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**1The hidden side of a major marine biogeographic boundary: a wide  
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18

19Running title: A mosaic tension zone at the Atlantic-Mediterranean divide

20

21

## 22Abstract

23The Almeria-Oran Front (AOF) is a recognised hotspot of genetic differentiation in  
24the sea, with genetic discontinuities reported in more than 50 species. The AOF is  
25a barrier to dispersal and an ecological boundary, and both facts can explain the  
26position of these genetic breaks. However, the maintenance of genetic  
27differentiation is likely reinforced by genetic barriers. A general drawback of  
28previous studies is an insufficient density of sampling sites at the transition zone  
29with a conspicuous lack of samples from the southern coastline. We analysed the  
30fine-scale genetic structure in the mussel *Mytilus galloprovincialis* with a few  
31ancestry-informative loci previously identified from genome scans. We discovered  
32a 600 km wide mosaic hybrid zone eastward of the AOF along the Algerian  
33coasts. This mosaic zone provides a new twist to our understanding of the  
34Atlantic-Mediterranean transition because it demonstrates the two lineages can  
35live in sympatry with ample opportunities to interbreed in a large area, but hardly  
36do. This implies some form of reproductive isolation must exist to maintain the  
37two genetic backgrounds locally cohesive. The mosaic zone ends with an abrupt  
38genetic shift at a barrier to dispersal in the Gulf of Bejaia, Eastern Algeria.  
39Simulations of endogenous or exogenous selection in models that account for the  
40geography and hydrodynamic features of the region support the hypothesis that  
41sister hybrid zones could have been differentially trapped at two alternative  
42barriers to dispersal and/or environmental boundaries, at Almeria in the north  
43and Bejaia in the south. A preponderantly unidirectional north-south gene flow  
44next to the AOF can also maintain a patch of an intrinsically maintained genetic  
45background in the south and the mosaic structure, even in the absence of local  
46adaptation. Our results concur with the coupling hypothesis that suggests natural  
47barriers mostly explain the position of genetic breaks while their maintenance  
48must additionally require genetic barriers.

49

50**Keywords:** Barrier to gene flow, mosaic hybrid zone, reproductive isolation,  
51marine connectivity, Almeria-Oran Front, *Mytilus galloprovincialis*.

52

## 53Introduction

54Natural populations are often subdivided into discrete patches within which  
55apparent panmixia is observed or where genetic differentiation smoothly  
56increases with geographic distance (Charlesworth *et al*, 2003). These roughly  
57homogeneous genetic patches are bordered by abrupt genetic discontinuities  
58maintained by “barriers to gene flow” (Arnold, 2006 ; Slatkin, 1987; Hewitt,  
591989). Barriers to gene flow allow divergence between populations and possibly  
60the evolution of reproductive isolation and speciation (Barton and Bengtsson,  
611986; Palumbi, 1994; Charlesworth *et al*, 2003). They also guarantee the  
62maintenance of the beta component (i.e. between-populations component) of  
63genetic and species diversity. Barriers to gene flow are therefore crucial in  
64structuring and maintaining biodiversity. The study of their origin, their location  
65and the processes involved in their functioning, is therefore a central issue in  
66evolutionary biology and ecology.

67When genetic discontinuities are spatially concordant among different species, a  
68parsimonious explanation is that the same factors contribute to the barrier across  
69species. For instance, species can share a common history (e.g. shared zones of  
70secondary contact sometimes called suture zones; [Remington, 1968](#); [Hewitt,](#)  
71[1996](#); Avise, 2000; Hewitt, 2000; Swenson and Howard, 2005), a comparable  
72mode of dispersal (e.g. planktonic dispersers should be similarly affected by  
73marine connectivity; Pelc *et al*, 2009) or a similar ecological niche (e.g.  
74adaptation to the same habitat such as brackish water in the Baltic Sea;  
75Johannesson and Andre, 2006). In the marine realm, decades of research in  
76population genetics have allowed researchers to identify and describe hotspots of  
77genetic differentiation (Rocha and Bowen, 2008; Hellberg, 2009; Riginos and  
78Liggins, 2013; see Table 1). Probably because many marine species have large  
79population sizes and high dispersal potential via the larval phase, genetic  
80homogeneity is almost always the rule within patches delineated by these  
81barriers and the concentration of genetic breaks at some locations is obvious in  
82the sea (Hellberg, 2009; Riginos *et al*, 2011; Gagnaire *et al*, 2015). Barriers to  
83gene flow in the marine environment are found at locations of strong  
84environmental gradients or oceanographic currents which prevent dispersal along  
85shores (Hellberg *et al*, 2002; Teske *et al*, 2014). Many factors can be involved:  
86physical (oceanic fronts, local and global oceanic currents; Patarnello *et al*, 2007),  
87ecological (temperature, salinity, tide level; Johannesson *et al*, 2010; Stanley *et*

