



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

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ABSTRACT

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

INTRODUCTION

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

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

It is predicted that genetic diversity is lowest in recently colonized areas and highest in refugial areas where long-term persistence was possible (e.g., Hewitt, 1996; Comps et al., 2001; Hewitt, 2004; Kennedy et al., 2017). However, contemporary demographic processes can either mask or even erase genetic signatures of population expansions or retreats (Smith et al., 2011). High levels of gene flow may homogenize genetic diversity among previously structured populations. On the other hand, nonrandom mating with individuals in close geographic proximity can generate genetic structuring within a continuous population (Slatkin, 1993). Intrinsic characteristics of the species such as dispersal ability, migration patterns and changes in population densities can further confound any historical signature (e.g., Mims et al., 2015; Chust et al., 2016; Assis et al., 2018).

Biogeographical transition regions provide a good framework for exploring and understanding genetic structuring of species through space and time. These are areas of overlap and segregation between different biotic components, and geographically separated clades often coincide with these transition zones (Ferro and Morrone, 2014). In the marine realm, phylogeographic breaks in biogeographical transition regions are generally attributed to historical processes or contemporary dispersal barriers, such as upwelling phenomena and currents that may limit along-shore dispersal, environmental differences boosting local adaptation and/or reproductive strategies maintaining self-recruitment (Gilg and Hilbish, 2003; Zardi et al., 2007; Selkoe et al., 2010).

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

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

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

In this study, we use phylogeographic analyses and Lagrangian Particle Simulations (LPS) coupled with network analyses to evaluate the levels of congruence between dispersal potential and the patterns of present-day genetic differentiation and diversity in the estuarine seaweed *Fucus ceranoides* along these two biogeographic transition zones. This species is perennial, dioecious and restricted to estuarine intertidal areas. Fucoid seaweeds have no planktonic dispersal stage and have restricted gamete dispersal (Serrão et al., 1997). However, adult individuals can achieve long distance gene flow via the rafting of whole or partially detached thalli with reproductive structures (Thiel and Haye, 2006; McKenzie and Bellgrove, 2008), a form of population connectivity strongly influenced by hydrodynamic forces and coastal topography. Currently, *F. ceranoides* is distributed from northern Portugal to northern Norway (Lein, 1984) and Iceland (Munda, 1999), covering both past non-glaciated and glaciated regions of Europe. Previous studies have shown the occurrence of two divergent genetic lineages in this species between the south and the north of Europe, the phylogeographic break being localized in Northwest France near the English Channel (Neiva et al., 2012a; Neiva et al., 2012b). Specifically, the dominant Northwest Iberian haplotypes of

this species was found in southern Brittany but not after the genetic break in northern Brittany (Neiva et al., 2010). We discuss three scenarios for the concordance between present-day oceanographic dispersal barriers and the observed genetic differentiation among *F. ceranoides* estuarine populations: 1) Contemporary oceanographic barriers to dispersal are responsible for the origin, the position and the maintenance (i.e. delaying genetic homogenization) of the genetic differentiation; 2) Contemporary oceanographic circulation patterns explain the position, the maintenance but not the origin of the genetic differentiation; 3) Reproductive isolation, in addition to contemporary oceanographic patterns, limits genetic homogenisation thus contributing to the position and the maintenance of the genetic differentiation.

MATERIALS

Genetic data

The two study areas (NW France and NW Spain) are peninsulas characterized by complex and variable circulation patterns (Puillat et al., 2004; Varela et al., 2005; Ruiz-Villarreal et al., 2006; Ayata et al., 2011). Because of that, sampling of only a limited number of localities would be inappropriate. We therefore decided to sample a small number of individuals at as many sites along the two coastlines as possible, rather than obtaining large numbers of individuals from a limited number of sites (e.g., Sotka et al., 2004; Teske et al., 2007). This decision was also supported by the very low genetic diversity within localities for this species (Neiva et al., 2010; 2012b; Neiva et al., 2012a). As a result, two sets of sequences of *Fucus ceranoides* were prepared and analyzed separately. The first data set (Data set 1) comprised sequences of individuals collected in the estuaries of all major rivers between Hennebont (HB, southern Brittany) and Camarel (CM, northern Brittany) in northwest France (n = 2 from each site; Table SI1). The second dataset (Data set 2) consisted of sequences previously analysed in Neiva et al. (Neiva et al., 2010; 2012b; Neiva et al., 2012a) and sampled across northern Iberia between Viana do Castelo (VIA, northern Portugal) and Porcia (POR, northern Spain). To

allow a comparison between data sets, a random subsample of 2 individuals from each site was used for Data set 2. The random subsampling in NW Spain was repeated to ensure consistency in the results obtained.

