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Congruence between fine-scale genetic breaks and dispersal potential in an estuarine seaweed across multiple transition zones

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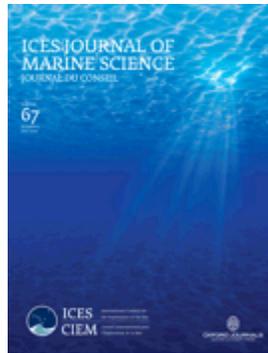
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3 1 **Congruence between fine-scale genetic breaks and dispersal potential in an**
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5 2 **estuarine seaweed across multiple transition zones.**
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55 23 **Running head:** Congruence between fine-scale genetic breaks and dispersal potential.

56
57 24 **Keywords:** Biogeography, physical modelling, gene flow, *Fucus* spp.
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25 **ABSTRACT**

26 Genetic structure in biogeographical transition zones can be shaped by several factors
27 including limited dispersal across barriers, admixture following secondary contact, differential
28 selection and mating incompatibility. A striking example is found in Northwest France and
29 Northwest Spain , where the estuarine seaweed *Fucus ceranoides* L. exhibits sharp, regional
30 genetic clustering. This pattern has been related to historical population fragmentation and
31 divergence into distinct glacial refugia, followed by post-glacial expansion and secondary
32 contact. The contemporary persistence of sharp ancient genetic breaks between nearby
33 estuaries has been attributed to prior colonization effects (density barriers) but the effect of
34 oceanographic barriers has not been tested. Here, through a combination of mesoscale
35 sampling (15 consecutive populations) and population genetic data (mtIGS) in NW France,
36 we define regional genetic disjunctions similar to those described in NW Iberia. Most
37 importantly, using high resolution dispersal simulations for Brittany and Iberian populations,
38 we provide evidence for a central role of contemporary hydrodynamics in maintaining genetic
39 breaks across these two major biogeographic transition zones. Our findings further show the
40 importance of a comprehensive understanding of oceanographic regimes in hydrodynamically
41 complex coastal regions to explain the maintenance of sharp genetic breaks along
42 continuously populated coastlines.

44 **INTRODUCTION**

45 Fueled by current concerns about the impacts of global change on biodiversity, there is a
46 renewed interest in understanding the processes affecting a species' range dynamics as well
47 as the factors shaping its genetic diversity. Generally, both historical and contemporary
48 processes are invoked to explain the distribution and phylogeography of a species. Tectonic
49 events and past climate fluctuations created topographic, environmental and hydrologic
50 barriers that were key in shaping phylogeographic structure of many plant and animal species.
51 Of these, the Last Glacial Maximum is probably the most significant and recent historical event

1
2
3 52 (e.g., Hewitt, 2000; Barnes et al., 2002; Liang et al., 2017; Neiva et al., 2018). During this time,
4
5 53 ice sheets covered much of current cold and temperate zones of the Northern Hemisphere,
6
7 54 triggering range fragmentation and contractions of entire ecosystems to more southern
8
9 55 latitudes, while during the present interglacial, widespread range shifts and poleward
10
11 56 expansions have occurred.

12
13 57 It is predicted that genetic diversity is lowest in recently colonized areas and highest in refugial
14
15 58 areas where long-term persistence was possible (e.g., Hewitt, 1996; Comps et al., 2001;
16
17 59 Hewitt, 2004; Kennedy et al., 2017). However, contemporary demographic processes can
18
19 60 either mask or even erase genetic signatures of population expansions or retreats (Smith et
20
21 61 al., 2011). High levels of gene flow may homogenize genetic diversity among previously
22
23 62 structured populations. On the other hand, nonrandom mating with individuals in close
24
25 63 geographic proximity can generate genetic structuring within a continuous population (Slatkin,
26
27 64 1993). Intrinsic characteristics of the species such as dispersal ability, migration patterns and
28
29 65 changes in population densities can further confound any historical signature (e.g., Mims et al.,
30
31 66 2015; Chust et al., 2016; Assis et al., 2018)

32
33 67 Biogeographical transition regions provide a good framework for exploring and understanding
34
35 68 genetic structuring of species through space and time. These are areas of overlap and
36
37 69 segregation between different biotic components, and geographically separated clades often
38
39 70 coincide with these transition zones (Ferro and Morrone, 2014). In the marine realm,
40
41 71 phylogeographic breaks in biogeographical transition regions are generally attributed to
42
43 72 historical processes or contemporary dispersal barriers, such as upwelling phenomena and
44
45 73 currents that may limit along-shore dispersal, environmental differences boosting local
46
47 74 adaptation and/or reproductive strategies maintaining self-recruitment (Gilg and Hilbish, 2003;
48
49 75 Zardi et al., 2007; Selkoe et al., 2010).

50
51 76 There are well known biogeographical boundaries in all oceans, some of which are associated
52
53 77 with oceanographic features that generate contemporary barriers to dispersal. For example,
54
55 78 the strong southward-flowing Agulhas Current, which runs about 10 km offshore along most
56
57 79 of South Africa's east and southeast coast, impedes larval dispersal and thus promotes local

1
2
3 80 adaptation (Teske et al., 2011; Zardi et al., 2011). Dispersal and gene flow around Point
4
5 81 Conception in southern California are also strongly affected by extensive upwelling of colder
6
7 82 sub-surface waters and by the southward California Current (Wares et al., 2001; Hohenlohe,
8
9 83 2004; Johansson et al., 2015).

10
11 84 Here, we investigated the contribution of contemporary oceanographic connectivity in
12
13 85 maintaining geographically separated genetic clades within a continuously distributed
14
15 86 seaweed species along the biogeographic transition areas of Brittany (northwest France,
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17 87 Europe) and northwest Iberia (northern Spain, Europe; Fig. 1). These two areas are highly
18
19 88 relevant for studying this question and marine connectivity in general. Both areas delimit the
20
21 89 boundaries between cold-temperate and warm-temperate regions (Spalding et al., 2007), they
22
23 90 are refugial zones for numerous species (Provan, 2013) and, over the past decades, they
24
25 91 have undergone significant changes in macroalgae assemblages due to climate change
26
27 92 (Nicastro et al., 2013; Gallon et al., 2014; Assis et al., 2017).

28
29
30 93 In this study, we use phylogeographic analyses and Lagrangian Particle Simulations
31
32 94 (LPS) coupled with network analyses to evaluate the levels of congruence between dispersal
33
34 95 potential and the patterns of present-day genetic differentiation and diversity in the estuarine
35
36 96 seaweed *Fucus ceranoides* along these two biogeographic transition zones. This species is
37
38 97 perennial, dioecious and restricted to estuarine intertidal areas. Furoid seaweeds have no
39
40 98 planktonic dispersal stage and have restricted gamete dispersal (Serrão et al., 1997).
41
42 99 However, adult individuals can achieve long distance gene flow via the rafting of whole or
43
44 100 partially detached thalli with reproductive structures (Thiel and Haye, 2006; McKenzie and
45
46 101 Bellgrove, 2008), a form of population connectivity strongly influenced by hydrodynamic forces
47
48 102 and coastal topography. Currently, *F. ceranoides* is distributed from northern Portugal to
49
50 103 northern Norway (Lein, 1984) and Iceland (Munda, 1999), covering both past non-glaciated
51
52 104 and glaciated regions of Europe. Previous studies have shown the occurrence of two divergent
53
54 105 genetic lineages in this species between the south and the north of Europe, the
55
56 106 phylogeographic break being localized in Northwest France near the English Channel (Neiva
57
58 107 et al., 2012a; Neiva et al., 2012b). Specifically, the dominant Northwest Iberian haplotypes of