88al. 2018), historical (secondary contact; [Quesada et al, 1995](#); Avise, 2000), or  
89genetic (reproductive isolation; Bierne et al, 2011). While barriers to gene flow  
90are more likely to result from a combination of factors acting synergistically  
91(Barton and Hewitt, 1985; Bierne et al, 2011; Cordero et al, 2014), a single factor  
92is often emphasised to explain the genetic structure in any one case. In addition,  
93the origin (primary divergence vs. secondary contact), localisation (ecotone vs.  
94natural barrier vs. suture zone) and maintenance (dispersal barrier vs. local  
95adaptation vs. reproductive isolation) of the genetic differentiation need to be  
96treated as different questions. For instance, the position of a genetic cline at a  
97barrier to dispersal does not necessarily mean that the genetic differentiation is  
98due to low dispersal at this location; it is equally likely to be the legacy of  
99divergence during past vicariance and/or the additional effect of a genetic barrier  
100trapped by the natural barrier (Barton 1979). Demographic reconstruction can  
101provide insight about the origin of the differentiation that the simple description  
102of the contemporary genetic structure does not reveal. However, to better  
103understand the maintenance of genetic breaks, the genetic analysis of distant  
104samples far from the transition zone is hardly sufficient, even with high-  
105throughput genomic data (Cruickshank and Hahn, 2014; Meirmans, 2015;  
106Harrison and Larson, 2016). Such genome-wide analyses allow reconstructing the  
107long term history of populations and identifying highly differentiated loci or  
108genomic islands (Tine et al, 2014; Fraïsse et al, 2016), but tell little about how  
109genetic lineages have the opportunity to interbreed at the boundary. A major  
110shortcoming of many genome-wide studies is that they do not undertake detailed  
111sampling at these points of geographic transition, though such sampling is critical  
112for teasing apart competing explanations. Ultimately, one also needs to conduct  
113experiments in the lab and in the field to obtain direct evidence of the isolation  
114mechanisms at play (Harrison, 1993).

115The Almeria-Oran Front (AOF) is a well-known marine barrier to gene flow  
116between populations of the Atlantic Ocean and the Mediterranean Sea (Quesada  
117et al, 1995b; Borsa et al, 1997; Borrero-Pérez et al, 2011; Chevolut et al, 2006;  
118Patarnello et al, 2007; Palero et al, 2008; Schunter et al. 2011; Tine et al, 2014).  
119The front is generated by the convergence of Mediterranean and Atlantic waters.  
120Atlantic waters enter into the Alboran Sea through the strait of Gibraltar and  
121produce anticyclonic gyres westward of the AOF, the Western and Eastern  
122Alboran Gyres, and a north-south unidirectional current at the AOF (see Figure 1).  
123In addition, part of the flow of the Eastern Alboran Gyre is trapped at the AOF to

124contribute to the Algerian current that flows eastward of Oran along the Algerian  
125coastline (Viúdez and Tintoré, 1995).

126Among the examples of genetic breaks at the AOF, one of the first described was  
127found in the marine mussel *Mytilus galloprovincialis* (Quesada *et al*, 1995a;  
1281995b, Sanjuan *et al*. 1994). Since the early reports, the origin of the genetic  
129break has been considered a secondary contact between two lineages isolated in  
130Mediterranean and Atlantic glacial refugia (Quesada *et al*, 1995a), as for other  
131species such as sea bass (Lemaire *et al*, 2005; Tine *et al*, 2014; Duranton *et al*,  
1322018). The genetic differentiation between the two mussel lineages proved to be  
133highly heterogeneous among loci (Gosset and Bierne, 2013; Fraïsse *et al*, 2016).  
134Heterogeneous differentiation is expected for a semi-permeable genetic barrier  
135maintained by partial reproductive isolation (Barton and Hewitt, 1985; Harrison,  
1361993) or because of heterogeneous divergence caused by linked selection  
137(Cruickshank and Hahn 2014; Ravinet *et al*. 2017), or both (Duranton *et al*. 2018).  
138To date only the northern coast near Almeria in Spain has been intensively  
139sampled, and contains an abrupt shift in allele frequency on each side of a 290  
140km wide no-mussel zone between Almeria and Alicante (Quesada *et al*, 1995a).  
141Although some studies have identified weak genetic differentiation between  
142Europe and North Africa east of the AOF (Ouagajjou and Preza 2015; Lourenço *et al*.  
143a. 2015), the geographic structure of the transition zone along the southern  
144coast in Algeria was not well characterised. This is an important sampling gap to  
145fill, especially considering that Atlantic waters enter the Mediterranean Sea  
146through the South by the Algerian current described above. The southern side of  
147the transition is indeed a ubiquitous sampling lacuna in the study of the Atlantic-  
148Mediterranean genetic divide.

149In the present study we aimed to advance our understanding of the marine  
150transition zone at the AOF by analysing four ancestry-informative loci (one  
151mitochondrial and three nuclear) at a fine-grained spatial scale. These loci were  
152previously identified to be among the ten most differentiated loci in two genome  
153scans, one with 388 AFLP loci (Gosset and Bierne, 2013), and another with 1269  
154targeted contigs (~50,000 SNPs, Fraïsse *et al*, 2016). We would like to make it  
155clear that our aim in the present study was not to infer the history of gene flow  
156between populations nor the genomic heterogeneity of differentiation, which  
157requires the analysis of a high number of loci and has been treated elsewhere  
158(Fraïsse *et al*, 2016). Our objective was to investigate the spatial structure of the

159 transition zone and how the two genetic backgrounds meet and interact when in  
160 contact, which requires analysing an extensive geographic sample with  
161 informative loci (Vines *et al*, 2016). We accomplished this in three steps. First, as  
162 a precaution we re-analysed the shift in allele frequency in South-Eastern Spain  
163 that was reported twenty years ago. We observed the same position of the break  
164 in Spain as earlier studies, confirming results from Diz and Presa (2008). Second,  
165 we sampled a new area along the Algerian coast between Oran and Tunisia, over  
166 a distance of 1330 km. We report a 600 km wide mosaic hybrid zone with  
167 populations of mixed ancestry. Third, we explored simple stepping-stone  
168 simulation models which show that the mosaic structure observed can be  
169 explained by the local geographic and hydrodynamic characteristics of the  
170 coastlines. We used a Y-shaped bi-unidimensional structure of the coastlines to  
171 reflect the shape of the coastlines that allows north-south gene exchange west of  
172 the AOF but only along coastlines to the east of the AOF because the distance  
173 between Algerian and Spanish coasts become too large for larval dispersal. We  
174 also included two alternative barriers to larval dispersal and/or environmental  
175 boundaries (one at the AOF and one in the Gulf of Bejaia), and a preponderantly  
176 unidirectional north-south gene flow at the AOF.

