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Research Article

Reproductive strategies and population genetic structure of *Fucus spp*. across a northeast Atlantic biogeographic transition☆

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Abstract – Geographical discontinuities in the composition of species assemblages are often mirrored by genetic clines and local adaptation in species that extend across such biogeographic disjunction. Species distributed across such biogeographic discontinuities are thus more prone to develop genetic clines and adaptations to environmental variation. The northwest coast of France encompasses a biogeographic boundary between cold- and warm-temperate marine ecosystems. Distinct hydrographic features characterize northern and southern shores, promoting physical oceanographic breaks that can affect dispersal and connectivity between populations. Furthermore, mosaics of contrasting conditions may affect local patterns of species assemblages and potential adaptive pressures. Along this stretch of coast, the intertidal habitat is largely dominated by brown algae of the genus *Fucus*, key structuring species common along North Atlantic shorelines. *Fucus spiralis*, *F. guiryi* and *F. vesiculosus* are sister species with different mating systems. They have extensive sympatric geographical distributions and distinct but overlapping vertical distributions in the intertidal zone. We examined genetic structure and diversity across this major environmental transition zone using neutral microsatellite markers to investigate patterns of differentiation between populations of each species inhabiting the two different biogeographic regions. We found contrasting results between the dioecious species (*F. vesiculosus*) and the two selfing hermaphroditic lineages (*F. spiralis* and *F. guiryi*). Genetic differentiation of northern and southern populations of *F. vesiculosus* followed the expectation from a hypothetical oceanographic discontinuity across this biogeographical transition zone, but this was not the case for the two hermaphroditic species. The former had higher genetic diversity and structure along the distribution range investigated whereas selfing hermaphrodites had less variability and were not geographically structured. Our results suggest that genetic patterns are correlated with this biogeographical transition zone but this effect is dependent on mating system, a determining factor affecting population structure. Additionally, other factors such as intertidal elevation may also play a role in observed difference in genetic structuring.

Keywords: Genetic diversity / Microsatellites / Fucus / Biogeographic transition zones / Mating system

1 Introduction

Biogeographic transitions are areas where different physical and environmental conditions and ecological factors lead to significant changes in species assemblages. Hence, species living throughout these environmental discontinuities are more prone to genetic clines, although they do not necessarily show consistent structuring (Lima et al., 2007; Neiva et al., 2012, 2016; Guillemin et al., 2016). These regions represent ideal settings for the investigation of species limits, range shifts and adaptations to changes in environmental conditions (Martinez et al., 2012; Assis et al., 2014; Robuchon et al., 2014). Transition zones can be reflected in dissimilarities in the genetic background throughout the continuum of a species' distribution. In marine ecosystems, these are generally attributed to dispersal barriers (e.g. currents, upwelling) that may limit along-shore dispersal, to environmental discontinuities acting through divergent natural selection or to reproductive strategies promoting self-recruitment (Gilg and Hilbish, 2003; Selkoe et al., 2010). Major biogeographic boundaries have been identified and associated with genetic

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breaks for several species, particularly coastal ones (e.g. fishes, Williams and Benzie, 1998; marine invertebrates, Haye et al., 2014; seaweeds, Tellier et al., 2009; Zardi et al., 2015a). Hence, these regions represent ideal settings for the investigation of species limits, range shifts and adaptations to changes in environmental conditions (Pujol et al., 2009; Martinez et al., 2012; Provan, 2013; Assis et al., 2014; Leys et al., 2014; Robuchon et al., 2014).

A biogeographic boundary between cold- and warm-temperate marine ecosystems is found on the northwest coast of France (Jolly et al., 2005; Gallon et al., 2014). This stretch of coast outlines the transition between the Celtic Sea and the South European Atlantic Shelf ecoregions which belong to distinct cohesive units, the Northern European Seas and the Lusitanian provinces, respectively (Spalding et al., 2007). At the northwest endpoint of Brittany, in the Ushant front, the Gulf Stream diverts into two main trajectories, one flowing South, in the direction of the Bay of Biscay, and one towards the English Channel (Billot et al., 2003). Distinct hydrographic features characterize northern and southern shores. Hydrodynamics on the southern coast are characterized by several mesoscale structures such as low salinity lenses, river plumes and fronts (Ayata et al., 2011). Additionally, upwelling occurs south of the Brittany peninsula (north of Bay of Biscay), linked to favorable westerly and northwesterly winds and weak tidal currents (Puillat et al., 2004, 2006). On the north coast of Brittany, eddies and diverted circulation related to the complex topography of the rocky shore characterize near shore hydrodynamics (Salomon and Breton, 1993; Billot et al., 2003).

This biogeographic discontinuity is coincident with distributional limits for a number of taxa (Breeman, 1988; Lüning, 1990). The study of this unique region is thus important to understand the contribution of both environmental factors (present and past) and life-history traits influencing species distribution (Engel et al., 2004; Mieszkowska and Sugden, 2016).

The intertidal habitat of this coastline is largely dominated by brown algae belonging to the genus *Fucus*. These form a group of dominant structuring species with wide geographic ranges along North Atlantic shorelines (Coyer et al., 2006; Hoarau et al., 2007; Billard et al., 2010). *Fucus spiralis*, *F. guiryi* and *F. vesiculosus* are genetically closely related, belonging to the same phylogenetic clade (Cánovas et al., 2011; Zardi et al., 2011). They are characterized by distinct mating systems (Zardi et al., 2011). These three species have extensive sympatric distributions and, of the three, only *F. guiryi* extends further south on the open coast along southern Iberia and Morocco (Zardi et al., 2015b), where *F. vesiculosus* also occurs but only inside estuaries and coastal lagoons (Ladah et al., 2003). When in sympatry, they are vertically zoned (Billard et al., 2010 where *F. guiryi* was named *F. spiralis* low; Zardi et al., 2011). On the upper shore *F. spiralis* occurs above *F. guiryi*, both selfing hermaphroditic species. The dioecious *F. vesiculosus* occurs lower in the intertidal (Zardi et al., 2011). Importantly, the distribution and the abundance of these species at the southern range have been affected by ongoing climate change (Nicastro et al., 2013; Lourenço et al., 2016), and future range shifts are predicted (Assis et al., 2014), highlighting the significance of understanding population genetic structure, environmental determinants and their variability.