1
2
3 108 this species was found in southern Brittany but not after the genetic break in northern Brittany
4
5 109 (Neiva et al., 2010). We discuss three scenarios for the concordance between present-day
6
7 110 oceanographic dispersal barriers and the observed genetic differentiation among *F.*
8
9 111 *ceranoides* estuarine populations: 1) Contemporary oceanographic barriers to dispersal are
10
11 112 responsible for the origin, the position and the maintenance (i.e. delaying genetic
12
13 113 homogenization) of the genetic differentiation; 2) Contemporary oceanographic circulation
14
15 114 patterns explain the position, the maintenance but not the origin of the genetic differentiation;
16
17 115 3) Reproductive isolation, in addition to contemporary oceanographic patterns, limits genetic
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19 116 homogenisation thus contributing to the position and the maintenance of the genetic
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21 117 differentiation.
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24 118

27 119 **MATERIALS**

30 120 **Genetic data**

31
32 121 The two study areas (NW France and NW Spain) are peninsulas characterized by complex
33
34 122 and variable circulation patterns (Puillat et al., 2004; Varela et al., 2005; Ruiz-Villarreal et al.,
35
36 123 2006; Ayata et al., 2011). Because of that, sampling of only a limited number of localities would
37
38 124 be inappropriate. We therefore decided to sample a small number of individuals at as many
39
40 125 sites along the two coastlines as possible, rather than obtaining large numbers of individuals
41
42 126 from a limited number of sites (e.g., Sotka et al., 2004; Teske et al., 2007). This decision was
43
44 127 also supported by the very low genetic diversity within localities for this species (Neiva et al.,
45
46 128 2010; 2012b; Neiva et al., 2012a). As a result, two sets of sequences of *Fucus ceranoides*
47
48 129 were prepared and analyzed separately. The first data set (Data set 1) comprised sequences
49
50 130 of individuals collected in the estuaries of all major rivers between Hennebont (HB, southern
51
52 131 Brittany) and Camarel (CM, northern Brittany) in northwest France (n = 2 from each site;
53
54 132 Table SI1). The second dataset (Data set 2) consisted of sequences previously analysed in
55
56 133 Neiva et al. (Neiva et al., 2010; 2012b; Neiva et al., 2012a) and sampled across northern Iberia
57
58 134 between Viana do Castelo (VIA, northern Portugal) and Porcia (POR, northern Spain). To
59
60

1
2
3 135 allow a comparison between data sets, a random subsample of 2 individuals from each site
4
5 136 was used for Data set 2. The random subsampling in NW Spain was repeated to ensure
6
7 137 consistency in the results obtained.
8

9 138 Sampling was performed in 2014-2015 and conducted with similar *criteria* for individuals used
10
11 139 in both data sets. All collection sites were characterized by monospecific belts of *F.*
12
13 140 *ceranoides* attached to hard substrata and were exposed to steep salinity fluctuations
14
15 141 throughout the tidal cycle. At each site, 5-10 cm tips of apical vegetative tissue were collected
16
17 142 from individuals sampled in the mid distributional range of the species. Neighboring sites were
18
19 143 at an average proximity of about 50 (± 15) and 33 (± 17) km for Data sets 1 and 2 respectively.
20
21 144 All samples were individually stored dehydrated in silica-gel crystals until DNA extraction.
22

23 145 *DNA isolation and sequencing of data set 1*

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25
26 146 To compile Data set 1, genomic DNA was extracted from approximately 10 mg of dried tissue
27
28 147 using the Nucleospin® Multi-96 plant kit (Macherey-Nagel Duren, Germany), according to the
29
30 148 manufacturer's protocol. Individuals were sequenced for the mitochondrial 23 S/trnK
31
32 149 intergenic spacer (mtIGS, Neiva et al., 2010). Primer sequences and amplification details were
33
34 150 the same as in Neiva et al. (Neiva et al., 2010; 2012b; Neiva et al., 2012a). Amplified fragments
35
36 151 were run in an ABI PRISM 3130xl automated capillary sequencer (Applied Biosystems,
37
38 152 CCMAR Portugal). MtDNA sequences were aligned, proofread and edited in GENEIOUS 3.8
39
40 153 (Drummond et al., 2011).
41
42

43 154 *Data analyses*

44
45 155 For both data sets, haplotype frequencies were estimated using DnaSP 5.0 (Librado and
46
47 156 Rozas, 2009). The relationships among the MtIGS haplotypes were inferred using statistical
48
49 157 parsimony with Tcs v. 1.13 (Clement et al., 2000). Because additional subsampled dataset for
50
51 158 the Iberia provided similar results (Table SI2 and Fig. SI1), only one was used for the
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53 159 simulations.
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55 160 **Dispersal simulations**

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57 161 The main oceanographic regions in northwest France and northwest Iberia (~550km and
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59 162 ~600km of coastlines, respectively) were identified by coupling Lagrangian Particle
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3 163 Simulations (LPS) with network analyses (least cost distance and community algorithm, e.g.,
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5 164 Assis et al., 2015; Klein et al., 2016; Assis et al., 2018). The simulations used daily data of
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7 165 ocean currents assembled from the Hybrid Coordinate Ocean Model (HYCOM), a resolution
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9 166 product with a spatial resolution of 0.08° (approx. 6–9 km), forced by wind speed, wind stress,
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11 167 precipitation and heat flux. This model can resolve oceanic fronts, meandering currents,
12
13 168 filaments and eddies (Chassignet et al., 2007), important mesoscale processes to properly
14
15 169 simulate ocean dispersal (Assis et al., 2015; Klein et al., 2016).

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17
18 170 Both regions of simulation were gridded to a common spatial resolution of 0.01° (approx. 1km).
19
20 171 A polygon representing global coastlines - OpenStreetMap geographic information (Haklay
21
22 172 and Weber, 2008)- was used to define intertidal source and sink cells. Passive particles
23
24 173 simulating rafts of *F. ceranoides* adult individuals were released from each gridded cell every
25
26 174 12 hours and allowed to drift for 60 full days; an extreme period for long-lived rafts of brown
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28 175 macroalgae (Monteiro et al., 2016; Assis et al., 2018). This approach aimed to capture the
29
30 176 rare, long-distance dispersal events, allowing gene flow at the scales of both regions (Monteiro
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32 177 et al., 2016; Assis et al., 2018). After the 60 days period, or when ending up on shore, the
33
34 178 particles were removed from the simulation. The geographic position of all particles was
35
36 179 calculated every hour with bilinear interpolation on the ocean velocity fields (with a spatial
37
38 180 resolution of 0.08°), while combining a 4th Order Runge-Kutta adaptive time-step on the path
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40 181 equations (e.g., Lett et al., 2008; Klein et al., 2016).

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42
43 182 The degree of connectivity between all pairs of gridded cells was determined by dividing the
44
45 183 number of unique particles released from cell *i* that ended up in cell *j*, by the total number of
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47 184 particles released from cell *i*. To account for the inter-annual variability in the ocean data, the
48
49 185 simulations ran independently per year (from January to December), for the most recent 10-
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51 186 year period of data, available in HYCOM (i.e., 2003 to 2012). Asymmetrical connectivity
52
53 187 matrices were determined by averaging the outcomes of the annual simulations.

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55
56 188 The connectivity matrices were used in network analyses (i.e., graph theory) to infer the major
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58 189 oceanographic regions of northwest Iberia and northwest France. To this end, network
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60 190 percolation removed weak probabilities to a threshold maintaining all cells (nodes) connected

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3 191 into a single network (Rozenfeld et al. 2008; Cunha et al., 2017), while maximizing modularity,
4
5 192 which quantified the strength of the backbone structure (or goodness of fit) of the networks
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7 193 (Newman, 2006). This allowed the removal of surplus connections with unimportant
8
9 194 information. The leading eigenvector algorithm (Newman, 2006) was applied to the percolated
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11 195 networks to assign a unique membership to the nodes. This approach allowed the detection
12
13 196 of communities in the networks (e.g., Munwes et al., 2010), which in practice translated into a
14
15 197 delineation of oceanographic regions in northwest Iberia and northwest France structured by
16
17 198 connectivity of ocean currents (Assis et al., 2018). The statistical significance of the
18
19 199 membership assignment to the nodes was inferred by testing the proportion of 9999
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21 200 membership randomizations that retrieved a higher modularity than that observed.