177

178

## 179 MATERIALS AND METHODS

### 180 *Sampling and molecular markers*

181 *Mytilus galloprovincialis* (Lamarck, 1819) samples were collected from 13  
182 locations on the southern coast of the Alboran and Mediterranean Seas from  
183 Nador (Morocco) to Bizerte (Tunisia) and in 7 locations on the Northern coast from  
184 Manilva (Spain) to Peniscola (Table S1, Figure 1). Mitochondrial DNA sequences  
185 proved that all the samples were *Mytilus galloprovincialis* (see below) as  
186 expected in the study area. We also analysed reference samples already reported  
187 in previous studies (Gosset and Bierne, 2013) in Faro (Portugal) and Sète  
188 (France). DNA was extracted from gills using the QIAGEN DNeasy Blood & Tissue  
189 Kit following the instructions of the manufacturer. DNA concentration was  
190 measured for each sample using a NanoDrop8000 Spectrophotometer (Thermo  
191 Scientific) and standardised to a DNA concentration of 100 ng  $\mu$ L<sup>-1</sup>.

192 A 350-bp fragment of the F-mtDNA cytochrome oxidase subunit III was PCR  
193 amplified and sequenced with primers *FOR1* (5'-TATGTACCAGGTCCAAGTCCGTG-  
194 3') and *REV1* (5'-TGCTCTTCTTGAATATAA GCGTA-3') (Zouros *et al*, 1994).  
195 Sequence reactions were precipitated using a standard EDTA/ethanol protocol,  
196 suspended in 15  $\mu$ l Hi-Di formamide and sequenced on an ABI 3130XL automated  
197 sequencer.

198 Based on previous genome scans, three nuclear markers were chosen based on  
199 both their strong differentiation between the Atlantic and Mediterranean  
200 backgrounds of *M. galloprovincialis* and for their ease of analysis. All three  
201 produced length-polymorphism of PCR products. *EFbis* is a widely used marker in  
202 mussels that was amplified with the following two primers: *EFbis-F* 5'-  
203 ACAAGATGGACAATACCGAACCACC-3' and *EFbis-R* 5'-CTCAAT  
204 CATGTTGTCTCCATGCC-3' (Bierne *et al*, 2002). *EF2* has been described in Gosset  
205 and Bierne (2013) and was amplified with the following two primers: *EF2-F* 5'-  
206 GGAAATCCCATGGGTGATTTAGCGG-3' and *EF2-R* 5'-  
207 GTCAAATAAATACTGAAACACAGTGACTTC-3'. A contig containing the *Precollagen-D*  
208 gene was identified from a genome scan of 1269 contigs as the most  
209 differentiated contig between Atlantic and Mediterranean *M. galloprovincialis*  
210 populations (Fraïsse *et al*, 2016). Using publicly available sequences (Qin *et al*,  
211 1997) we designed primers to amplify the fifth intron of the gene with the 3' end  
212 of each primer positioned at the exon-intron junction, which prevented



213 amplification of paralogous sequences of the gene family. The primers used to  
214 amplify *Precol-D* locus were *Precol-D-F* 5'-GACAAGGACCAGCAGGTACCATATT-3'  
215 and *Precol-D-R* 5'-GAGTGGTCCGGCTGGTCCTAAGAA-3'. Indel polymorphisms in  
216 the intron produced nine length alleles in our samples with strong allele  
217 frequency differences between Atlantic and Mediterranean samples. Standard  
218 PCR protocols were used with annealing temperatures set at 54°C for *EFbis* and  
219 *EF2*, and 49°C for *Precol-D*. 2 µl of PCR products were mixed with Hi-Di  
220 formamide/ROX 500 size standard (12.8 µl formamide and 02 µl ROX), and the  
221 mixtures were then loaded on an ABI 3130XL capillary automated sequencer.  
222 GeneMapper® v4.5 software (Applied Biosystems) was used to read the resulting  
223 chromatograms.

#### 224 **Data analysis**

225 *COIII* sequences were aligned using the ClustalW multiple alignment algorithm in  
226 BIOEDIT V7.1.3.0 and revised manually. Aligned sequences were then used to  
227 construct a Neighbour-Joining tree with MEGA software v6 (Tamura *et al.*, 2013).  
228 Allelic and genotyping frequencies were computed using Genetix software  
229 v4.0.5.2 (Belkhir *et al.*, 2002). Number of haplotypes ( $h$ ), nucleotide diversity ( $\pi$ ),  
230 average number of nucleotide substitutions per site between populations ( $D_{xy}$ )  
231 and net number of nucleotide substitutions per site between populations ( $D_a$ )  
232 were calculated using DnaSP V5.10.1 (Librado and Rozas, 2009). Individuals were  
233 assigned to the Mediterranean and Atlantic lineages with a discriminant analysis  
234 of principal components (DAPC) implemented in the adegenet package in R  
235 (Jombart and Ahmed, 2011). The individual ancestries were examined by a  
236 Bayesian clustering method implemented in STRUCTURE 2.3.4 (Falush *et al.*,  
237 2003). Analysis with STRUCTURE was conducted for various numbers of clusters  
238  $K$  under the admixture model, assuming that the allele frequencies are correlated  
239 across populations, with a burn-in period of 50.000 steps and a run length of  
240 100.000 iterations. We used NewHybrids software (Anderson and Thompson,  
241 2002) to determine the hybrid status of individuals in the hybrid zones. We used  
242 a model with six categories of genotypes corresponding to two parental lineages  
243 and four categories of hybrids: F1 and F2 hybrids and the two types of  
244 backcrosses. Note that there are many more categories of hybrid genotypes in  
245 natural hybrid zones. However, this analysis allows investigating the frequency of  
246 early generation hybrids (expected to be rare in natural bimodal hybrid zones).  
247 Individual posterior probabilities of belonging to each category were obtained by