Here, we examine the genetic structure and genetic diversity of three sister species of macroalgae across a known marine biogeographic transition zone in northwest France. Specifically, we applied a population genetic approach using seven microsatellite markers to investigate differentiation patterns between populations of each species inhabiting the two different biogeographic regions. We also aim to infer the possible influence of mating system on population structure along this region, by choosing model species with distinct reproductive modes (selfing hermaphrodites versus dioecious species).

2 Methods

Samples were collected between March 2009 (populations of Roscoff and Dossen) and February 2012 (populations of Le Havre, St. Malo, Larmore and Cotinière). Collection was based on morphometric identification (Zardi et al., 2011) and position on the shore (Table 1). Individuals were sampled approximately 2 m apart to avoid partially, overlapping zones (Zardi et al., 2011) and any intermediate morphotype.

2.1 DNA extraction and microsatellite amplification

Total DNA was extracted from 5 to 10 mg of dried tissue using the CTAB method as in Coyer et al. (2009). Seven microsatellite loci (Engel et al., 2003; Wallace et al., 2004; Coyer et al., 2009) were used. Polymerase Chain Reactions (PCR) were performed with a Thermal Cycler 2720 (Applied Biosystems) following conditions detailed in Table S1. The lengths of PCR products were analysed on an automated sequencer ABI PRISM 3130 (Applied Biosystems) using as size standards 350 ROX (L20, L38, L58, L78, L94, F12) and 500 LIZ (F26II, F42) on the software GeneScan. Raw allele sizes were scored using STRand (Toonen and Hughes, 2001) and binned into allele classes with MsatAllele R (Alberto, 2009).

2.2 Data analyses

All analyses were conducted for each species independently. Presence of null alleles and scoring errors were tested with MicroChecker (van Oosterhout et al., 2004). Allelic richness (Â) was estimated and standardised to the smallest sample size within each species ($n = 30$, $n = 31$ and $n = 22$ for *F. guiryi*, *F. spiralis* and *F. vesiculosus*, respectively) using StandArich R (Alberto et al., 2006). Nei's gene diversity (unbiased expected heterozygosity, H_E; Nei, 1978) and observed heterozygosity (H_O) were estimated with GENETIX 4.05 (Belkhir et al., 2004) and used on tests of departure from random mating within each population. Significance of F_{IS} was estimated after 10^4 permutations with GENETIX 4.05 (Belkhir et al., 2004).

Genetic differentiation between pairs of populations was calculated across loci with the F_{ST} estimator (θ) (Weir and Cockerham, 1984). Significance was tested with 10^4 random permutations using a threshold adjusted and q-value correction for multiple comparisons (Storey, 2002). Patterns of genetic structure were depicted through Factorial Correspondence Analysis (FCA) of individual allelic frequencies. All the above analyses were performed using GENETIX 4.05 (Belkhir et al., 2004). Pairwise genetic differentiation was also estimated with D_{Jost} (Jost, 2008) using R package DEMEtics

Table 1. Genetic diversity parameters for (A) *Fucus spiralis*, (B) *F. guiryi* and (C) *F. vesiculosus*. Sampled locations and codes, coordinates, number of individuals (N), unbiased gene diversity (H_E), observed heterozygosity (H_O), inbreeding coefficient multilocus estimates (F_{IS}), allelic richness standardized for the smallest sample size (Â), standard deviation (SD). (*) Significant deviation from Hardy–Weinberg expectations with q-value correction for multiple comparisons (q-value < 0.01).

(A)

Location	Latitude	Longitude	N	H_E	H_O	F_{IS}	Â ± SD
Le Havre (LH)	49°38'26.95"N	0°08'54.47"E	32	0.068	0.018	0.741*	1.14±0
St. Malo (SM)	48°39'10.75"N	2°01'49.95"W	32	0.046	0.013	0.709*	1.29±0
Roscoff (RF)	48°43'41.14"N	3°59'17.69"W	32	0.103	0.040	0.613*	1.97±0.08
Dossen (DS)	48°42'15.27"N	4°04'18.73"W	31	0.091	0.014	0.851*	1.43±0
Larmore (LA)	47°42'02.11"N	3°23'11.21"W	31	0.206	0.018	0.912*	1.86±0

(B)

Location	Latitude	Longitude	N	H_E	H_O	F_{IS}	Â ± SD
St. Malo (SM)	48°39'10.75"N	2°01'49.95"W	32	0.009	0.000	1.000*	1.13±0.04
Roscoff (RF)	48°43'41.14"N	3°59'17.69"W	30	0.153	0.067	0.570*	3.57±0
Dossen (DS)	48°42'15.27"N	4°04'18.73"W	30	0.019	0.010	0.498*	1.43±0
Larmore (LA)	47°42'02.11"N	3°23'11.21"W	32	0.087	0.009	0.899*	1.43±0
Cotinière (CT)	45°54'54.64"N	1°20'00.03"W	31	0.031	0.005	0.853*	1.29±0

(C)

Location	Latitude	Longitude	N	H_E	H_O	F_{IS}	Â ± SD
Roscoff (RF)	48°43'41.14"N	3°59'17.69"W	32	0.735	0.603	0.182*	8.57±0.3
Dossen (DS)	48°42'15.27"N	4°04'18.73"W	31	0.701	0.590	0.160*	6.50±0.3
Larmore (LA)	47°42'02.11"N	3°23'11.21"W	22	0.679	0.630	0.074	6.71±0

(Gerlach et al., 2010). Significance was tested with 10^4 bootstrap resamplings and p-value correction for multiple comparisons with the Benjamini and Hochberg (1995) method. Additionally, confidence intervals were calculated for both estimators of genetic differentiation with R package diveRsity (Keenan et al., 2013).