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23
24 201 Lagrangian Particle Simulations and network analyses were performed in R (R Development
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26 202 Core Team, 2016) using the packages: data.table (Dowle et al., 2019), dismo (Hijmans et al.,
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28 203 2017), igraph (Kamvar et al., 2014), parallel (Team, 2018), raster (Lamigueiro et al., 2018)
29
30 204 and vegan (Oksanen et al., 2018).

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32
33 205

34 206 **RESULTS**

35
36 207 In Data set 1 (NW France), six mtIGS haplotypes were identified in 30 individuals of *Fucus*
37
38 208 *ceranoides* in 15 sampled sites. In NW France, the network analyses showed two dominant
39
40 209 haplotypes (A and D) plus three derived ones (B, C and E), each private to one population
41
42 210 (Fig 1a). Haplotype frequency distribution revealed a geographical segregation of the two main
43
44 211 haplotypes. Haplotype 1 was present in individuals from regions R1 and R2 while Haplotype
45
46 212 D was restricted to more northern sites within region R3.

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48
49 213 Out of 415 sequences retrieved from the GenBank, 52 sequences were randomly selected for
50
51 214 Data set 2 (northwest Iberia). The network showed seven main haplotypes of which two were
52
53 215 shared among six to ten populations and three were shared by two to three populations. The
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55 216 remaining two haplotypes were private to one single population. In the frequency distribution,
56
57 217 the main haplotype was restricted to region R5 and haplotype F was present only in region
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3 218 R4. Haplotype A was present in regions R3 and R1 while haplotype B was confined to region

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5 219 **R2. Dispersal simulations**

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7 220 The LPS using HYCOM ocean currents over the 10-year period released 7300 particles per
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9 221 cell (7.80×10^6 and 7.88×10^6 particles in total in northwest France and northwest Iberia,
10
11 222 respectively). Particles drifted for longer distances in northwest Iberia than in northwest France
12
13 223 (up to 431.2 km; Table 1; Fig. SI2). The maximum period of drifting time was also higher in
14
15 224 northwest Iberia (26.7 days), but on average, particles drifted for longer periods in northwest
16
17 225 France (3.61 ± 2.63 days). The maximum probability of connectivity between the pairs of cells
18
19 226 was observed in northwest France (western Brittany; 0.721). However, the average cell
20
21 227 probabilities within regions did not vary considerably (Table 1; Fig. SI2).

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23
24 228 The assignment of oceanographic regions performed by the leading eigenvector algorithm
25
26 229 (network analysis) for northwest France and northwest Iberia showed significant modularity
27
28 230 values of 0.41 and 0.57 (p-values < 0.001), respectively. The algorithm identified three regions
29
30 231 in northwest France (Fig. 1a), with breaks in Penmarch and Porspoder, and five regions in
31
32 232 northwest Iberia (Fig. 1b), with breaks in Ria de Arousa, Corrubedo, Camelle (northern Costa
33
34 233 da Morte) and Cabo Ortegal (Cariño). The average probability of connectivity within the
35
36 234 oceanographic regions of northwest France (diagonal of Fig. 1d) was 10-fold higher than
37
38 235 between regions, with the exception of those between R1 and R2 (Fig. 1d), which were of the
39
40 236 same order of magnitude. Following a similar pattern, the probabilities of connectivity in
41
42 237 northwest Iberia were 10 to 100-fold higher within regions than between regions (diagonal of
43
44 238 Fig. 1e), with a marked increase as the distance between groups increased.

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51 240 **DISCUSSION**

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54 241 Our results show an overall strong match between oceanographic regions identified
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56 242 by dispersal simulations and fine-scale genetic discontinuities in the estuarine seaweed *Fucus*
57
58 243 *ceranoides* inhabiting north Atlantic shores (Fig. 1).

1
2
3 244 Predictions of oceanographic transport made with Lagrangian particle simulations are
4
5 245 highly sensitive to the inner spatial and temporal resolution of circulation models (Putman and
6
7 246 He, 2013). While we preserved the raw circulation processes modelled by Hycom at the scales
8
9 247 of days and tens of kilometers, a main limitation may arise if additional oceanographic
10
11 248 processes occurring at smaller scales are important for realistic connectivity events shaping
12
13 249 the genetic structure of *F. ceranoides*. For instance, circulation models with coarse spatial
14
15 250 resolutions may underestimate drifting times up to a factor of ~2. In the same way, weekly or
16
17 251 even daily temporal time steps may not be a realistic representation of what organisms
18
19 252 continuously experience (Fossette et al., 2012). Regardless of such potential limitations, our
20
21 253 results compared with independent genetic data, as well as additional studies comparing
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23 254 connectivity estimates with satellite-tracked organisms (e.g., Fossette et al., 2012) suggest
24
25 255 that, overall, particles advected by Hycom data provide a reliable estimate of the main
26
27 256 processes shaping current flow.

30 257 Previous studies have shown that mtIGS differentiation and contemporary *F.*
31
32 258 *ceranoides* genetic structuring in NW Iberia is most likely the result of complex, past range
33
34 259 dynamics (Neiva et al., 2012a). High levels of endemism and diversity highlighted by genetic
35
36 260 analyses of *F. ceranoides* populations inhabiting this region indicate long-term persistence in
37
38 261 glacial refugia. Despite the refugial role played by NW Iberia, sea level changes associated
39
40 262 with glacial/inter-glacial expansion and melting of ice-sheets had significant effects on near-
41
42 263 shore habitats (Chao et al., 2002; Roucoux et al., 2005). The current fine-scale genetic breaks
43
44 264 in Iberian *F. ceranoides* are the result of past fragmentation and divergence of populations
45
46 265 into distinct refugia (estuarine refugia within regional refugia), followed by expansion and
47
48 266 secondary contact of vicariant phylogroups (Neiva et al., 2012b).

51 267 In addition to southern European refugia, the ice-free paleo-shores of northwest
52
53 268 France (western Brittany) together with south western Ireland and the English Channel have
54
55 269 been recognized as northern periglacial refugia for several species (*Palmaria palmata* (Provan
56
57 270 et al., 2005); *Celleporella hyalina* (Gomez et al., 2007); *Fucus serratus* (Hoarau et al., 2007);
58
59 271 *Neomysis integer* (Remerie et al., 2009); *Ascophyllum nodosum* (Olsen et al., 2010)

1
2
3 272 Potentially, periodic sea level changes associated to Pleistocene glacial/interglacial cycles
4
5 273 could have caused continuous rearrangements of estuaries triggering *F. ceranoides*
6
7 274 population contraction/expansion dynamics similar to those described for Iberian shores;
8
9 275 these rearrangements could have then eventually led to the sharp genetic differentiation in
10
11 276 Brittany reported here. In the light of these earlier findings and observations the scenario of
12
13 277 contemporary oceanographic barriers being responsible for the origin the genetic
14
15 278 differentiation among *F. ceranoides* estuarine populations is rejected. Our results point to the
16
17 279 preponderant role of oceanography in determining the position and possibly maintaining the
18
19 280 break between vicariant lineages. This is further supported by previous studies showing
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21 281 shared haplotypes between Brittany (southern) and Iberia (Neiva et al., 2010; Neiva et al.,
22
23 282 2012a; Neiva et al., 2012b).

24
25
26 283 The persistent integrity of the sharp, fine-scale genetic discontinuities at secondary
27
28 284 contact zones can have a number of non-exclusive explanations. Previous studies assessing
29
30 285 this fine-scale phylogeographic structure within *F. ceranoides* in NW Iberia have highlighted
31
32 286 that contemporary dispersal between established populations is effectively too low to erase
33
34 287 historical divergence stemming from past fragmentation processes (Neiva et al., 2012b). In
35
36 288 this instance, sporadic inter-estuarine dispersal and density barriers have been invoked as the
37
38 289 main driver of limited connectivity.