248running NewHybrids with uniform priors, a burn-in period of 50 000 steps  
249followed by a run length of 100 000 iterations. Because parental lineages tend to  
250be more introgressed locally within a mosaic hybrid zone than outside of the zone  
251in allopatric populations (Bierne *et al.*, 2003) we did not use allopatric populations  
252as references in the analysis. In this context including allopatric samples would  
253have inflated the posterior probabilities of locally introgressed parental genotype  
254to be backcrosses, which is not desired. To depict allele frequency clines, all four  
255loci were transformed into bi-allelic loci by pooling alleles according to their  
256frequencies in reference samples (sample 1 Faro Portugal for the Atlantic lineage  
257and sample N9 Sète France for the Mediterranean lineage, two localities often  
258studied in previous genetic studies of *M. galloprovincialis*). Finally, the average  
259departure from Hardy-Weinberg equilibrium was measured by  $F_{is}$  and the average  
260pairwise linkage disequilibrium across all loci,  $D$ , was estimated using the  
261variance in the hybrid index as described in Barton and Gale (1993). Departure  
262from Hardy-Weinberg and linkage equilibrium was tested by permutations with  
263the Genetix software combining p-values using Fisher's method.

#### 264**Simulations**

265We used a model of evolution in a metapopulation of 2 x 60 demes arranged in  
266two parallel linear stepping-stones (Bierne *et al.*, 2011; 2013). The purpose of the  
267simulations was to account for the geographic and hydrodynamic characteristics  
268of the region and to compare intrinsic reproductive isolation with local adaptation  
269at two different spatial scales (fine- or coarse-grained environmental  
270heterogeneity). At generation zero, two partially reproductively isolated  
271backgrounds meet and start to exchange genes. The auto-recruitment rate was 1  
272-  $2m$ , and migration to adjacent demes was  $m$ . A weak barrier to dispersal was  
273set between demes 20 and 21 in the northern chain to simulate the AOF, and  
274another barrier to dispersal in the southern chain between demes 40 and 41 to  
275simulate the Gulf of Bejaia Barrier (GBB). The migration rate at barriers to  
276dispersal was set to a value  $m_{bar}$ , with  $m_{bar} < m$ . Bidirectional migration was  
277possible between the northern and the southern chain for the first 20 demes (left  
278of the first barrier to dispersal, i.e. in the Alboran Sea) with the same rate of  
279migration  $m$ . For a few more demes (from 1 to 10) bidirectional or unidirectional  
280north-south gene flow was possible between the north and the south and then  
281stopped for the remaining demes. The aim of the parameterization was to  
282account for the fact that the Spanish and Algerian coasts east of the AOF become

283too distant to be connected directly by a single generation of larval dispersal,  
284which is thought to be roughly around  $50\text{km gen}^{-1}$  in mussels (McQuaid and Phillips  
2852000, Gilg and Hilbish 2003). Selection acted at a local adaptation locus  
286(exogenous selection) or against recombinant genotypes (intrinsic selection) at  
287two freely recombining reproductive isolation loci (Bierne *et al*, 2011). Allelic  
288fitnesses at the exogenous locus were  $W(C) = 1$  and  $W(c) = 1 - t$  in habitat 1 and  
289 $W(C) = 1 - t$  and  $W(c) = 1$  in habitat 2. The two-locus fitnesses at the  
290incompatible alleles were  $W(AB) = W(ab) = 1$  and  $W(Ab) = W(aB) = 1 - s$ . We did  
291not consider the interaction between the two types of selection here (see Bierne  
292*et al*. 2011) but consider either exogenous or endogenous selection alone. A  
293neutral marker was positioned at a recombination map distance of 1cM to a  
294selected locus.

295In order to simulate the trapping of a hybrid zone by a barrier to dispersal or an  
296environmental boundary, we need clines to overlap with barriers at their initial  
297position (Goldberg and Lande, 2007) or to move toward the barrier (Barton and  
298Turelli, 2011). We could have chosen the initial conditions and the parameter  
299values such that the northern cline overlapped with the AOF (between demes 20  
300and 21) and the southern cline overlapped with the GBB (between demes 40 and  
30141 of the southern chain). However, we have chosen to exemplify the arguably  
302more realistic situation of initially moving hybrid zones. Local adaptation clines  
303move to environmental boundaries driven by local selection. However, tension  
304zones maintained by selection against recombinant genotypes stay at their initial  
305contact position in a purely deterministic genetic model with equal fitnesses of  
306parental genotypes and isotropic migration. There are three main reasons why  
307tension zones could move. First, they are expected to move down gradients of  
308population density and to be trapped by density troughs (Abbott *et al*, 2013;  
309Barton, 1979; Hewitt, 1975). This demographic effect is not accounted for in our  
310purely genetic model, although the tension zone can be trapped by barriers to  
311dispersal providing it moves towards the barriers for other reasons. Second,  
312tension zones can move because one parental genotype is fitter. These moving  
313tension zones can nonetheless easily be halted by density troughs or barriers to  
314dispersal owing to their bi-stable nature (Barton and Turelli, 2011). Random drift  
315is expected to ultimately free such tension zones (Barton 1979, Pialek and Barton  
3161997) but the trapping can last for very long time. Finally, tension zones can  
317move haphazardly because of stochastic processes - genetic drift within  
318populations and stochastic dispersal between populations. Here, we used the