The question of whether there are distinct genetic clusters, their number (K) and the assignment of individual multilocus genotypes to those clusters were performed for *F. vesiculosus* using STRUCTURE (Pritchard et al., 2000). Analyses were performed for K ranging from 1 to 4 (number of locations plus one) without any prior population assignment, with correlated allele frequencies assumed and admixture allowed. For each K, ten independent runs were performed using a burning length of 5×10^4 iterations and 1×10^4 Markov Chain Monte Carlo (MCMC) iterations. The most likely number of genetic clusters was selected based on ΔK (Evanno et al., 2005) implemented in Structure Harvester (Earl and von Holdt, 2012).

3 Results

3.1 Genetic diversity and mating system

Null alleles at high frequencies (>0.2) were detected for F26II (Fig. S1) and thus, to avoid an overestimation of F_{IS} and F_{ST} estimators (Chapuis and Estoup, 2007), this locus was removed from all subsequent analyses.

A total of 132 distinct alleles were obtained from the 398 individuals genotyped. Different levels of polymorphism were observed among loci, ranging from 1 to 20 alleles per locus. *Fucus spiralis* was the least polymorphic species (monomorphic for loci L38 and L58) and the highest (3–20 alleles per locus) was *F. vesiculosus*. Loci L20 and F12 showed the highest numbers of alleles (30) for all species, compared to all other loci (Fig. S2).

Gene diversity and allelic richness of *F. spiralis* were low and very similar across locations (H_E: 0.046–0.206; Â: 1.14–1.97, Table 1A). Diversity was also low in *F. guiryi* (H_E: 0.009–0.153; Â: 1.13–3.57, Table 1B), with the highest values in Roscoff. In contrast, *F. vesiculosus* had much higher genetic diversity across all sites compared to the other species (H_E: 0.679–0.735; Â: 6.50–8.57, Table 1C).

With the exception of *F. vesiculosus* in Larmore, F_{IS} values (Table 1) were significantly positive (heterozygote deficit) for all species and locations, with much higher estimates for both hermaphroditic species (*F. spiralis* and *F. guiryi*) than for *F. vesiculosus*.

3.2 Population genetic structure and biogeographic patterns

The distribution of genetic variation, as illustrated by Factorial Correspondence Analysis, revealed distinct patterns between species.

Populations of the species *F. spiralis*, revealed in the FCA plot (Fig. 1B) some overlapping between individuals belonging to different locations (Le Havre, St. Malo and Dossen), associated with low genetic variability and equal allele size

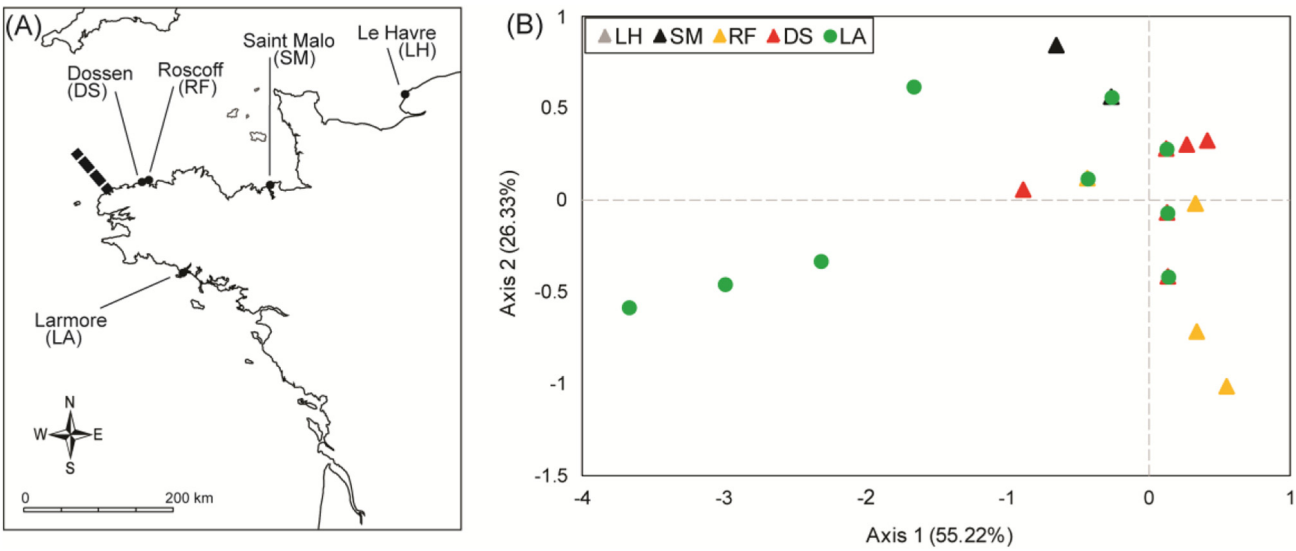

Fig. 1. Sampling locations and genetic structure for *Fucus spiralis*. (A) Map of the study area; dots indicate sampled locations; code of each site is in brackets; the biogeographic discontinuity is indicated by a dashed line, following Ayata et al. (2010) and Gallon et al. (2014). (B) Factorial Correspondence Analysis (FCA) based on allele frequencies at four microsatellite loci. Percentages of inertia are shown between parentheses for each axis.

at these locations. Conversely, Larmore displayed the highest distribution of individuals along the second axis, corresponding to the highest variance in allele frequencies within this location (Fig. S2). This was further illustrated by low levels of pairwise genetic differentiation parameters, particularly D_{EST} estimates (Table 2A).

