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

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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 (mtIGS) 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.

Keywords: biogeography, Fucus spp, gene flow, physical modelling

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,
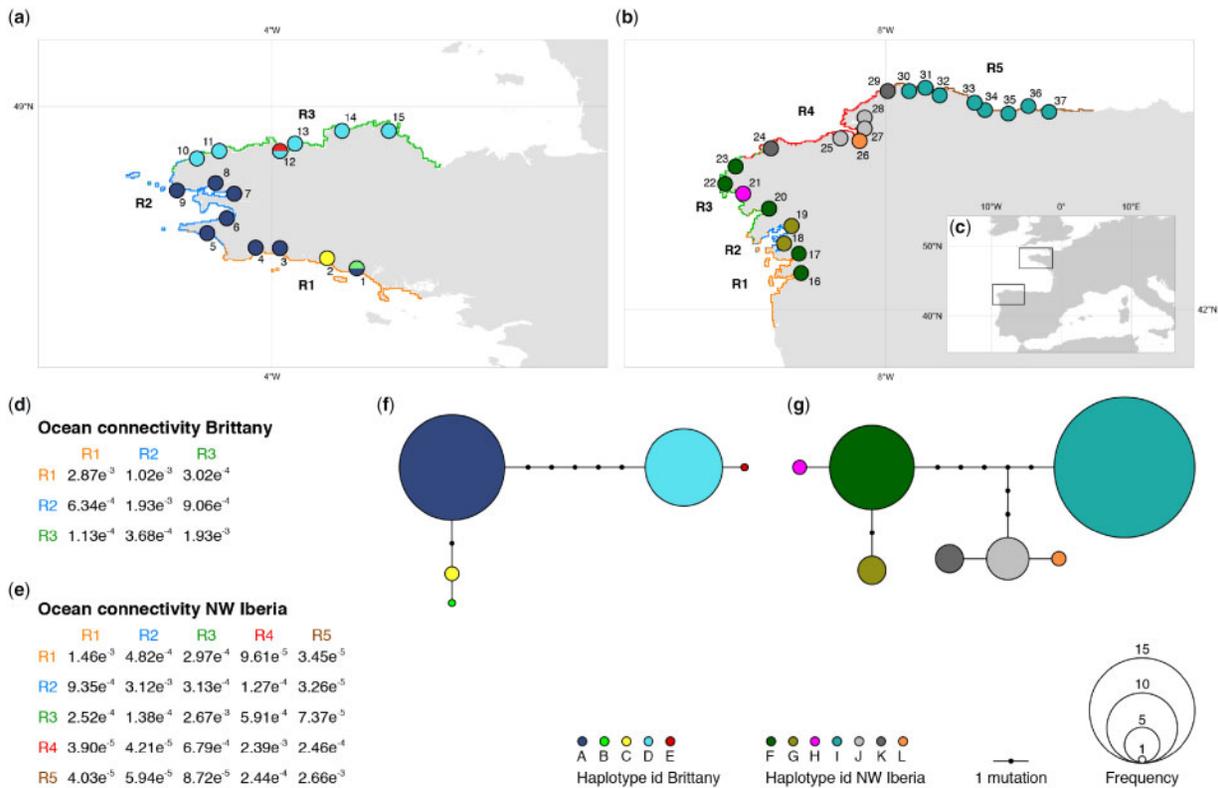
Figure 1. Haplotype distribution of *F. ceranoides* in the coastlines of (a) Northwester France and (b) Northwest Iberia. The colours along coastlines (a, b) depict the different oceanographic regions (R) identified in network analysis. A pairwise matrix of directional connectivity between oceanographic regions identified in (d) western Brittany and (e) northwest Iberia. Matrix header colours 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).

triggering range fragmentation and contractions of entire ecosystems to more southern latitudes, whilst 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 amongst 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; Figure 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, b). 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 amongst *F. ceranoides* estuarine populations: (i) Contemporary oceanographic barriers to dispersal are responsible for the origin, the position, and the maintenance (i.e. delaying genetic homogenization) of the genetic differentiation; (ii) Contemporary oceanographic circulation patterns explain the position, the maintenance but not the origin of the genetic differentiation; (iii) Reproductive isolation, in addition to contemporary oceanographic patterns, limits genetic homogenization thus contributing to the position and the maintenance of the genetic differentiation.