319latter two processes to simulate tension zone movement. We used a slight fitness  
320advantage  $a$  ( $W(AB)=1+a$ ) of the Mediterranean parental genotype starting from  
321a contact within the Mediterranean Sea (at deme 50), or a slight fitness  
322advantage of the Atlantic parental genotype ( $W(ab)=1+a$ ) starting from a contact  
323on the Atlantic side (at deme 10). Alternatively we introduced random drift by  
324using multinomial sampling of genotypes within each deme at each generation  
325( $N = 500$  per deme). This second way of simulating tension zone movement  
326results in various outcomes from the same starting position, because the  
327movement is not directional. We used this alternative only to show that results  
328are qualitatively similar regardless of the “engine” of the tension zone movement  
329and we did not intend to complete an extensive analysis of the effect of drift on  
330the outcomes, as this is far from the purpose of the present work.

331

## 332 RESULTS

### 333 **Analysis of genetic diversity**

334 The analysis of 568 *COIII* sequences revealed 150 haplotypes and a high  
335 nucleotide diversity ( $\pi = 0.023$ ). Average and net nucleotide divergence  
336 measures between Atlantic and Mediterranean populations were also high ( $D_{xy} =$   
337  $0.029$ ,  $D_a = 0.011$ ). The NJ-tree is presented in the supplementary Figure S1. Two  
338 clades of haplotypes could be defined according to their phylogenetic  
339 relationships and their frequency in Atlantic and Mediterranean samples (Figure  
340 S1). The clade nearly fixed in Atlantic samples is known to be due to introgression  
341 of alleles from the sister species *M. edulis* (Quesada *et al*, 1998). We used  
342 phylogenetic relationships to define the Mediterranean and the Atlantic  
343 haplogroups. Nine size-alleles were detected at the new locus *Precol-D* and allele  
344 frequencies are presented in Table S2. *EF2* was found to be bi-allelic as in Gosset  
345 and Bierne (2013). The use of capillary electrophoresis allowed us to distinguish  
346 *EFbis* size-alleles with 1bp differences that were not detected previously with  
347 acrylamide gels. We observed 22 alleles and the correspondence with previous  
348 allele names is given in Table S2. Clustering analysis was performed with multi-  
349 allelic data. In order to represent allele frequency clines we transformed multi-  
350 allelic loci into bi-allelic loci by pooling alleles according to their frequency in  
351 reference samples, sample 1 (Faro, Portugal) for the Atlantic lineage and sample  
352 N9 (Sète, France) for the Mediterranean lineage (see Table S2).

### 353 **Spatial genetic structure**

354 The frequencies of the Mediterranean allele at the mitochondrial *COIII* locus and  
355 the three nuclear markers (*Precol-D*, *EFbis* and *EF2*) in each sample are presented  
356 in Figure 2A and 2B. Clustering methods did not provide meaningful results with a  
357 number of genetic clusters parameterized above  $K=2$  (no improvement of the  
358 likelihood in the STRUCTURE analysis, low contribution of secondary axes in  
359 multivariate analyses, and lack of spatial structure of additional clusters) and we  
360 provide the results with  $K=2$ . As reported 20 years ago (Quesada *et al*, 1995b,  
361 Sanjuan *et al*. 1994) and 10 years ago (Diz and Presa 2008), the northern  
362 transect along the Spanish coast contained an abrupt change in allele  
363 frequencies in the zone of transition between Almeria and Cartagena with all four  
364 loci. The three samples collected in Atlantic waters (1-Faro, N2-Manilva and N3-  
365 Almeria) have high frequencies of the Atlantic alleles (Figure 2A), uniformly high

366Atlantic cluster membership probabilities in the DAPC analysis (Figure 1, sup file  
367text S1), and a high proportion of Atlantic ancestry in the STRUCTURE analysis  
368(Figure 2E). Conversely, samples from Mediterranean waters (N6-Tabarca, N7-  
369Nules, N8-Peñíscola del Pinatar, and N9-Sète) have high frequencies of  
370Mediterranean alleles (Figure 2B), uniformly high Mediterranean cluster  
371membership probabilities in the DAPC analysis (Figure 1), and a high proportion  
372of Mediterranean ancestry in the STRUCTURE analysis (Figure 2F). Two  
373populations (N4-Cartagena and N5-San Pedro) were obtained from the region  
374reported to be devoid of mussels 20 years ago. These samples were  
375predominantly of Mediterranean ancestry, but some individuals were assigned to  
376the Atlantic genetic cluster with high confidence and a few mussels with a  
377genome of mixed ancestry were also present (Figure 1 and 2E). Departure from  
378Hardy-Weinberg and linkage equilibrium was maximal in these intermediate  
379samples (Figure 2C) as expected from hybrid zone theory (Barton and Gale, 1993)  
380and the departure was significantly different from zero in sample N4-Cartagena.  
381These samples are crucial for our understanding of the functioning of the AOF  
382barrier to gene flow as they show Atlantic mussels are found in observable  
383numbers east of the AOF within the Mediterranean Sea.