39
40
41 290 Although post-glacial range expansion shows that *F. ceranoides* can effectively drift
42
43 291 across large spatial scales (Neiva et al., 2012a), dispersal among colonized estuaries is
44
45 292 expected to be limited. *F. ceranoides* is dioecious, and therefore prerequisites for successful
46
47 293 long-distance, inter-estuarine colonization are dispersal of fertile male and female fronds and
48
49 294 synchronous gamete release to produce zygotes at the new location. In addition, coastal
50
51 295 topography and estuarine morphology can curb circulation patterns, retention times and,
52
53 296 consequently, connectivity through drifting (Muhlin et al., 2008; Nicastro et al., 2008; Pardo et
54
55 297 al., 2019). The sheltered nature of estuarine habitats can significantly limit gamete dispersal
56
57 298 and the intrinsic features of geomorphology of each estuary can modulate circulation velocity
58
59 299 and intensity (Day et al., 1989). It has been suggested that pronounced meander curvatures

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2
3 300 contribute to reduced dispersal efficiency and the variable patterns of gene flow between
4
5 301 coastal and estuarine habitats (Zardi et al., 2013).
6

7 302 Density barrier effects are usually particularly marked in species such as *F. ceranoides*
8
9 303 characterized by rapid population growth and consequent habitat saturation. The dense,
10
11 304 monospecific *F. ceranoides* canopies typical of European northern Atlantic estuaries act as a
12
13 305 demographic buffer against numerically rare inter-estuarine immigrants favoring the
14
15 306 conservation of pre-existing genetic structure.
16
17

18 307 Clearly, the abundance of estuaries and their proximity strongly suggest that distance
19
20 308 can be excluded from the list of determinants maintaining *F. ceranoides* genetic breaks along
21
22 309 these shores. In NW Iberia, the mean distance between populations inhabiting neighboring
23
24 310 estuaries is not significantly different than that between bordering populations across
25
26 311 phylogeographic breaks (Neiva et al., 2012b). Similar distributional patterns can be found in
27
28 312 Brittany where several edge populations are spatially closer to populations across regional
29
30 313 genetic disjunctions than they are to their adjacent population within the same genetic clade.
31
32 314 While some studies carried out between cold- and warm-temperate marine ecosystems along
33
34 315 the northwest coast of France have invoked distinct mesoscale hydrographic features as
35
36 316 drivers of genetic patterns (Goldson et al., 2001; Jolly et al., 2005; Couceiro et al., 2013;
37
38 317 Almeida et al., 2017), others have highlighted lack of evidence for the role of hydrodynamics
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40 318 as dispersal determinants for the observed genetic discontinuities along NW Iberian shores
41
42 319 (Neiva et al., 2012b). The latter works have also stressed the difficulties to track drifters'
43
44 320 movements at a scale relevant for the organism to estimate migration rates among estuaries
45
46 321 and phylogroups. In NW Iberia, circulation dynamics are complex with high seasonal variability
47
48 322 and lack of persistent oceanographic patterns (Ruiz-Villarreal et al., 2006; Alvarez et al.,
49
50 323 2009). Here, through the use of large scale, dispersal simulations we reveal several
51
52 324 oceanographic regions matching haplotype segregation. Our findings add important evidence
53
54 325 to previous conclusions and support the scenario of key, mesoscale oceanographic processes
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56 326 having a determinant role in explaining the position of the observed high levels of regional
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58 327 genetic divergence. We also hypothesized that mesoscale oceanographic dispersal barriers
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3 328 are key to the maintenance of inter-estaurine genetic differentiation. In a neutral model of
4
5 329 secondary contact following allopatric differentiation, signs of secondary intergradation are
6
7 330 generally observed around oceanographic barriers (Woodruff, 1973; Barton and Hewitt, 1985;
8
9 331 Bierne et al., 2011). Admixed nuclear background has only been reported between two
10
11 332 neighboring *F. ceranoides* Iberian populations (Neiva et al., 2012b), indicating that individuals
12
13 333 belonging to distinct phylogroups can interbreed. However, no signs of hybridization have
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15 334 been observed in other Iberian or French populations. The geographically restricted and
16
17 335 limited lineage admixture suggests that other factors may be at play in maintaining fine-scale
18
19 336 genetic differentiation. In particular, incipient reproductive isolation (pre- or post-zygotic) can
20
21 337 depress gene flow between divergent phylogroups (e.g., Tellier et al., 2011). Under this
22
23 338 scenario, limited dispersal across oceanographic barriers explains the position of the genetic
24
25 339 discontinuity while the delay in homogenisation is mainly explained by endogenous
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27 340 components of reproductive isolation. Future studies assessing spatial and temporal
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29 341 reproductive dynamics of distinct *F. ceranoides* lineages will be crucial to provide a direct
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31 342 testing of this hypothesis.
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343 **Conclusions**

344 Our study highlights the need to combine evidence from multiple sources for a comprehensive
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36 345 understanding of ecological and evolutionary mechanisms linked to phylogeographic breaks.
37
38 346 These conclusions are of great significance for other organisms with sporadic and spatially
39
40 347 limited dispersal, helping clarify the apparent inconsistency of extensive and sharp genetic
41
42 348 differentiation in geographically restricted regions. In addition to theoretical evolutionary
43
44 349 relevance, the identification of contemporary dynamics contributing to the maintenance of
45
46 350 significant units of intraspecific biodiversity is critical for efficient approaches of management
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48 351 and conservation efforts.
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3 **590 FIGURE LEGEND**
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6 **591 Fig. 1.** Haplotype distribution of *Fucus ceranoides* in the coastlines of (a) Northwest France
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8 **592** and (panel b) Northwest Iberia. The colors along coastlines (a, b) depict the different
9
10 **593** oceanographic regions (R) identified in network analysis. A pairwise matrix of directional
11
12 **594** connectivity between oceanographic regions identified in (d) western Brittany and (e)
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14 **595** northwest Iberia. Matrix header colors according to the oceanographic regions depicted in the
15
16 **596** top panels a and b. Haplotype frequency and differentiation degree in (f) western Brittany and
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18 **597** (g) northwest Iberia. Note that there is no correspondence of haplotypes between the two
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20 **598** panels (i.e., each dataset was treated separately).
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24 **599**

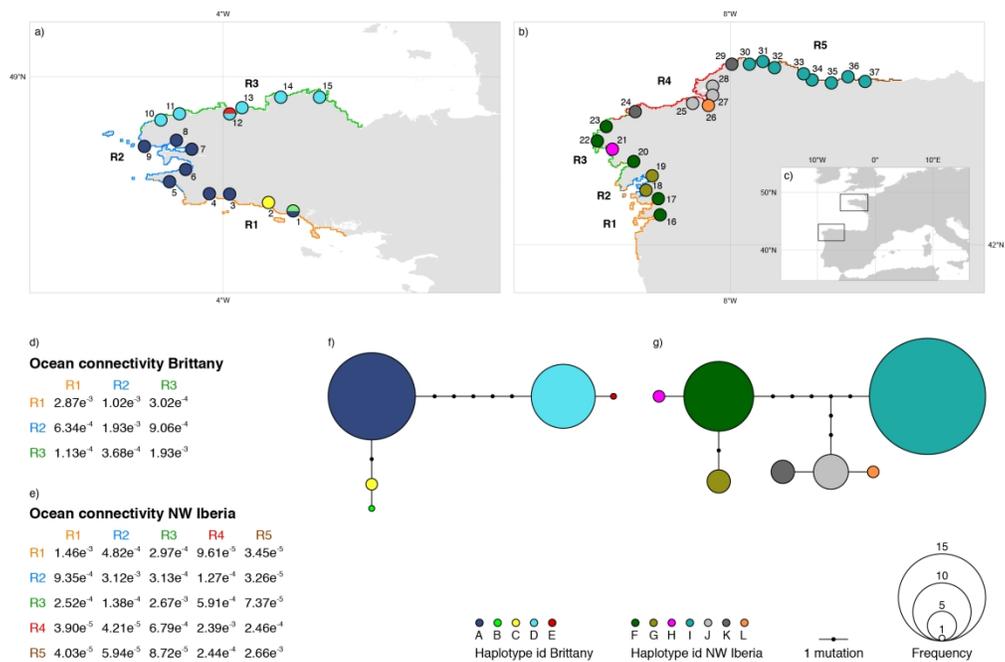
25
26 **600 TABLES**
27

28 **601 Table 1.** Maximum and average distances (km), drifting time (days) and probabilities produced
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30 **602** by the particles connecting different cells for the lagrangian particle simulations running in
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32 **603** Northwest France and Northwest Spain..
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34 **604**