For *F. guiryi*, the first axis of the FCA, which describes the highest variance between populations (72.23%), delimited the southern locations of Larmore and Cotinière (Fig. 2B) but all other locations did not retrieve any pattern of genetic structure. In addition, Roscoff exhibited a scattered distribution throughout the second axis of the FCA plot. This was further supported by pairwise estimates of genetic differentiation which were low for comparisons between all locations with the exception of Roscoff (Table 2B). The first axis of the FCA, which describes the highest variance between populations (36.61%), distinguished the northern from the southern locations (Fig. 2B).

The populations of *F. vesiculosus* comprised two clusters that were clearly geographically structured between northern and southern Brittany. The Bayesian analyses implemented in STRUCTURE revealed two genetic groups (Fig. S3) that were geographically consistent with a biogeographic boundary. This pattern was also reflected in the FCA plot (Fig. 3B) and in both of the pairwise genetic differentiation estimators, F_{ST} and D_{EST} (Table 2C).

4 Discussion

4.1 The Brittany biogeographic transition zone

The hypothesis that the biogeographic transition zone between southern and northern Brittany would influence genetic structure of the three distinct fucoid species was rejected for the selfing hermaphroditic species, which showed very low diversity across the entire study area, but was supported by the patterns observed for the dioecious species. The very distinct levels of genetic diversity found on the northwest coast of France between the dioecious *Fucus vesiculosus* and the much less diverse hermaphroditic species, *F. spiralis* and *F. guiryi*, suggest highly contrasting strategies for population persistence and colonization, between these sister species.

The division between northern and southwestern populations observed for *F. vesiculosus* agrees with the zonation of the marine biogeographical provinces in the northeastern Atlantic Ocean (Spalding et al., 2007). Genetic patterns reflecting this physical geographic discontinuity region have been previously observed for sessile species, such as invertebrates (Goldson et al., 2001; Jolly et al., 2005), kelps (Couceiro et al., 2013) and fucoids (Neiva et al., 2012) and patterns of genetic differentiation have been correlated to surface currents in the region. Genetic differentiation patterns separating northern and southern Brittany have been associated with the major current trajectories flowing in the region following divergence in the Ushant front. However, a few exceptions exist to the concordance between genetic and large-scale physical patterns (e.g. kelps, Billot et al., 2003). In fact, local turbulence regimes created by the convoluted topography of the Brittany coast may be more important in coastal species and dilute the contribution from this major current regime (Billot et al., 2003). Moreover, currents in the English Channel are highly variable in intensity and orientation (Salomon and Breton, 1993) and thus, this may lead to significant divergence in local patterns, particularly on the northern coast, that prevail or overcome the large-scale dominant current pattern. This could possibly explain the genetic structuring features of both hermaphroditic species.

Note that two possible bias may explain such a pattern of genetic structure. First, the clearer pattern of genetic differentiation between northern and southwestern populations observed for *F. vesiculosus* could also be explained by a cumulative effect of spatial and temporal genetic differentiation since the

Table 2. Pairwise genetic differentiation for (A) *Fucus spiralis*, (B) *F. guiryi* and (C) *F. vesiculosus*. Mean values of F_{ST} with the estimator θ are reported above the diagonal, while mean D_{Jost} values are reported below the diagonal. Asterisks indicate significant deviation from null expectations with q-value correction for multiple comparisons: *<0.05; **<0.01; ***<0.001. 95% confidence intervals are in brackets. Codes correspond to locations in Table 1.

A.

	LH	SM	RF	DS	LA
LH		0.4248*** (0.2095,0.6288)	0.0278 (-0.0432,0.1966)	0.0722 (-0.0456,0.2829)	0.0735* (-0.0179,0.2156)
SM	0.0081** (0.0038,0.0128)		0.2100*** (0.0548,0.3768)	0.1627** (0.0194,0.3487)	0.1432*** (0.0437,0.2905)
RF	0.0009* (-0.0006,0.0043)	0.0041** (0.0008,0.0081)		0.0001 (-0.0480,0.0815)	0.0247 (-0.0255,0.1066)
DS	0.0018* (-0.0007,0.0061)	0.0030** (0.0003,0.0068)	0.0001 (-0.0009,0.0026)		0.0266 (-0.0250,0.1100)
LA	0.0081* (-0.0003,0.0259)	0.0061** (0.0004,0.0181)	0.0009* (-0.0036,0.0128)	0.0014* (-0.0030,0.0127)	

B.

	SM	RF	DS	LA	CT
SM		0.3292*** (0.1688,0.5330)	0.0034 (-0.0210,0.0530)	0.0734 (-0.0094,0.1800)	0.0091 (-0.0364,0.0801)
RF	0.0072** (0.0028,0.0123)		0.2812*** (0.1115,0.4818)	0.2597*** (0.1362,0.4141)	0.2980*** (0.1498,0.4817)
DS	0.0001 (0.0000,0.0004)	0.0066** (0.0021,0.0116)		0.0827* (0.0104,0.1784)	0.0192 (-0.0208,0.0812)
LA	0.0012** (-0.0005,0.0058)	0.0091** (0.0030,0.0181)	0.0019** (-0.0005,0.0068)		0.0532 (-0.0072,0.1421)
GT	0.0001 (-0.0001,0.0007)	0.0073** (0.0028,0.0125)	0.0003* (-0.0001,0.0011)	0.0010** (-0.0006,0.0048)	

C.