384The southern transect along the Algerian coast revealed a complex structure on a  
385much wider geographic scale, consisting of a mosaic pattern of alternation  
386between mostly Atlantic, mostly Mediterranean, and intermediate samples  
387(Figure 1 and 2). Individuals assigned to the Atlantic cluster predominated in the  
388sample from S2-Nador (Morocco) situated in the Alboran Sea (Figure 1 and 2).  
389The Mediterranean cluster predominated in three samples from eastern Algeria  
390(S11-Zaima Mansouriah, S12-Collo and S13-Skikda) and Tunisia (S14-Bizerta)  
391(Figure 1 and 2). From S3-Oran to S10-Bejaia, a mosaic hybrid zone was observed  
392with a tendency for the Mediterranean ancestry to decrease eastward along the  
393zone. The zone ends with an abrupt genetic shift in the Gulf of Bejaia (Gulf of  
394Bejaia Barrier, GBB), west of which are preponderantly Atlantic samples and east  
395of which is populated by Mediterranean mussels. Within the mosaic zone,  
396samples were found to be a mixture of individuals belonging to both clusters and  
397with mixed ancestry (Figure 1 and 2F). Again strong departures from Hardy-  
398Weinberg and linkage equilibrium (Figure 2D) attest to a strong deficit of hybrids  
399relative to random mating. The departure was strongly significant in S3-Oran and  
400S5-Sidi Lakdher and significant in S8-Tipaza and S9-Algiers (Figure 2D). We did  
401not obtain support for the existence of early generation hybrids in Algerian

402populations as none of the 183 individuals sampled in the hybrid zone obtained a  
403cumulative posterior probability above 0.8 to be F1, F2 or backcross in  
404NewHybrids (Supplementary Table S3). This is not surprising as early generation  
405hybrids must be extremely rare in nature for the genetic differentiation to be so  
406efficiently maintained between two backgrounds. Evidence for hybridization  
407nonetheless comes from allele frequencies and the comparison of ancestry  
408values which show Atlantic mussels from the hybrid zone have a higher fraction  
409of Mediterranean ancestry and Mediterranean mussels a higher fraction of  
410Atlantic ancestry than mussels from peripheral allopatric populations (Figure 2F).  
411This local introgression of parental backgrounds within the mosaic hybrid zone  
412also explains the lack of power to characterise hybrid genotypes despite the fact  
413that our markers are strongly differentiated between reference samples well  
414outside of the hybrid zone.

415

416***Modeling a Y-shape bi-unidirectional stepping stone that accounts for***  
417***the seascape features of the AOF transition zone***

418Our simple model in a Y-shape bi-unidimensional stepping stone allowed us to  
419obtain useful indications about how the principal features of the seascape around  
420the AOF area could produce the mosaic structure observed.

421***Endogenous selection***- Let us begin with endogenous selection. It is important  
422to remember that in the tension zone model, selection against hybrids maintains  
423the clinal structure but, in contrast to exogenous selection, the position of the  
424cline is not stabilized by selection. Theory predicts that tension zones should be  
425trapped by and coincide with natural barriers to dispersal, i.e. zones of low  
426population density such as mountains, rivers or oceanic fronts (Barton, 1979).  
427First, we describe the results observed with deterministic simulations at a  
428selected locus in the case of a tension zone moving as a consequence of a fitness  
429advantage of one parental genotype. The objective is not to explore the  
430conditions in which the trapping process occurs, which are well known (Barton  
431and Turelli, 2011; Barton, 1979), but to illustrate how tension zone trapping can  
432occur in an unusual spatial and connectivity context such as the one in the AOF  
433area. Second, we will provide an example with a neutral locus introgressing  
434through the barrier and incorporating genetic drift. Again, we do not treat the  
435effect of linkage and random drift that are known (Barton, 1986; Polechová and

436Barton 2011); our aim is simply to exemplify that the model can retrieve a  
437pattern which resembles the true data.

438Figure 3 presents the results of the deterministic model: movement of  
439endogenous clines along the northern coast, characterized by a barrier to  
440dispersal between demes 20 and 21 (called AOF in Figure 3), and the southern  
441coast, characterized by a barrier to dispersal between demes 40 and 41 (called  
442GBB in Figure 3). We obtained qualitatively similar results when we added a  
443barrier to dispersal between demes 20 and 21 of the southern chain (i.e. Oran)  
444and provide the results with no barrier to exemplify the trapping of the cline even  
445when the barrier is restricted to the northern coast (i.e. Almeria). The most  
446interesting result is a contact within the Mediterranean Sea (between demes 50  
447and 51) and a westward propagation of the cline owing to a slight fitness  
448advantage of the Mediterranean parental genotype. The clines propagate along  
449the southern and northern coasts and a barrier to dispersal is first met by the  
450southern cline between demes 40 and 41 (GBB), where it is trapped while the  
451northern cline continues to propagate westward (Figure 3A). The northern cline is  
452subsequently trapped by the AOF barrier between demes 20 and 21 when it  
453comes to overlap with it (blue cline). When migration is symmetrical between the  
454north and the south, we end with a pair of shifted clines, one trapped by the AOF  
455in the North and one trapped by the GBB in the south (see inset in Figure 3A). In  
456this case the Algerian coast is inhabited by the Atlantic lineage. However, when  
457migration is asymmetrical from the north to the south, the Mediterranean  
458genotype can establish and be maintained in the south, generating a zone of  
459coexistence around the AOF in the south (Figure 3A bottom panel). This  
460simulation shows that a mosaic hybrid zone can be produced in the South with  
461purely intrinsic reproductive isolation when the major hydrodynamic  
462characteristics of the region are taken into account. We also considered the  
463situation of a contact on the Atlantic side and an eastward propagation of clines  
464owing to a slight fitness advantage of the Atlantic parental genotype. The clines  
465propagate and meet the AOF barrier between demes 20 and 21 where they are  
466trapped (Figure 3B). The southern cline remains trapped at the AOF, even when  
467the barrier is simulated only in the northern chain (migration between demes 20  
468and 21 is fixed at  $m_{bar}$  in the northern chain, at Almeria, and at  $m$  in the  
469southern chain, at Oran). The southern cline does not have the opportunity to  
470meet the barrier to dispersal at the GBB. It is well established that tension zones  
471are expected to be trapped by the first minor barrier encountered (Barton 1979,