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Region	Distance (km)		Time (days)		Probability	
	Maximum	Mean (\pm SD)	Maximum	Mean (\pm SD)	Maximum	Mean (\pm SD)
W Brittany	382.6	62.6 \pm 54.6	24.6	3.61 \pm 2.63	0.721	0.004 \pm 0.020
NW Iberia	431.2	105.9 \pm 90.8	26.7	2.09 \pm 1.81	0.607	0.004 \pm 0.021

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3 1 **Congruence between fine-scale genetic breaks and dispersal potential in an**
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5 2 **estuarine seaweed across multiple transition zones.**
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10 4 Katy R. Nicastr¹, Jorge Assis¹, Ester A. Serrão¹, Gareth A. Pearson¹, João Neiva¹, Myriam
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55 23 **Running head:** Congruence between fine-scale genetic breaks and dispersal potential.
56

57
58 24 **Keywords:** Biogeography, physical modelling, gene flow, *Fucus* spp.
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60

25 **ABSTRACT**

26 Genetic structure in biogeographical transition zones can be shaped by several factors
27 including limited dispersal across barriers, admixture following secondary contact, differential
28 selection and mating incompatibility. A striking example is found in Northwest France and
29 Northwest Spain , where the estuarine seaweed *Fucus ceranoides* L. exhibits sharp, regional
30 genetic clustering. This pattern has been related to historical population fragmentation and
31 divergence into distinct glacial refugia, followed by post-glacial expansion and secondary
32 contact. The contemporary persistence of sharp ancient genetic breaks between nearby
33 estuaries has been attributed to prior colonization effects (density barriers) but the effect of
34 oceanographic barriers has not been tested. Here, through a combination of mesoscale
35 sampling (15 consecutive populations) and population genetic data (mtlGS) in NW France,
36 we define regional genetic disjunctions similar to those described in NW Iberia. Most
37 importantly, using high resolution dispersal simulations for Brittany and Iberian populations,
38 we provide evidence for a central role of contemporary hydrodynamics in maintaining genetic
39 breaks across these two major biogeographic transition zones. Our findings further show the
40 importance of a comprehensive understanding of oceanographic regimes in hydrodynamically
41 complex coastal regions to explain the maintenance of sharp genetic breaks along
42 continuously populated coastlines.

44 **INTRODUCTION**

45 Fueled by current concerns about the impacts of global change on biodiversity, there is a
46 renewed interest in understanding the processes affecting a species' range dynamics as well
47 as the factors shaping its genetic diversity. Generally, both historical and contemporary
48 processes are invoked to explain the distribution and phylogeography of a species. Tectonic
49 events and past climate fluctuations created topographic, environmental and hydrologic
50 barriers that were key in shaping phylogeographic structure of many plant and animal species.
51 Of these, the Last Glacial Maximum is probably the most significant and recent historical event

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3 52 (e.g., Hewitt, 2000; Barnes et al., 2002; Liang et al., 2017; Neiva et al., 2018). During this time,
4
5 53 ice sheets covered much of current cold and temperate zones of the Northern Hemisphere,
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7 54 triggering range fragmentation and contractions of entire ecosystems to more southern
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9 55 latitudes, while during the present interglacial, widespread range shifts and poleward
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11 56 expansions have occurred.

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13 57 It is predicted that genetic diversity is lowest in recently colonized areas and highest in refugial
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15 58 areas where long-term persistence was possible (e.g., Hewitt, 1996; Comps et al., 2001;
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17 59 Hewitt, 2004; Kennedy et al., 2017). However, contemporary demographic processes can
18
19 60 either mask or even erase genetic signatures of population expansions or retreats (Smith et
20
21 61 al., 2011). High levels of gene flow may homogenize genetic diversity among previously
22
23 62 structured populations. On the other hand, nonrandom mating with individuals in close
24
25 63 geographic proximity can generate genetic structuring within a continuous population (Slatkin,
26
27 64 1993). Intrinsic characteristics of the species such as dispersal ability, migration patterns and
28
29 65 changes in population densities can further confound any historical signature (e.g., Mims et al.,
30
31 66 2015; Chust et al., 2016; Assis et al., 2018)

32
33 67 Biogeographical transition regions provide a good framework for exploring and understanding
34
35 68 genetic structuring of species through space and time. These are areas of overlap and
36
37 69 segregation between different biotic components, and geographically separated clades often
38
39 70 coincide with these transition zones (Ferro and Morrone, 2014). In the marine realm,
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41 71 phylogeographic breaks in biogeographical transition regions are generally attributed to
42
43 72 historical processes or contemporary dispersal barriers, such as upwelling phenomena and
44
45 73 currents that may limit along-shore dispersal, environmental differences boosting local
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47 74 adaptation and/or reproductive strategies maintaining self-recruitment (Gilg and Hilbish, 2003;
48
49 75 Zardi et al., 2007; Selkoe et al., 2010).

50
51 76 There are well known biogeographical boundaries in all oceans, some of which are associated
52
53 77 with oceanographic features that generate contemporary barriers to dispersal. For example,
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55 78 the strong southward-flowing Agulhas Current, which runs about 10 km offshore along most
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57 79 of South Africa's east and southeast coast, impedes larval dispersal and thus promotes local

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3 80 adaptation (Teske et al., 2011; Zardi et al., 2011). Dispersal and gene flow around Point
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5 81 Conception in southern California are also strongly affected by extensive upwelling of colder
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7 82 sub-surface waters and by the southward California Current (Wares et al., 2001; Hohenlohe,
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9 83 2004; Johansson et al., 2015).

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11 84 Here, we investigated the contribution of contemporary oceanographic connectivity in
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13 85 maintaining geographically separated genetic clades within a continuously distributed
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15 86 seaweed species along the biogeographic transition areas of Brittany (northwest France,
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17 87 Europe) and northwest Iberia (northern Spain, Europe; Fig. 1). These two areas are highly
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19 88 relevant for studying this question and marine connectivity in general. Both areas delimit the
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21 89 boundaries between cold-temperate and warm-temperate regions (Spalding et al., 2007), they
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23 90 are refugial zones for numerous species (Provan, 2013) and, over the past decades, they
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25 91 have undergone significant changes in macroalgae assemblages due to climate change
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27 92 (Nicastro et al., 2013; Gallon et al., 2014; Assis et al., 2017).