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

DNA isolation and sequencing of data set 1

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

Data analyses

For both data sets, haplotype frequencies were estimated using DnaSP 5.0 (Librado and Rozas, 2009). The relationships among the MtIGS haplotypes were inferred using statistical parsimony with Tcs v. 1.13 (Clement et al., 2000). Because additional subsampled dataset for the Iberia provided similar results (Table SI2 and Fig. SI1), only one was used for the simulations.

Dispersal simulations

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

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

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

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

The connectivity matrices were used in network analyses (i.e., graph theory) to infer the major oceanographic regions of northwest Iberia and northwest France. To this end, network 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,
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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
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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
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13 196 of communities in the networks (e.g., Munwes et al., 2010), which in practice translated into a
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15 197 delineation of oceanographic regions in northwest Iberia and northwest France structured by
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17 198 connectivity of ocean currents (Assis et al., 2018). The statistical significance of the
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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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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)
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30 204 and vegan (Oksanen et al., 2018).
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35 206 RESULTS

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37 207 In Data set 1 (NW France), six mtIGS haplotypes were identified in 30 individuals of *Fucus*
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39 208 *ceranoides* in 15 sampled sites. In NW France, the network analyses showed two dominant
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41 209 haplotypes (A and D) plus three derived ones (B, C and E), each private to one population
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43 210 (Fig 1a). Haplotype frequency distribution revealed a geographical segregation of the two main
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45 211 haplotypes. Haplotype 1 was present in individuals from regions R1 and R2 while Haplotype
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47 212 D was restricted to more northern sites within region R3.
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49 213 Out of 415 sequences retrieved from the GenBank, 52 sequences were randomly selected for
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51 214 Data set 2 (northwest Iberia). The network showed seven main haplotypes of which two were
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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,
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57 217 the main haplotype was restricted to region R5 and haplotype F was present only in region
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218 R4. Haplotype A was present in regions R3 and R1 while haplotype B was confined to region

219 R2. Dispersal simulations

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

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

240 DISCUSSION

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

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

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

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

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

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

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

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

Density barrier effects are usually particularly marked in species such as *F. ceranoides* characterized by rapid population growth and consequent habitat saturation. The dense, monospecific *F. ceranoides* canopies typical of European northern Atlantic estuaries act as a demographic buffer against numerically rare inter-estuarine immigrants favoring the conservation of pre-existing genetic structure.

Clearly, the abundance of estuaries and their proximity strongly suggest that distance can be excluded from the list of determinants maintaining *F. ceranoides* genetic breaks along these shores. In NW Iberia, the mean distance between populations inhabiting neighboring estuaries is not significantly different than that between bordering populations across phylogeographic breaks (Neiva et al., 2012b). Similar distributional patterns can be found in Brittany where several edge populations are spatially closer to populations across regional genetic disjunctions than they are to their adjacent population within the same genetic clade. While some studies carried out between cold- and warm-temperate marine ecosystems along the northwest coast of France have invoked distinct mesoscale hydrographic features as drivers of genetic patterns (Goldson et al., 2001; Jolly et al., 2005; Couceiro et al., 2013; Almeida et al., 2017), others have highlighted lack of evidence for the role of hydrodynamics as dispersal determinants for the observed genetic discontinuities along NW Iberian shores (Neiva et al., 2012b). The latter works have also stressed the difficulties to track drifters' movements at a scale relevant for the organism to estimate migration rates among estuaries and phylogroups. In NW Iberia, circulation dynamics are complex with high seasonal variability and lack of persistent oceanographic patterns (Ruiz-Villarreal et al., 2006; Alvarez et al., 2009). Here, through the use of large scale, dispersal simulations we reveal several oceanographic regions matching haplotype segregation. Our findings add important evidence to previous conclusions and support the scenario of key, mesoscale oceanographic processes having a determinant role in explaining the position of the observed high levels of regional 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
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5 329 secondary contact following allopatric differntiation, signs of secondary intergradation are
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7 330 generally observed around oceanographic barriers (Woodruff, 1973; Barton and Hewitt, 1985;
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9 331 Bierne et al., 2011). Admixed nuclear background has only been reported between two
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11 332 neighboring *F. ceranoides* Iberian populations (Neiva et al., 2012b), indicating that individuals
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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
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17 335 limited lineage admixture suggests that other factors may be at play in maintaining fine-scale
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19 336 genetic differentiation. In particular, incipient reproductive isolation (pre- or post-zygotic) can
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21 337 depress gene flow between divergent phylogroups (e.g., Tellier et al., 2011). Under this
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23 338 scenario, limited dispersal across oceanographic barriers explains the position of the genetic
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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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35 343 **Conclusions**