Material and methods
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, 2012a, b). As a result, two sets of sequences of *F. ceranoides* were prepared and analysed 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; Supplementary Table S1). The second dataset (Data set 2) consisted of sequences previously analysed in Neiva *et al.* (Neiva *et al.*, 2010, 2012a, b) 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 two 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. Neighbouring 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.* (2010, 2012a, b). 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.*, 2010).

Data analyses
For both data sets, haplotype frequencies were estimated using DnaSP 5.0 (Librado and Rozas, 2009). The relationships amongst the MtIGS haplotypes were inferred using statistical parsimony with Tcs v. 1.13 (Clement *et al.*, 2000). Because additional sub-sampled dataset for the Iberia provided similar results (Supplementary Table S2 and Supplementary Figure S1), only one was used for the simulations.

Dispersal simulations
The main oceanographic regions in northwest France and northwest Iberia (∼550 and ∼600 km of coastlines, respectively) were identified by coupling LPS with network analyses (least cost distance and community algorithm, e.g. Assis *et al.*, 2015, 2018; Klein *et al.*, 2016). 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°), whilst combining a Fourth 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 ten-year period of data, available in HYCOM (i.e. 2003–2012). 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 into a single network (Cunha *et al.*, 2017), whilst 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 Core Team, 2016) using the packages: data.table (Dowle *et al.*, 2019), dismo (Hijmans *et al.*, 2017), igraph (Kamvar *et al.*, 2014), parallel, raster (Lamigueiro *et al.*, 2019), and vegan (Oksanen *et al.*, 2010).

Results

In Data set 1 (NW France), 6 mtIGS haplotypes were identified in 30 individuals of *F. 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 (Figure 1a). Haplotype frequency distribution revealed a geographical segregation of the two main haplotypes. Haplotype 1 was present in individuals from regions R1 and R2 whilst 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 amongst 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 R4. Haplotype A was present in regions R3 and R1, whilst haplotype B was confined to region R2.

Dispersal simulations

The LPS using HYCOM ocean currents over the ten-year period released 7300 particles per cell (7.80×10^6 and 7.88×10^6 particles in total in northwest France and northwest Iberia, respectively). Particles drifted for longer distances in northwest Iberia than in northwest France (up to 431.2 km; Table 1; Supplementary Figure S2). The maximum period of drifting time was also higher in northwest Iberia (26.7 days), but on average, particles drifted for longer periods in northwest France (3.61 ± 2.63 days). The maximum probability of connectivity between the pairs of cells was observed in northwest France (western Britany; 0.721). However, the average cell probabilities within regions did not vary considerably (Table 1; Supplementary Figure S2).

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

Discussion

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

Predictions of oceanographic transport made with LPS are highly sensitive to the inner spatial and temporal resolution of circulation models (Putman and He, 2013). Whilst we preserved the raw circulation processes modelled by Hycom at the scales of days and tens of kilometres, a main limitation may arise if additional oceanographic processes occurring at smaller scales are

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

Region	Distance (km)		Time (days)		Probability	
	Maximum	Mean ($\pm SD$)	Maximum	Mean ($\pm SD$)	Maximum	Mean ($\pm SD$)
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

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); and *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 amongst *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, 2012a, b).

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 amongst colonized estuaries is expected to be limited.

Fucus 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 favouring 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 neighbouring 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.

Whilst 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 amongst 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-estuarine 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 neighbouring *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 whilst the delay in homogenization 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 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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Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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