	RF	DS	LA
RF		0.0233*** (0.0039,0.0480)	0.1303*** (0.0946,0.1727)
DS	0.0561** (0.0121,0.1066)		0.1320*** (0.0996,0.1679)
LA	0.2217** (0.1423,0.3207)	0.2260** (0.1570,0.2927)	

population of Lamore was sampled in 2012 while the two populations from Northern Brittany were sampled in 2009. Second, patterns of genetic structure for hermaphroditic species could also be directly influenced by the low level of polymorphism of the microsatellites used in this study. The set of microsatellites was chosen in order to compare to previous studies for these species (e.g. Coleman and Brawley, 2005; Engel et al., 2005; Billard et al., 2010). Other microsatellites (i.e. more informative) specifically designed for *F. spiralis* (Perrin et al., 2007) and/or with higher mutation rate could help to improve estimates of the genetic parameters for the hermaphroditic species (Chakraborty et al., 1997; Ellegren, 2004; Engel et al., 2005).

4.2 Genetic diversity and mating system

Although all three species showed signs of high inbreeding (heterozygote deficiencies), these were much stronger in

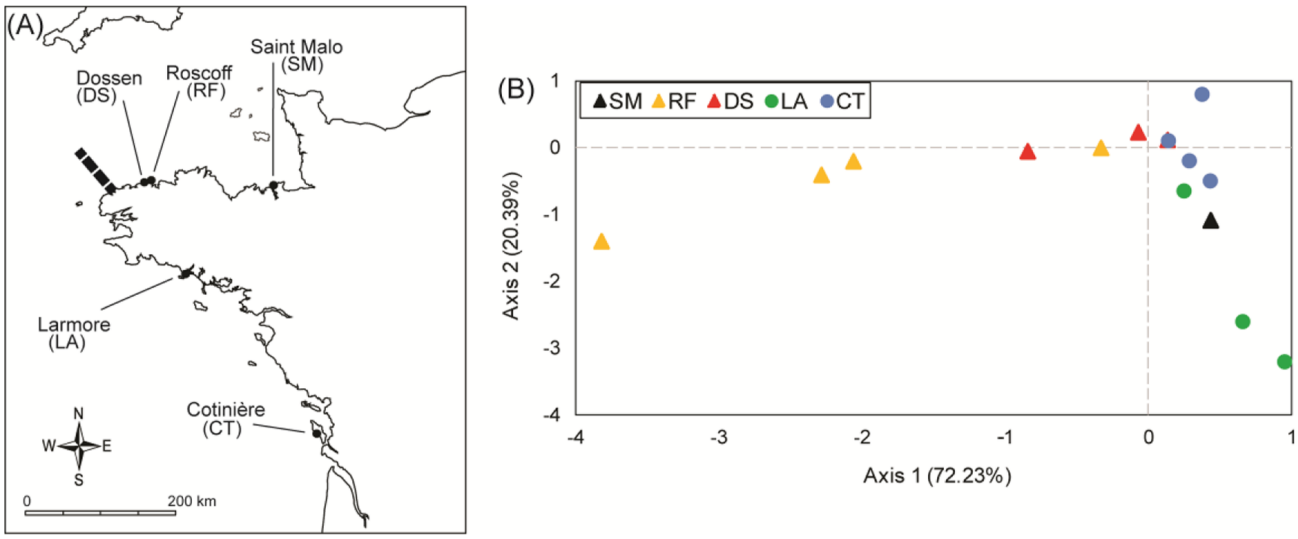

Fig. 2. Sampling locations and genetic structure for *Fucus guiryi*. (A) Map of the study area; dots indicate sampled locations; code of each site is in brackets; the biogeographic discontinuity is indicated by a dashed line, following Ayata et al. (2010) and Gallon et al. (2014). (B) Factorial Correspondence Analysis (FCA) based on allele frequencies at six microsatellite loci. Percentages of inertia are shown between parentheses for each axis.

the selfing hermaphrodites *F. spiralis* and *F. guiryi*, than in *F. vesiculosus*. This dioecious species also showed high genetic diversity across all sampled locations. This was expected, since the area has been acknowledged as a long term, persistent refugial region for marine species during Quaternary cycles and particularly for *F. vesiculosus* (Assis et al., 2014; reviewed in Neiva et al., 2016).

The differences in genetic diversity among species with different mating system are in accordance with previous studies of these lineages for comparable coastlines using the same molecular markers (Engel et al., 2005; Billard et al., 2010). Heterozygote deficits were expected for the selfing hermaphrodites (Perrin et al., 2007), but have also been consistently observed for *F. vesiculosus* here and in previous studies (Teixeira et al., 2016 and many references therein) throughout the entire European range. Exceptions to this general pattern were found in several of the very isolated southernmost populations in the eastern and western Atlantic (Assis et al., 2014, Teixeira et al., 2016) distributional ranges of *F. vesiculosus* (Muhlin et al., 2008; Muhlin and Brawley, 2009; Assis et al., 2014). Temporal Wahlund effect and limited gamete dispersal were suggested for this pattern (Engel et al., 2005; Teixeira et al., 2016). The genetic background of *F. vesiculosus* has the contribution from several alleles at low frequency; this could result from the mixing of individuals from groups with different allelic frequencies or deriving from genetically differentiated cohorts of recruits, causing a departure from Hardy-Weinberg equilibrium (i.e. Wahlund effect; Johnson and Black, 1984). Alternatively, biparental inbreeding possibly due to short gamete dispersal could also likely explain the significant heterozygosity deficiencies observed (Serrão et al., 1997; Teixeira et al., 2016). Previously, evidence was found for inbreeding depression based on higher heterozygote deficit in recruits than in adults (Teixeira et al., 2016).