472Barton and Turelli 2011). Despite this prediction, it is usually not well  
473acknowledged that hotspots for hybrid zones (i.e. suture zones) are more likely to  
474be localised at the barrier to dispersal that is closest to an area of frequent  
475contact rather than at the strongest barrier to dispersal across the overall  
476distribution area.

477The deterministic model shows that sister tension zones can be differentially  
478trapped at two alternative barriers to larval dispersal, at Almeria in the North and  
479Bejaia in the South and that a preponderantly asymmetrical north-south  
480migration rate at the AOF can maintain a “pocket” of the Mediterranean  
481background east of Oran in the South. In order to model the true data more  
482closely, we considered a neutral locus linked to a selected locus, which allowed  
483us to account for introgression, and introduced genetic drift. A simulation output  
484is presented in Figure 4A, with the two coastlines superposed in the same figure  
485and compared to true data in Figure 4B. In this simulation the two parental  
486genotypes have the same fitness, which shows that the pocket of Mediterranean  
487background in the South is not due to a fitness advantage but to the balance  
488between migration from the North and selection against hybrids. A comparison  
489with Figure 3 shows that introgression of Mediterranean alleles onto the Atlantic  
490background and of Atlantic alleles onto the Mediterranean background is stronger  
491in the mosaic zone between the two barriers (AOF and GBB) than in peripheral  
492populations. This is expected in mosaic hybrid zones as already explained in  
493another mussel hybrid zone (Bierne *et al*, 2003). Small patches of parental  
494populations enclosed within a mosaic hybrid zone and flanked by patches of  
495populations of the alternative genetic background are expected to introgress  
496faster than large and broadly distributed peripheral populations.

497**Exogenous selection**- We now consider exogenous selection. We explored two  
498kinds of seascape, a fine-grained mosaic structure in the hybrid zone, or coarse-  
499grained environmental variation. In the first model we have a mosaic of habitat 1  
500(Atlantic-like) that alternates randomly with habitat 2 (Mediterranean-like) in the  
501central area of the southern stepping stone (corresponding to the area between  
502the AOF and the GBB in Algeria). This model corresponds to a fine-grained mosaic  
503of habitats. As expected, notwithstanding that genotypes adapted to habitat 1  
504and genotypes adapted to habitat 2 flow from peripheral populations, this kind of  
505selection generates a mosaic structure at the selected locus that correlates with  
506habitat variation (Figure 4A). Despite the strong selection coefficient ( $s=0.2$ ) and

507with the recombination rate we used (1 cM) introgression proceeds quickly at the  
508neutral locus in the mosaic zone (Figure 4A presents the results at generation  
5091000) and the neutral marker loses the association with both the selected locus  
510and the habitat. We can of course increase selection and decrease recombination  
511to maintain the association for longer periods, but the parameters we used are  
512already strong selection and tight linkage. Our objective here was to briefly verify  
513the well-established result that micro-geographic adaptation generates a very  
514weak barrier to neutral gene flow (Flaxman et al. 2012; Thiebert-Plante and  
515Hendry 2015). Secondly, we simulated coarse-grained environmental variation  
516(Figure 3B). As for endogenous selection, we observed two clines at the two  
517environmental boundaries we simulated, the AOF in the North and the GBB in the  
518south, when north-south migration was symmetrical. In order to obtain the  
519maintenance of genotypes adapted to habitat 2 (i.e. Mediterranean-like) in the  
520south, asymmetrical north-south migration at the AOF was required. The result  
521obtained is very similar to that obtained with endogenous selection. Introgression  
522proceeds much more slowly than in the fine-grained habitat model, although  
523faster than with endogenous selection (with the same recombination rate of 1  
524cM). Another difference between the exogenous and endogenous models is that  
525under exogenous selection, the habitat 2 genetic background (Mediterranean-  
526like) cannot be maintained without migration from the north, because it is  
527counter-selected in the south. In the endogenous model however, we can  
528imagine that a sufficiently big patch of Mediterranean background can persist in  
529the south, at least transiently, as soon as it has been established by an episode  
530of north-south migration.

