	0.356	0.245	0.239	0.246	0.206	0.183	0.179	0.203	0.205	0.189	0.168	0.186	0.159	0.178	0.18	0.24	0.248	0.207	0.225	0.221	0.214	0.273	0.284	0.267	0.278	0.248	0.223	0.189		NS	NS	NS	NS	

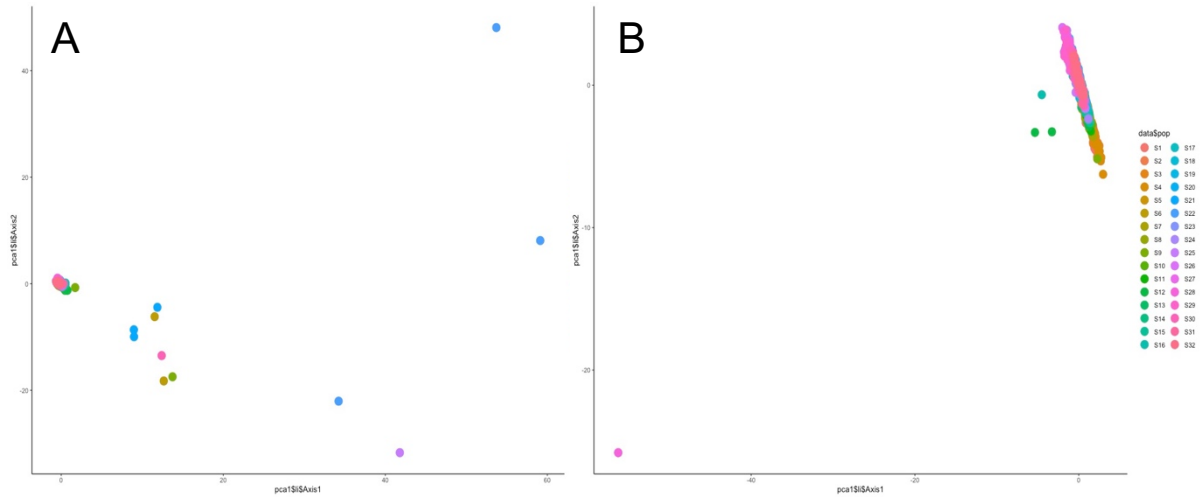


Figure S1. **A.** The PCA run on the whole dataset enabled to identify 11 outliers: S6 (2 ind.), S9 (1 ind.), S21 (3 ind.), S22 (3 ind.), S25 (1 ind.) and S30 (1 ind.). **B.** The PCA run on the dataset after taking the 11 outliers identified previously enabled to identify another outlier coming from S28.

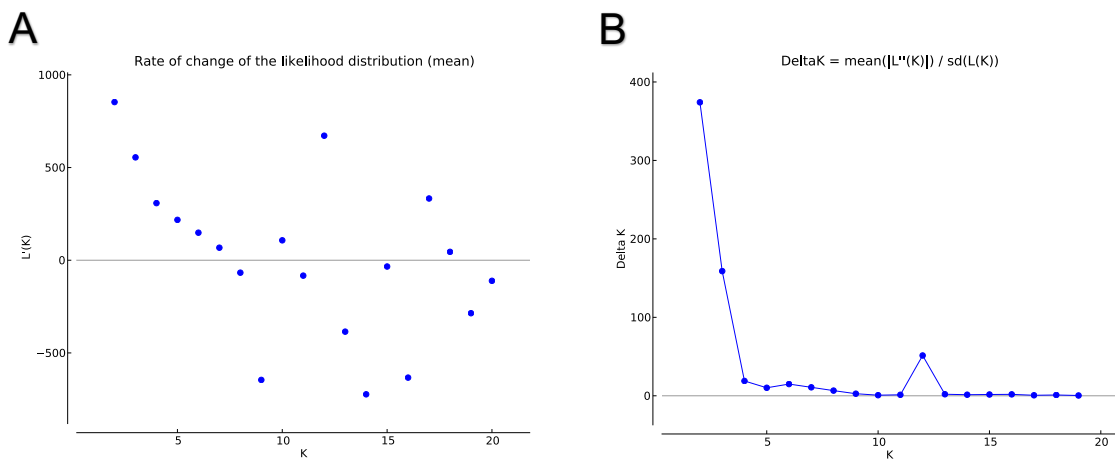


Figure S2. **A.** Rate of likelihood distribution (Pritchard & Wen 2003) and **B.** Delta K method (Evanno et al. 2005) associated to the STRUCTURE analyses.