Nevertheless, the magnitude of the inbreeding coefficients found for hermaphroditic species could also reflect the contribution of the high proportion of null alleles which was observed for some loci (Fig. S1). Deviations from the HWE may be attributed to both biological factors (e.g. inbreeding, Wahlund effect) and the occurrence of null alleles (Chapuis and Estoup, 2007) and distinguishing the contribution from these two factors is usually based on the evaluation of concordance of patterns across loci (Dakin and Avise, 2004; but see Dharmarajan et al., 2013). The occurrence of null alleles has been acknowledged to inflate values of F_{IS} (Chybicki and Burczyk, 2009). In our study all polymorphic loci revealed the presence of null alleles for *F. spiralis*, although the same pattern was not observed for *F. guiryi*. Maximum values for the inbreeding coefficient ($F_{IS} = 1.0$) were observed for loci with a high proportion of null alleles (L20, F12 and F42 for *F. guiryi*; L20 and F12 for *F. spiralis*), and could be considered as a factor contributing to the high inbreeding coefficients observed in the hermaphroditic species.

4.3 Population genetic structure

Patterns of genetic structure differed greatly among species, particularly between hermaphroditic and dioecious species. Both hermaphroditic species revealed relatively weak population structuring with variability in allele patterns common across different locations, mainly reflecting the high proportion of fixed alleles present in both species. As reported previously (Engel et al., 2005; where *F guiryi* was named "*F. spiralis* sympatric"), hermaphroditic species show extremely low polymorphism at all the loci. In contrast, *F. vesiculosus* displayed a clearly distinct clustering pattern that separated northern from southern populations, and a clear differentiation between the three populations that revealed a highly structured distribution of this species in the region.

Differences between species were especially striking between opposite mating systems, suggesting that mating