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37 344 Our study highlights the need to combine evidence from multiple sources for a comprehensive
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39 345 understanding of ecological and evolutionary mechanisms linked to phylogeographic breaks.
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41 346 These conclusions are of great significance for other organisms with sporadic and spatially
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43 347 limited dispersal, helping clarify the apparent inconsistency of extensive and sharp genetic
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45 348 differentiation in geographically restricted regions. In addition to theoretical evolutionary
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47 349 relevance, the identification of contemporary dynamics contributing to the maintenance of
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49 350 significant units of intraspecific biodiversity is critical for efficient approaches of management
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51 351 and conservation efforts.
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56 353 **ACKNOWLEDGMENTS**
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FIGURE LEGEND

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Fig. 1. Haplotype distribution of *Fucus ceranoides* in the coastlines of (a) Northwester France

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and (panel b) Northwest Iberia. The colors along coastlines (a, b) depict the different

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oceanographic regions (R) identified in network analysis. A pairwise matrix of directional

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connectivity between oceanographic regions identified in (d) western Brittany and (e)

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northwest Iberia. Matrix header colors according to the oceanographic regions depicted in the

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top panels a and b. Haplotype frequency and differentiation degree in (f) western Brittany and

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(g) northwest Iberia. Note that there is no correspondence of haplotypes between the two

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panels (i.e., each dataset was treated separately).

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TABLES

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Table 1. Maximum and average distances (km), drifting time (days) and probabilities produced

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by the particles connecting different cells for the lagrangian particle simulations running in

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Northwest France and Northwest Spain..

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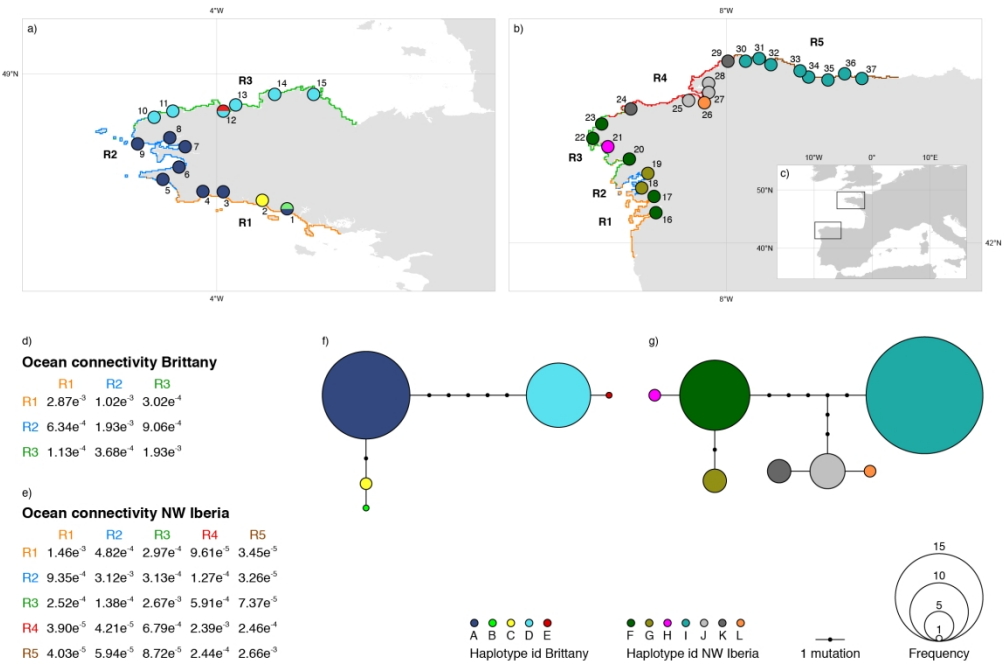
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	Distance (km)		Time (days)		Probability	
Region	Maximum	Mean (±SD)	Maximum	Mean (±SD)	Maximum	Mean (±SD)
W Brittany	382.6	62.6±54.6	24.6	3.61±2.63	0.721	0.004±0.020
NW Iberia	431.2	105.9±90.8	26.7	2.09±1.81	0.607	0.004±0.021