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30 93 In this study, we use phylogeographic analyses and Lagrangian Particle Simulations
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32 94 (LPS) coupled with network analyses to evaluate the levels of congruence between dispersal
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34 95 potential and the patterns of present-day genetic differentiation and diversity in the estuarine
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36 96 seaweed *Fucus ceranoides* along these two biogeographic transition zones. This species is
37
38 97 perennial, dioecious and restricted to estuarine intertidal areas. Furoid seaweeds have no
39
40 98 planktonic dispersal stage and have restricted gamete dispersal (Serrão et al., 1997).
41
42 99 However, adult individuals can achieve long distance gene flow via the rafting of whole or
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44 100 partially detached thalli with reproductive structures (Thiel and Haye, 2006; McKenzie and
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46 101 Bellgrove, 2008), a form of population connectivity strongly influenced by hydrodynamic forces
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48 102 and coastal topography. Currently, *F. ceranoides* is distributed from northern Portugal to
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50 103 northern Norway (Lein, 1984) and Iceland (Munda, 1999), covering both past non-glaciated
51
52 104 and glaciated regions of Europe. Previous studies have shown the occurrence of two divergent
53
54 105 genetic lineages in this species between the south and the ~~North-north~~ of Europe, the
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56 106 phylogeographic break being localized in Northwest France near the English Channel (Neiva
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58 107 et al., 2012a; Neiva et al., 2012b). Specifically, the dominant Northwest Iberian haplotypes of

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3 108 this species was found in southern Brittany but not after the genetic break in northern Brittany
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5 109 (Neiva et al., 2010). We discuss three scenarios for the concordance between present-day
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7 110 oceanographic dispersal barriers and the observed genetic differentiation among *F.*
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9 111 *ceranoides* estuarine populations: 1) Contemporary oceanographic barriers to dispersal are
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11 112 responsible for the origin, the position and the maintenance (i.e. delaying genetic
12
13 113 homogenization) of the genetic differentiation; 2) Contemporary oceanographic circulation
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15 114 patterns explain the position, the maintenance but not the origin of the genetic differentiation;
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17 115 3) Reproductive isolation, in addition to contemporary oceanographic patterns, limits genetic
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19 116 homogenisation thus contributing to the position and the maintenance of the genetic
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21 117 differentiation.
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27 119 **MATERIALS**

30 120 **Genetic data**

31
32 121 The two study areas (NW France and NW Spain) are peninsulas characterized by complex
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34 122 and variable circulation patterns (Puillat et al., 2004; Varela et al., 2005; Ruiz-Villarreal et al.,
35
36 123 2006; Ayata et al., 2011). Because of that, sampling of only a limited number of localities would
37
38 124 be inappropriate. We therefore decided to sample a small number of individuals at as many
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40 125 sites along the two coastlines as possible, rather than obtaining large numbers of individuals
41
42 126 from a limited number of sites (e.g., Sotka et al., 2004; Teske et al., 2007). This decision was
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44 127 also supported by the very low genetic diversity within localities for this species (Neiva et al.,
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46 128 2010; 2012b; Neiva et al., 2012a). As a result, two sets of sequences of *Fucus ceranoides*
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48 129 were prepared and analyzed separately. The first data set (Data set 1) comprised sequences
49
50 130 of individuals collected in the estuaries of all major rivers between Hennebont (HB, southern
51
52 131 Brittany) and Camarel (CM, northern Brittany) in northwest France (n = 2 from each site;
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54 132 Table SI1). The second dataset (Data set 2) consisted of sequences previously analysed in
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56 133 Neiva et al. (Neiva et al., 2010; 2012b; Neiva et al., 2012a) and sampled across northern Iberia
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58 134 between Viana do Castelo (VIA, northern Portugal) and Porcia (POR, northern Spain). To
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3 135 allow a comparison between data sets, a random subsample of 2 individuals from each site
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5 136 was used for Data set 2. The random subsampling in NW Spain was repeated to ensure
6
7 137 consistency in the results obtained.
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9 138 Sampling was performed in 2014-2015 and conducted with similar *criteria* for individuals used
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11 139 in both data sets. All collection sites were characterized by monospecific belts of *F.*
12
13 140 *ceranoides* attached to hard substrata and were exposed to steep salinity fluctuations
14
15 141 throughout the tidal cycle. At each site, 5-10 cm tips of apical vegetative tissue were collected
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17 142 from individuals sampled in the mid distributional range of the species. Neighboring sites were
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19 143 at an average proximity of about 50 (± 15) and 33 (± 17) km for Data sets 1 and 2 respectively.
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21 144 All samples were individually stored dehydrated in silica-gel crystals until DNA extraction.
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23 145 *DNA isolation and sequencing of data set 1*

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26 146 To compile Data set 1, genomic DNA was extracted from approximately 10 mg of dried tissue
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28 147 using the Nucleospin® Multi-96 plant kit (Macherey-Nagel Duren, Germany), according to the
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30 148 manufacturer's protocol. Individuals were sequenced for the mitochondrial 23 S/trnK
31
32 149 intergenic spacer (mtIGS, Neiva et al., 2010). Primer sequences and amplification details were
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34 150 the same as in Neiva et al. (Neiva et al., 2010; 2012b; Neiva et al., 2012a). Amplified fragments
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36 151 were run in an ABI PRISM 3130xl automated capillary sequencer (Applied Biosystems,
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38 152 CCMAR Portugal). MtDNA sequences were aligned, proofread and edited in GENEIOUS 3.8
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40 153 (Drummond et al., 2011).
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42 154 *Data analyses*

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45 155 For both data sets, haplotype frequencies were estimated using DnaSP 5.0 (Librado and
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47 156 Rozas, 2009). The relationships among the MtIGS haplotypes were inferred using statistical
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49 157 parsimony with Tcs v. 1.13 (Clement et al., 2000). Because additional subsampled dataset for
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51 158 the Iberia provided similar results (Table SI2 and Fig. SI1), only one was used for the
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53 159 simulations.
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55 160 **Dispersal simulations**

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58 161 The main oceanographic regions in northwest France and northwest Iberia (~550km and
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60 162 ~600km of coastlines, respectively) were identified by coupling Lagrangian Particle

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3 163 Simulations (LPS) with network analyses ~~–least cost and community algorithms–~~(least cost
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5 164 distance and community algorithm, e.g., Assis et al., 2015; Klein et al., 2016; Assis et al.,
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7 165 2018). The simulations used daily data of ocean currents assembled from the Hybrid
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9 166 Coordinate Ocean Model (HYCOM), a ~~high~~-resolution product with a spatial resolution of 0.08°
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11 167 (approx. 6–9 km), ~~forced~~ by wind speed, wind stress, precipitation and heat flux. This model
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14 168 can resolve oceanic fronts, meandering currents, filaments and eddies (Chassignet et al.,
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16 169 2007), important mesoscale processes to properly simulate ocean dispersal (Assis et al.,
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18 170 2015; Klein et al., 2016).

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20 171 Both regions of simulation were gridded to a common spatial resolution of 0.01° (approx. 1km).
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22 172 A polygon representing global coastlines - OpenStreetMap geographic information (Haklay
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24 173 and Weber, 2008)- was used to define intertidal source and sink cells. Passive particles
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26 174 simulating rafts of *F. ceranoides* adult individuals were released from each gridded cell every
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28 175 12 hours and allowed to drift for 60 full days; an extreme period for long-lived rafts of brown
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30 176 macroalgae (Monteiro et al., 2016; Assis et al., 2018). This approach aimed to capture the
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32 177 rare, long-distance dispersal events, allowing gene flow at the scales of both regions (Monteiro
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34 178 et al., 2016; Assis et al., 2018). After the 60 days period, or when ending up on shore, the
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36 179 particles were removed from the simulation. The geographic position of all particles was
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38 180 calculated every hour with bilinear interpolation on the ocean velocity fields (with a spatial
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40 181 resolution of 0.08°), while combining a 4th Order Runge-Kutta adaptive time-step on the path
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42 182 equations (e.g., Lett et al., 2008; Klein et al., 2016).

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45 183 The degree of connectivity between all pairs of gridded cells was determined by dividing the
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47 184 number of unique particles released from cell *i* that ended up in cell *j*, by the total number of
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49 185 particles released from cell *i*. To account for the inter-annual variability in the ocean data, the
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51 186 simulations ran independently per year (from January to December), for the most recent 10-
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53 187 year period of data, available in HYCOM (i.e., 2003 to 2012). Asymmetrical connectivity
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55 188 matrices were determined by averaging the outcomes of the annual simulations.