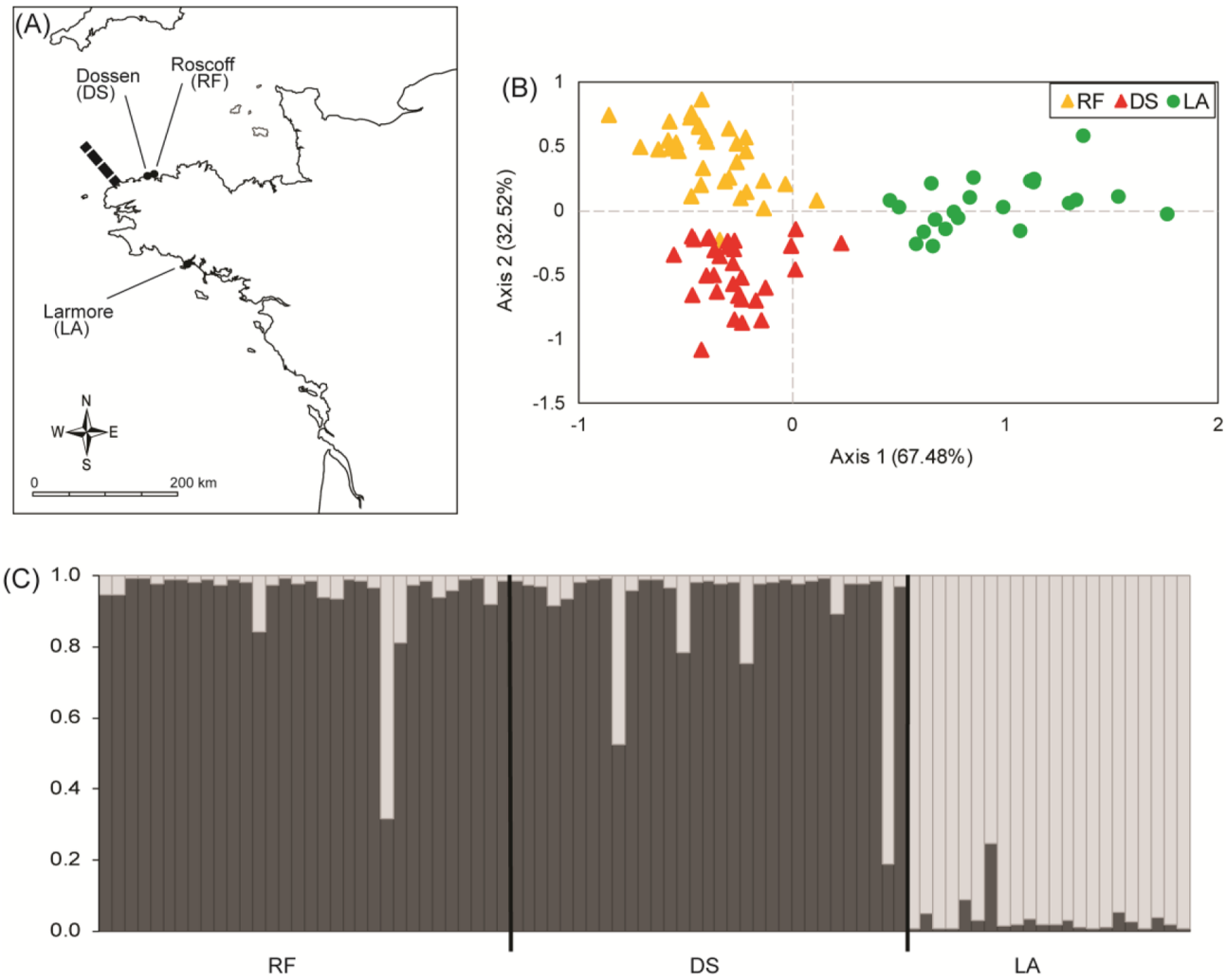

Fig. 3. Sampling locations and genetic structure for *Fucus vesiculosus*. (A) Map of the study area; dots indicate sampled locations; code of each site is in brackets; the biogeographic discontinuity is indicated by a dashed line, following Ayata et al. (2010) and Gallon et al. (2014). (B) Factorial Correspondence Analysis based on allele frequencies at six microsatellite loci. Percentages of inertia are shown between parentheses for each axis. (C) Genetic subdivision into clusters as defined by STRUCTURE where each vertical bar represents an individual. Proportions of multilocus genotypes for each individual assigned to each K cluster ($K = 2$) is illustrated by different colours. Codes correspond to locations in section A of this same figure.

system is a major factor explaining the observed patterns. The low population differentiation in the hermaphroditic species were similar to those previously observed for *F. spiralis* in the western Atlantic (Coleman and Brawley, 2005) using the same molecular markers. Low differentiation for *F. spiralis* was previously suggested to reflect a recent colonization history of these populations, with insufficient time for strong genetic differentiation to have evolved (Coleman and Brawley, 2005). Alternatively, large scale dispersal could be possible if extensive episodic recruitment leads to the dominance of one or more age cohorts, which could contribute to the spreading of gametes on scales larger than predicted by life history characteristics alone (Ladah et al., 2003; Coleman and Brawley, 2005). Brief periods of massive gamete release are known to occur in broadcast spawners and have been reported for these species (Monteiro et al., 2012). Moreover, gamete release occurs preferentially during high tide immersion (Monteiro et al., 2016), reducing spawning opportunities particularly for upper shore species such as *F. spiralis* that live on a narrow stretch of the intertidal area. A short immersion time (18–35%) (Zardi et al., 2011) for spawning while submerged may increase synchrony and genetic admixture, although the likelihood of selfing counteracts this effect. Alternatively, stochastic factors such as high genetic drift, which is facilitated in selfing hermaphrodites, may also play a role in the genetic patterns observed. Rare alleles are highly prone to genetic drift. With such high proportions of fixed alleles across loci, any new allele with extremely low frequency could (randomly) dictate the overall genetic structuring. Another hypothesis that cannot be totally discarded is the possibility of occurrence of clonal reproduction in the hermaphroditic species, although there is no known biological mechanism by which these species could propagate clonally on an exposed shore. This hypothesis is less likely

because negative F_{IS} values would be expected for populations with clonal reproduction (Balloux et al., 2003) and the potential for clonal reproduction has never been shown on exposed shores, only in highly sheltered subtidal habitats where vegetative fragments of *Fucus spp.* are able to settle for long time periods (Tatarenkov et al., 2005; Johannesson et al., 2011). Still, the hypothesis of high selfing rates has several consequences that are similar to clonality yet result in highly positive F_{IS} as observed here.

An alternative explanation for the different levels of genetic structure observed between species and particularly the pattern of allele fixation in *F. spiralis* could be the potential role of height on the shore. Previous studies have found significant differences in genetic structure according to zonation patterns in the intertidal habitat (Engel et al., 2004; Kelly and Palumbi, 2010; Valero et al., 2011; Krueger-Hadfield et al., 2013). And some have found an increase in species' genetic structure with a decreasing height on the shore (Innes, 1988; Marko, 2004). This was suggested to be related to greater exposure to abiotic stress in the high shore, which particularly during glacial periods could have determined changes in intertidal assemblages by favoring the persistence of low-shore species over upper-intertidal ones (Marko, 2004). On the other hand, a greater adaptation of low-shore species to seawater physical properties could determine the higher differentiation between locations (Innes, 1988). This region is characterized by wide tidal amplitude (Garreau, 1993) and particularly *F. spiralis* has been found to occur in a narrow band (*F. spiralis*-High in Billard et al., 2010; Zardi et al., 2011), high above the mid-tide point (2.5 m) where a high percentage of time is spent emersed (78%, Billard et al., 2010; 65–82%, Zardi et al., 2011). Hence, greater exposure to abiotic stressors (desiccation, temperature) combined with limited gene flow due to selfing may promote adaptation to high shore ecophysiological conditions (i.e. resilience to air exposure) (e.g. Zardi et al., 2011). This could contribute to the allele fixation patterns observed in this study that may overcome processes favouring differentiation between populations. In contrast, *F. vesiculosus* occupies a wider vertical band along the intertidal and spends more time immersed (50%, Billard et al., 2010; 31–63%, Zardi et al., 2011), Additionally, the Brittany region has been suggested as a long term persistent refugial area for *F. vesiculosus* (Assis et al., 2014). Hence, local adaptation to hydrological conditions (e.g. sea surface temperature) combined with long persistence in this region could contribute to genetic divergence between regional units.

However, F_{ST} estimates for *F. spiralis* revealed quite high values for pairwise comparisons with population of St. Malo (Table 2A). This could possibly be related with the lack of within-population variability, a factor known to affect F_{ST} estimates (Slatkin, 1995; reviewed in Meirmans and Hedrick, 2011).