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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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54 23 **Running head:** Congruence between fine-scale genetic breaks and dispersal potential.
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57 24 **Keywords:** Biogeography, physical modelling, gene flow, *Fucus* spp.
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ABSTRACT

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

INTRODUCTION

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

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

It is predicted that genetic diversity is lowest in recently colonized areas and highest in refugial areas where long-term persistence was possible (e.g., Hewitt, 1996; Comps et al., 2001; Hewitt, 2004; Kennedy et al., 2017). However, contemporary demographic processes can either mask or even erase genetic signatures of population expansions or retreats (Smith et al., 2011). High levels of gene flow may homogenize genetic diversity among previously structured populations. On the other hand, nonrandom mating with individuals in close geographic proximity can generate genetic structuring within a continuous population (Slatkin, 1993). Intrinsic characteristics of the species such as dispersal ability, migration patterns and changes in population densities can further confound any historical signature (e.g., Mims et al., 2015; Chust et al., 2016; Assis et al., 2018).

Biogeographical transition regions provide a good framework for exploring and understanding genetic structuring of species through space and time. These are areas of overlap and segregation between different biotic components, and geographically separated clades often coincide with these transition zones (Ferro and Morrone, 2014). In the marine realm, phylogeographic breaks in biogeographical transition regions are generally attributed to historical processes or contemporary dispersal barriers, such as upwelling phenomena and currents that may limit along-shore dispersal, environmental differences boosting local adaptation and/or reproductive strategies maintaining self-recruitment (Gilg and Hilbish, 2003; Zardi et al., 2007; Selkoe et al., 2010).

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

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

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

In this study, we use phylogeographic analyses and Lagrangian Particle Simulations (LPS) coupled with network analyses to evaluate the levels of congruence between dispersal potential and the patterns of present-day genetic differentiation and diversity in the estuarine seaweed *Fucus ceranoides* along these two biogeographic transition zones. This species is perennial, dioecious and restricted to estuarine intertidal areas. Fucoid seaweeds have no planktonic dispersal stage and have restricted gamete dispersal (Serrão et al., 1997). However, adult individuals can achieve long distance gene flow via the rafting of whole or partially detached thalli with reproductive structures (Thiel and Haye, 2006; McKenzie and Bellgrove, 2008), a form of population connectivity strongly influenced by hydrodynamic forces and coastal topography. Currently, *F. ceranoides* is distributed from northern Portugal to northern Norway (Lein, 1984) and Iceland (Munda, 1999), covering both past non-glaciated and glaciated regions of Europe. Previous studies have shown the occurrence of two divergent genetic lineages in this species between the south and the ~~North-north~~ of Europe, the phylogeographic break being localized in Northwest France near the English Channel (Neiva et al., 2012a; Neiva et al., 2012b). Specifically, the dominant Northwest Iberian haplotypes of

this species was found in southern Brittany but not after the genetic break in northern Brittany (Neiva et al., 2010). We discuss three scenarios for the concordance between present-day oceanographic dispersal barriers and the observed genetic differentiation among *F. ceranoides* estuarine populations: 1) Contemporary oceanographic barriers to dispersal are responsible for the origin, the position and the maintenance (i.e. delaying genetic homogenization) of the genetic differentiation; 2) Contemporary oceanographic circulation patterns explain the position, the maintenance but not the origin of the genetic differentiation; 3) Reproductive isolation, in addition to contemporary oceanographic patterns, limits genetic homogenisation thus contributing to the position and the maintenance of the genetic differentiation.