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58 189 The connectivity matrices were used in network analyses (i.e., graph theory) to infer the major
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60 190 oceanographic regions of northwest Iberia and northwest France. To this end, network

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3 191 percolation removed weak probabilities to a threshold maintaining all cells (nodes) connected
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5 192 into a single network (Rozenfeld et al. 2008; Cunha et al., 2017), while maximizing modularity,
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7 193 which quantified the strength of the backbone structure (or goodness of fit) of the networks
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9 194 (Newman, 2006). This allowed the removal of surplus connections with unimportant
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11 195 information. The leading eigenvector algorithm (Newman, 2006) was applied to the percolated
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13 196 networks to assign a unique membership to the nodes. This approach allowed the detection
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15 197 of communities in the networks (e.g., Munwes et al., 2010), which in practice translated into a
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17 198 delineation of oceanographic regions in northwest Iberia and northwest France structured by
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19 199 connectivity of ocean currents (Assis et al., 2018). The statistical significance of the
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21 200 membership assignment to the nodes was inferred by testing the proportion of 9999
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23 201 membership randomizations that retrieved a higher modularity than that observed.
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25

26 202 Lagrangian Particle Simulations and network analyses were performed in R (R Development
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28 203 Core Team, 2016) using the packages: data.table (Dowle et al., 2019), dismo (Hijmans et al.,
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30 204 2017), igraph (Kamvar et al., 2014), parallel (Team, 2018), raster (Lamigueiro et al., 2018)
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32 205 and vegan (Oksanen et al., 2018).
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36 207 **RESULTS**

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38 208 In Data set 1 (NW France), six mtIGS haplotypes were identified in 30 individuals of *Fucus*
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40 209 *ceranoides* in 15 sampled sites. In NW France, the network analyses showed two dominant
41
42 210 haplotypes (A and D) plus three derived ones (B, C and E), each private to one population
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44 211 (Fig 1a). Haplotype frequency distribution revealed a geographical segregation of the two main
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46 212 haplotypes. Haplotype 1 was present in individuals from regions R1 and R2 while Haplotype
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48 213 D was restricted to more northern sites within region R3.

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50 214 Out of 415 sequences retrieved from the GenBank, 52 sequences were randomly selected for
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52 215 Data set 2 (northwest Iberia). The network showed seven main haplotypes of which two were
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54 216 shared among six to ten populations and three were shared by two to three populations. The
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56 217 remaining two haplotypes were private to one single population. In the frequency distribution,
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58 218 the main haplotype was restricted to region R5 and haplotype F was present only in region
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3 219 R4. Haplotype A was present in regions R3 and R1 while haplotype B was confined to region

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5 220 **R2. Dispersal simulations**

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7 221 The LPS using HYCOM ocean currents over the 10-year period released 7300 particles per
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9 222 cell (7.80×10^6 and 7.88×10^6 particles in total in northwest France and northwest Iberia,
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11 223 respectively). Particles drifted for longer distances in northwest Iberia than in northwest France
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13 224 (up to 431.2 km; Table 1; Fig. SI2). The maximum period of drifting time was also higher in
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15 225 northwest Iberia (26.7 days), but on average, particles drifted for longer periods in northwest
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17 226 France (3.61 ± 2.63 days). The maximum probability of connectivity between the pairs of cells
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19 227 was observed in northwest France (western Brittany; 0.721). However, the average cell
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21 228 probabilities within regions did not vary considerably (Table 1; Fig. SI2).

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23
24 229 The assignment of oceanographic regions performed by the leading eigenvector algorithm
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26 230 (network analysis) for northwest France and northwest Iberia showed significant modularity
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28 231 values of 0.41 and 0.57 (p-values < 0.001), respectively. The algorithm identified three regions
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30 232 in northwest France (Fig. 1a), with breaks in Penmarch and Porspoder, and five regions in
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32 233 northwest Iberia (Fig. 1b), with breaks in Ria de Arousa, Corrubedo, Camelle (northern Costa
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34 234 da Morte) and Cabo Ortegal (Cariño). The average probability of connectivity within the
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36 235 oceanographic regions of northwest France (diagonal of Fig. 1d) was 10-fold higher than
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38 236 between regions, with the exception of those between R1 and R2 (Fig. 1d), which were of the
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40 237 same order of magnitude. Following a similar pattern, the probabilities of connectivity in
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42 238 northwest Iberia were 10 to 100-fold higher within regions than between regions (diagonal of
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44 239 Fig. 1e), with a marked increase as the distance between groups increased.

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51 241 **DISCUSSION**

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54 242 Our results show an overall strong match between oceanographic regions identified
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56 243 by dispersal simulations and fine-scale genetic discontinuities in the estuarine seaweed *Fucus*
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58 244 *ceranoides* inhabiting north Atlantic shores (Fig. 1).

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3 245 Predictions of oceanographic transport made with Lagrangian particle simulations are
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5 246 highly sensitive to the inner spatial and temporal resolution of circulation models (Putman and
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7 247 He, 2013). While we preserved the raw circulation processes modelled by Hycom at the scales
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9 248 of days and tens of kilometers, a main limitation may arise if additional oceanographic
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11 249 processes occurring at smaller scales are important for realistic connectivity events shaping
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13 250 the genetic structure of *F. ceranoides*. For instance, circulation models with coarse spatial
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15 251 resolutions may underestimate drifting times up to a factor of ~2. In the same way, weekly or
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17 252 even daily temporal time steps may not be a realistic representation of what organisms
18
19 253 continuously experience (Fossette et al., 2012). Regardless of such potential limitations, our
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21 254 results compared with independent genetic data, as well as additional studies comparing
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23 255 connectivity estimates with satellite-tracked organisms (e.g., Fossette et al., 2012) suggest
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25 256 that, overall, particles advected by Hycom data provide a reliable estimate of the main
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27 257 processes shaping current flow.

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29
30 258 Previous studies have shown that mtIGS differentiation and contemporary *F.*
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32 259 *ceranoides* genetic structuring in NW Iberia is most likely the result of complex, past range
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34 260 dynamics (Neiva et al., 2012a). High levels of endemism and diversity highlighted by genetic
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36 261 analyses of *F. ceranoides* populations inhabiting this region indicate long-term persistence in
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38 262 glacial refugia. Despite the refugial role played by NW Iberia, sea level changes associated
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40 263 with glacial/inter-glacial expansion and melting of ice-sheets had significant effects on near-
41
42 264 shore habitats (Chao et al., 2002; Roucoux et al., 2005). The current fine-scale genetic breaks
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44 265 in Iberian *F. ceranoides* are the result of past fragmentation and divergence of populations
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46 266 into distinct refugia (estuarine refugia within regional refugia), followed by expansion and
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48 267 secondary contact of vicariant phylogroups (Neiva et al., 2012b).

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51 268 In addition to southern European refugia, the ice-free paleo-shores of northwest
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53 269 France (western Brittany) together with south western Ireland and the English Channel have
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55 270 been recognized as northern periglacial refugia for several species (*Palmaria palmata* (Provan
56
57 271 et al., 2005); *Celleporella hyalina* (Gomez et al., 2007); *Fucus serratus* (Hoarau et al., 2007);
58
59 272 *Neomysis integer* (Remerie et al., 2009); *Ascophyllum nodosum* (Olsen et al., 2010)

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3 273 Potentially, periodic sea level changes associated to Pleistocene glacial/interglacial cycles
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5 274 could have caused continuous rearrangements of estuaries triggering *F. ceranoides*
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7 275 population contraction/expansion dynamics similar to those described for Iberian shores;
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9 276 these rearrangements could have then eventually led to the sharp genetic differentiation in
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11 277 Brittany reported here. In the light of these earlier findings and observations the scenario of
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13 278 contemporary oceanographic barriers being responsible for the origin the genetic
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15 279 differentiation among *F. ceranoides* estuarine populations is rejected. Our results point to the
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17 280 preponderant role of oceanography in determining the position and possibly maintaining the
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19 281 break between vicariant lineages. This is further supported by previous studies showing
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21 282 shared haplotypes between Brittany (southern) and Iberia (Neiva et al., 2010; Neiva et al.,
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23 283 2012a; Neiva et al., 2012b).