Additionally, patterns of genetic structure for hermaphroditic species could also be directly influenced by the microsatellites used in this study. The set of microsatellites was chosen in order to allow comparison with previous studies (e.g. Coleman and Brawley, 2005; Engel et al., 2005; Billard et al., 2010). Other (potentially more informative) microsatellites specifically designed for *F. spiralis* (Perrin et al., 2007) could help to improve estimates of genetic parameters for the hermaphroditic species (Chakraborty et al., 1997; Ellegren, 2004; Engel et al., 2005). Additionally, higher number of populations sampled along the study region could improve the resolution and robustness of these results.

4.4 Ecological implications

The large increase in sea surface temperatures in the northeast Atlantic over the last twenty years, including this region, is predicted to continue (Hawkins et al., 2003; Mieszkowska et al., 2007; Gallon et al., 2014; Robuchon et al., 2014). Distribution limits of marine species are usually directly correlated with their thermal tolerance limits and responses to climate change are particularly strong (Blanchette et al., 2008; Sorte et al., 2010; Pinsky et al., 2013).

Biogeographic boundaries impose unique constraints for marine life that entail sharp changes in the genetic configuration, demographic parameters and distributional limits of species (Zacherl et al., 2003; Lima et al., 2007; Sivasundar and Palumbi, 2010). Alteration in physical factors responsible for the delimitation of biogeographic boundaries (e.g. sea surface temperature) are likely to have particularly important consequences on future distributions of sessile marine species with limited dispersal. Hence, the study of marine biota in these regions is essential to understand the coupling between physiological and life-history traits along with environmental variables, which may give valuable insights into their resilience capacity (Zacherl et al., 2003; Lima et al., 2007; Belanger et al., 2012). In particular, intertidal species that live close to upper temperature tolerance limits, are unique models to study the impact that climatic changes may have on species assemblages (reviewed in Helmuth et al., 2006; Somero, 2010).

Canopy-forming macroalgae are crucial for structuring rocky intertidal ecosystems and supporting complex food webs, and thus have a potentially huge impact on economically important species (Golléty et al., 2010; Kordas et al., 2011; Dijkstra et al., 2012). Temperature is known to be a factor determining the distribution of seaweeds, influencing survival, recruitment, growth and reproduction (Eggert, 2012; reviewed in Harley et al., 2012). Shifts in distributional ranges have already been observed for a number of species in recent years (Lima et al., 2006, 2007; Wernberg et al., 2011; Gallon et al., 2014) and many more are predicted to occur (Müller et al., 2009; Jueterbock et al., 2013). We found low levels of genetic diversity for highly selfing species, *F. spiralis* and *F. guiryi.* These may be locally adapted to more strict physical conditions (e.g. on the coast of Portugal, southern populations of *F. vesiculosus* showed a higher resilience to heat stress than northern populations, Saada et al., 2016). However, reduced genetic diversity due to low effective population size may render these populations highly vulnerable since stochastic events (i.e. genetic drift) could eliminate important traits of ecological and/or physiological relevance, resulting in a reduced capacity to respond to environmental stressors (Stockwell et al., 2003; Pujol and Pannell, 2008). For the species considered in this study, *F. spiralis*, which displays the lowest genetic diversity, also has the most restricted distribution south of this region and may potentially be the most vulnerable. Hence, studies of marine genetic diversity are essential in order to track changes and understand consequences of climate changes. Specifically, multi-species studies where different life-history traits may be considered in regions exhibiting environmental variation are important in

order to investigate the link between biotic and abiotic factors determining species persistence in order to predict future impacts (Poloczanska et al., 2013; Mieszkowska et al., 2014). This approach could contribute to a clear view of conservation priorities and help in designing frameworks for active management and future research (e.g. Williams et al., 2008; Hoffmann et al., 2015).

5 Conclusions

Fucus vesiculosus showed genetic differentiation between the northern and the southern populations, in accordance with the hypothesis raised based on the oceanographic discontinuity of this region, but this pattern was not observed for the hermaphroditic species. Mating systems appeared to be determinant concerning population genetic variability and structure for this region, more than the physical abiotic differences prevailing in this region. Distinct levels of genetic diversity between the hermaphroditic *Fucus spiralis*, *F. guiryi* and the dioecious *F. vesiculosus* were found to be consistent with the mating system displayed by the species. Alternatively, possible effects related to altitude on the shore along with biogeographic history may be determinant on the current emergent patterns.

Supplementary Material

Figure S1. Null allele frequency for all loci for (A) *Fucus spiralis*, (B) *F. guiryi* and (C) *F. vesiculosus*. Dots correspond to the mean frequency across populations for each locus calculated using Estimator 1 from Brookfield (1996). Vertical bars represent the standard deviation for the estimated values.

Figure S2. Allelic frequencies for *Fucus spiralis*, *F. guiryi* and *F. vesiculosus*, for each locus and location. Dots of varying diameter represent the frequency of the allele classes indicated below. Codes correspond to locations in Table 1.

Figure S3. Magnitude of ΔK as a function of K for *F. vesiculosus*. The modal value of ΔK that is based on the rate of change in the log probability of data between successive K values is considered as the highest level of population structuring.

Table S1. PCR conditions. Mixture and program for the microsatellites amplified following Engel et al. (2003) for L20, L38, L58, L78, L94; Wallace et al. (2004) for F26II; Coyer et al. (2009) for F42. (*) indicates a touchdown step: decrease in 0.2 °C per cycle.

Table S2. Pairwise genetic differentiation for (A) *Fucus spiralis*, (B) *F. guiryi* and (C) *F. vesiculosus*. Mean values of F_{ST} with the estimator θ are reported above the diagonal, while mean D_{Jost} values are reported below the diagonal. 95% confidence intervals are in brackets. Codes correspond to locations in Table 1.

The Supplementary Material is available at http://www.alr-journal.org/10.1051/alr/2017012/olm.

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