MATERIALS

Genetic data

The two study areas (NW France and NW Spain) are peninsulas characterized by complex and variable circulation patterns (Puillat et al., 2004; Varela et al., 2005; Ruiz-Villarreal et al., 2006; Ayata et al., 2011). Because of that, sampling of only a limited number of localities would be inappropriate. We therefore decided to sample a small number of individuals at as many sites along the two coastlines as possible, rather than obtaining large numbers of individuals from a limited number of sites (e.g., Sotka et al., 2004; Teske et al., 2007). This decision was also supported by the very low genetic diversity within localities for this species (Neiva et al., 2010; 2012b; Neiva et al., 2012a). As a result, two sets of sequences of *Fucus ceranoides* were prepared and analyzed separately. The first data set (Data set 1) comprised sequences of individuals collected in the estuaries of all major rivers between Hennebont (HB, southern Brittany) and Camarel (CM, northern Brittany) in northwest France (n = 2 from each site; Table SI1). The second dataset (Data set 2) consisted of sequences previously analysed in Neiva et al. (Neiva et al., 2010; 2012b; Neiva et al., 2012a) and sampled across northern Iberia between Viana do Castelo (VIA, northern Portugal) and Porcia (POR, northern Spain). To

allow a comparison between data sets, a random subsample of 2 individuals from each site was used for Data set 2. The random subsampling in NW Spain was repeated to ensure consistency in the results obtained.

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

DNA isolation and sequencing of data set 1

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

Data analyses

For both data sets, haplotype frequencies were estimated using DnaSP 5.0 (Librado and Rozas, 2009). The relationships among the MtIGS haplotypes were inferred using statistical parsimony with Tcs v. 1.13 (Clement et al., 2000). Because additional subsampled dataset for the Iberia provided similar results (Table SI2 and Fig. SI1), only one was used for the simulations.

Dispersal simulations

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

1
2
3 163 Simulations (LPS) with network analyses ~~least cost and community algorithms~~ (least cost
4
5 164 distance and community algorithm, e.g., Assis et al., 2015; Klein et al., 2016; Assis et al.,
6
7 165 2018). The simulations used daily data of ocean currents assembled from the Hybrid
8
9 166 Coordinate Ocean Model (HYCOM), a ~~high~~-resolution product with a spatial resolution of 0.08°
10
11 167 (approx. 6–9 km), ~~forced~~ by wind speed, wind stress, precipitation and heat flux. This model
12
13 168 can resolve oceanic fronts, meandering currents, filaments and eddies (Chassignet et al.,
14
15 169 2007), important mesoscale processes to properly simulate ocean dispersal (Assis et al.,
16
17 170 2015; Klein et al., 2016).

18
19
20 171 Both regions of simulation were gridded to a common spatial resolution of 0.01° (approx. 1km).
21
22 172 A polygon representing global coastlines - OpenStreetMap geographic information (Haklay
23
24 173 and Weber, 2008)- was used to define intertidal source and sink cells. Passive particles
25
26 174 simulating rafts of *F. ceranoides* adult individuals were released from each gridded cell every
27
28 175 12 hours and allowed to drift for 60 full days; an extreme period for long-lived rafts of brown
29
30 176 macroalgae (Monteiro et al., 2016; Assis et al., 2018). This approach aimed to capture the
31
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
35
36 179 particles were removed from the simulation. The geographic position of all particles was
37
38 180 calculated every hour with bilinear interpolation on the ocean velocity fields (with a spatial
39
40 181 resolution of 0.08°), while combining a 4th Order Runge-Kutta adaptive time-step on the path
41
42 182 equations (e.g., Lett et al., 2008; Klein et al., 2016).

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44
45 183 The degree of connectivity between all pairs of gridded cells was determined by dividing the
46
47 184 number of unique particles released from cell *i* that ended up in cell *j*, by the total number of
48
49 185 particles released from cell *i*. To account for the inter-annual variability in the ocean data, the
50
51 186 simulations ran independently per year (from January to December), for the most recent 10-
52
53 187 year period of data, available in HYCOM (i.e., 2003 to 2012). Asymmetrical connectivity
54
55 188 matrices were determined by averaging the outcomes of the annual simulations.