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26 284 The persistent integrity of the sharp, fine-scale genetic discontinuities at secondary
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28 285 contact zones can have a number of non-exclusive explanations. Previous studies assessing
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30 286 this fine-scale phylogeographic structure within *F. ceranoides* in NW Iberia have highlighted
31
32 287 that contemporary dispersal between established populations is effectively too low to erase
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34 288 historical divergence stemming from past fragmentation processes (Neiva et al., 2012b). In
35
36 289 this instance, sporadic inter-estuarine dispersal and density barriers have been invoked as the
37
38 290 main driver of limited connectivity.

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41 291 Although post-glacial range expansion shows that *F. ceranoides* can effectively drift
42
43 292 across large spatial scales (Neiva et al., 2012a), dispersal among colonized estuaries is
44
45 293 expected to be limited. *F. ceranoides* is dioecious, and therefore prerequisites for successful
46
47 294 long-distance, inter-estuarine colonization are dispersal of fertile male and female fronds and
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49 295 synchronous gamete release to produce zygotes at the new location. In addition, coastal
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51 296 topography and estuarine morphology can curb circulation patterns, retention times and,
52
53 297 consequently, connectivity through drifting (Muhlin et al., 2008; Nicastro et al., 2008; Pardo et
54
55 298 al., 2019). The sheltered nature of estuarine habitats can significantly limit gamete dispersal
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57 299 and the intrinsic features of geomorphology of each estuary can modulate circulation velocity
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59 300 and intensity (Day et al., 1989). It has been suggested that pronounced meander curvatures

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3 301 contribute to reduced dispersal efficiency and the variable patterns of gene flow between
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5 302 coastal and estuarine habitats (Zardi et al., 2013).
6

7 303 Density barrier effects are usually particularly marked in species such as *F. ceranoides*
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9 304 characterized by rapid population growth and consequent habitat saturation. The dense,
10
11 305 monospecific *F. ceranoides* canopies typical of European northern Atlantic estuaries act as a
12
13 306 demographic buffer against numerically rare inter-estuarine immigrants favoring the
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15 307 conservation of pre-existing genetic structure.
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18 308 Clearly, the abundance of estuaries and their proximity strongly suggest that distance
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20 309 can be excluded from the list of determinants maintaining *F. ceranoides* genetic breaks along
21
22 310 these shores. In NW Iberia, the mean distance between populations inhabiting neighboring
23
24 311 estuaries is not significantly different than that between bordering populations across
25
26 312 phylogeographic breaks (Neiva et al., 2012b). Similar distributional patterns can be found in
27
28 313 Brittany where several edge populations are spatially closer to populations across regional
29
30 314 genetic disjunctions than they are to their adjacent population within the same genetic clade.
31
32 315 While some studies carried out between cold- and warm-temperate marine ecosystems along
33
34 316 the northwest coast of France have invoked distinct mesoscale hydrographic features as
35
36 317 drivers of genetic patterns (Goldson et al., 2001; Jolly et al., 2005; Couceiro et al., 2013;
37
38 318 Almeida et al., 2017), others have highlighted lack of evidence for the role of hydrodynamics
39
40 319 as dispersal determinants for the observed genetic discontinuities along NW Iberian shores
41
42 320 (Neiva et al., 2012b). The latter works have also stressed the difficulties to track drifters'
43
44 321 movements at a scale relevant for the organism to estimate migration rates among estuaries
45
46 322 and phylogroups. In NW Iberia, circulation dynamics are complex with high seasonal variability
47
48 323 and lack of persistent oceanographic patterns (Ruiz-Villarreal et al., 2006; Alvarez et al.,
49
50 324 2009). Here, through the use of large scale, dispersal simulations we reveal several
51
52 325 oceanographic regions matching haplotype segregation. Our findings add important evidence
53
54 326 to previous conclusions and support the scenario of key, mesoscale oceanographic processes
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56 327 having a determinant role in explaining the position of the observed high levels of regional
57
58 328 genetic divergence. We also hypothesized that mesoscale oceanographic dispersal barriers
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3 329 are key to the maintenance of inter-estaurine genetic differentiation. In a neutral model of
4
5 330 secondary contact following allopatric differentiation, signs of secondary intergradation are
6
7 331 generally observed around oceanographic barriers (Woodruff, 1973; Barton and Hewitt, 1985;
8
9 332 Bierne et al., 2011). Admixed nuclear background has only been reported between two
10
11 333 neighboring *F. ceranoides* Iberian populations (Neiva et al., 2012b), indicating that individuals
12
13 334 belonging to distinct phylogroups can interbreed. However, no signs of hybridization have
14
15 335 been observed in other Iberian or French populations. The geographically restricted and
16
17 336 limited lineage admixture suggests that other factors may be at play in maintaining fine-scale
18
19 337 genetic differentiation. In particular, incipient reproductive isolation (pre- or post-zygotic) can
20
21 338 depress gene flow between divergent phylogroups (e.g., Tellier et al., 2011). Under this
22
23 339 scenario, limited dispersal across oceanographic barriers explains the position of the genetic
24
25 340 discontinuity while the delay in homogenisation is mainly explained by endogenous
26
27 341 components of reproductive isolation. Future studies assessing spatial and temporal
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29 342 reproductive dynamics of distinct *F. ceranoides* lineages will be crucial to provide a direct
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31 343 testing of this hypothesis.
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344 **Conclusions**

345 Our study highlights the need to combine evidence from multiple sources for a comprehensive
346 understanding of ecological and evolutionary mechanisms linked to phylogeographic breaks.
347 These conclusions are of great significance for other organisms with sporadic and spatially
348 limited dispersal, helping clarify the apparent inconsistency of extensive and sharp genetic
349 clines differentiation in geographically restricted regions. In addition to theoretical evolutionary
350 relevance, the identification of contemporary dynamics contributing to the maintenance of
351 significant units of intraspecific biodiversity is critical for efficient approaches of management
352 and conservation efforts.
353

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3 591 **FIGURE LEGEND**
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6 592 **Fig. 1.** Haplotype distribution of *Fucus ceranoides* in the coastlines of (a) Northwest France
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8 593 and (panel b) Northwest Iberia. The colors along coastlines (a, b) depict the different
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10 594 oceanographic regions (R) identified in network analysis. A pairwise matrix of directional
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12 595 connectivity between oceanographic regions identified in (d) western Brittany and (e)
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14 596 northwest Iberia. Matrix header colors according to the oceanographic regions depicted in the
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16 597 top panels a and b. Haplotype frequency and differentiation degree in (f) western Brittany and
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18 598 (g) northwest Iberia. Note that there is no correspondence of haplotypes between the two
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20 599 panels (i.e., each dataset was treated separately).
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26 601 **TABLES**
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28 602 **Table 1.** Maximum and average distances (km), drifting time (days) and probabilities produced
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30 603 by the particles connecting different cells for the lagrangian particle simulations running in
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32 604 Northwest France and Northwest Spain..
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Region	Distance (km)		Time (days)		Probability	
	Maximum	Mean (\pm SD)	Maximum	Mean (\pm SD)	Maximum	Mean (\pm SD)
W Brittany	382.6	62.6 \pm 54.6	24.6	3.61 \pm 2.63	0.721	0.004 \pm 0.020
NW Iberia	431.2	105.9 \pm 90.8	26.7	2.09 \pm 1.81	0.607	0.004 \pm 0.021

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