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57
58 189 The connectivity matrices were used in network analyses (i.e., graph theory) to infer the major
59
60 190 oceanographic regions of northwest Iberia and northwest France. To this end, network

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

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

RESULTS

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

Out of 415 sequences retrieved from the GenBank, 52 sequences were randomly selected for Data set 2 (northwest Iberia). The network showed seven main haplotypes of which two were shared among six to ten populations and three were shared by two to three populations. The remaining two haplotypes were private to one single population. In the frequency distribution, the main haplotype was restricted to region R5 and haplotype F was present only in region

219 R4. Haplotype A was present in regions R3 and R1 while haplotype B was confined to region

220 R2. Dispersal simulations

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

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

241 DISCUSSION

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

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

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

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

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

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

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

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

Density barrier effects are usually particularly marked in species such as *F. ceranoides* characterized by rapid population growth and consequent habitat saturation. The dense, monospecific *F. ceranoides* canopies typical of European northern Atlantic estuaries act as a demographic buffer against numerically rare inter-estuarine immigrants favoring the conservation of pre-existing genetic structure.

Clearly, the abundance of estuaries and their proximity strongly suggest that distance can be excluded from the list of determinants maintaining *F. ceranoides* genetic breaks along these shores. In NW Iberia, the mean distance between populations inhabiting neighboring estuaries is not significantly different than that between bordering populations across phylogeographic breaks (Neiva et al., 2012b). Similar distributional patterns can be found in Brittany where several edge populations are spatially closer to populations across regional genetic disjunctions than they are to their adjacent population within the same genetic clade. While some studies carried out between cold- and warm-temperate marine ecosystems along the northwest coast of France have invoked distinct mesoscale hydrographic features as drivers of genetic patterns (Goldson et al., 2001; Jolly et al., 2005; Couceiro et al., 2013; Almeida et al., 2017), others have highlighted lack of evidence for the role of hydrodynamics as dispersal determinants for the observed genetic discontinuities along NW Iberian shores (Neiva et al., 2012b). The latter works have also stressed the difficulties to track drifters' movements at a scale relevant for the organism to estimate migration rates among estuaries and phylogroups. In NW Iberia, circulation dynamics are complex with high seasonal variability and lack of persistent oceanographic patterns (Ruiz-Villarreal et al., 2006; Alvarez et al., 2009). Here, through the use of large scale, dispersal simulations we reveal several oceanographic regions matching haplotype segregation. Our findings add important evidence to previous conclusions and support the scenario of key, mesoscale oceanographic processes having a determinant role in explaining the position of the observed high levels of regional genetic divergence. We also hypothesized that mesoscale oceanographic dispersal barriers

are key to the maintenance of inter-estaurine genetic differentiation. In a neutral model of secondary contact following allopatric differentiation, signs of secondary intergradation are generally observed around oceanographic barriers (Woodruff, 1973; Barton and Hewitt, 1985; Bierne et al., 2011). Admixed nuclear background has only been reported between two neighboring *F. ceranoides* Iberian populations (Neiva et al., 2012b), indicating that individuals belonging to distinct phylogroups can interbreed. However, no signs of hybridization have been observed in other Iberian or French populations. The geographically restricted and limited lineage admixture suggests that other factors may be at play in maintaining fine-scale genetic differentiation. In particular, incipient reproductive isolation (pre- or post-zygotic) can depress gene flow between divergent phylogroups (e.g., Tellier et al., 2011). Under this scenario, limited dispersal across oceanographic barriers explains the position of the genetic discontinuity while the delay in homogenisation is mainly explained by endogenous components of reproductive isolation. Future studies assessing spatial and temporal reproductive dynamics of distinct *F. ceranoides* lineages will be crucial to provide a direct testing of this hypothesis.

Conclusions

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

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FIGURE LEGEND

Fig. 1. Haplotype distribution of *Fucus ceranoides* in the coastlines of (a) Northwester France and (panel b) Northwest Iberia. The colors along coastlines (a, b) depict the different oceanographic regions (R) identified in network analysis. A pairwise matrix of directional connectivity between oceanographic regions identified in (d) western Brittany and (e) northwest Iberia. Matrix header colors according to the oceanographic regions depicted in the top panels a and b. Haplotype frequency and differentiation degree in (f) western Brittany and (g) northwest Iberia. Note that there is no correspondence of haplotypes between the two panels (i.e., each dataset was treated separately).

TABLES

Table 1. Maximum and average distances (km), drifting time (days) and probabilities produced by the particles connecting different cells for the lagrangian particle simulations running in Northwest France and Northwest Spain..

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