531

532

## 533 **DISCUSSION**

534 The Almeria-Oran Front (AOF) is arguably one of the most famous hotspots of  
535 genetic differentiation in the sea (Patarnello *et al.*, 2007), and *Mytilus*  
536 *galloprovincialis* one of the iconic species exhibiting a pronounced genetic break  
537 at the AOF (Quesada *et al.*, 1995a,b, Sanjuan *et al.* 1994). We already had indirect  
538 evidence that reproductive isolation might have evolved between Mediterranean  
539 and Atlantic refugia (i) in order to maintain genetic differentiation upon contact  
540 (Quesada *et al.*, 1995a), (ii) in order to maintain a sharp genetic break (Quesada  
541 *et al.*, 1995b), and (iii) in order to explain the semi-permeability of the barrier to  
542 gene flow (Fraisse *et al.* 2016). However, the story could not be definitively  
543 settled without more direct evidence that interbreeding opportunities exist at the  
544 transition zone, even if such opportunities are rare. Maybe due to this lack of  
545 evidence of reproductive isolation, the idea that the Atlantic-Mediterranean divide  
546 could simply be explained either by the AOF itself acting as a barrier to larval  
547 dispersal or by the ecological differences between Atlantic and Mediterranean  
548 waters remains strongly anchored in the marine literature. In addition, knowing  
549 Atlantic waters enter the Mediterranean Sea through the South by the Algerian  
550 current, the description of the southern side of the transition zone was a  
551 sampling lacuna that needed to be filled. Sampling that coast revealed far more  
552 than one could have expected. The unexplored side of the biogeographic  
553 boundary was hiding a 600 km wide mosaic hybrid zone. We will argue here that  
554 the existence of this large mosaic hybrid zone provides evidence-based support  
555 for the existence of partial reproductive isolation, which prevents gene flow when  
556 the two lineages live in sympatry/syntopy with the opportunity to interbreed and  
557 exchange genes in the absence of such reproductive isolation. We believe that  
558 the existence of partial reproductive isolation between heterogeneously-  
559 differentiated genetic backgrounds should supplement the disruption of  
560 population connectivity and selection against maladaptive migrants to provide a  
561 fuller explanation of genetic subdivision in marine (Bierne *et al.*, 2011, Gagnaire  
562 *et al.* 2015, Riginos *et al.* 2016) as well as terrestrial species (Barton and Hewitt  
563 1985, Hewitt 1989).

564 The previously-reported absence of mussels between Almeria and Alicante  
565 (Quesada *et al.*, 1995b) on the Spanish coast suggested that there was no strong  
566 opportunity for sympatry and interbreeding between the Atlantic and the  
567 Mediterranean lineages, in accordance with the AOF as an efficient barrier to

568dispersal. However, two populations were sampled south of Alicante in Cartagena  
569and San Pedro (N4 and N5 in Figure 1) with a low but non-negligible proportion of  
570these individuals assigned to the Atlantic genetic cluster. This is a sufficient  
571proportion of migrant mussels to refute the barrier to dispersal as strong enough  
572to explain the maintenance of the genetic structure. Along with the results from  
573the southern coast presented here, there remains no ambiguity that the Atlantic  
574lineage not only enters the Mediterranean Sea, but co-exists with the  
575Mediterranean lineage, sometimes in balanced proportions, across a widespread  
576area where mussels are numerous. Described as a strong barrier to larval  
577dispersal, the AOF is in fact rather a mix of Atlantic waters and Alboran surface  
578waters called 'Modified Atlantic water' (MAW, Font *et al*, 1998) in the Eastern  
579Alboran anticyclone and along the Algerian coast thanks to the Algerian current.  
580There are several species without a genetic break at the AOF -e.g. the European  
581flat oyster *Ostrea edulis* (Launey *et al*, 2002), the Mediterranean rainbow wrasse  
582*Coris julis* (Aurelle *et al*, 2003), or the saddled seabream *Oblada melanura*  
583(Galarza *et al*, 2009). These species share similar biological and ecological  
584characteristics with species that do exhibit a break and this observation was  
585already a strong argument against the hypothesis of a sufficiently reduced  
586dispersal rate at the AOF to explain the genetic differentiation observed in many  
587species.

588We now turn to the more complex issue of the nature of the genetic barrier  
589(extrinsic, intrinsic, or both). Given the contrasting environments inhabited by the  
590two lineages in the Mediterranean Sea and the Atlantic Ocean, there is little  
591doubt that differential adaptation must exist between the two lineages (including  
592phenotypic plasticity and epigenetic responses). However, the large zone of co-  
593existence in Algeria modifies our view of how the genetic barrier operates. We no  
594longer have to explain adaptation in the two seas but have to explain that the  
595two lineages are maintained genetically cohesive in sympatry along 600 km of  
596Algerian coasts. Without being able to refute exogenous selection, we argue here  
597that intrinsic pre- or post-zygotic isolation is equally likely, if not more likely. We  
598have shown with simple simulations that the mosaic genetic structure observed  
599in Algeria can indeed be obtained with intrinsic reproductive isolation alone  
600(Figure 3 and 4). It only requires asymmetric north-south dispersal at the AOF,  
601which seems a reasonable assumption. In addition, simulations of exogenous  
602selection to a coarse-grained environment also require the assumption of  
603asymmetric north-south dispersal at the AOF (Figure 5B), or a patch of

604maladapted Mediterranean mussels cannot be maintained in the south.  
605Adaptation to a patchy fine-grained environment might better explain the mosaic  
606structure but does not generate a strong barrier to gene flow if neutral markers  
607are not tightly linked to adaptive loci. We probably have not sampled the genome  
608sufficiently densely during our previous genome scans to argue for strong  
609physical linkage between our markers and local adaption genes (Hoban et al.  
6102016), and we therefore need a process able to generate a barrier to gene flow  
611on a large proportion of the genome (Bierne et al. 2011). Selection against  
612migrants that are maladapted to the local environment is often proposed as a  
613process able to generate a genome-wide barrier to gene flow (Marshall *et al*,  
6142010; Nosil *et al*, 2005). However, it is not well appreciated that local selection  
615needs to be extremely strong to generate a sufficiently effective barrier to gene  
616flow (Barton and Bengtsson, 1986; Feder and Nosil, 2010; Slatkin, 1973),  
617producing a strong segregation of each ecotype in its own favoured habitat. As  
618soon as lineages coexist in balanced proportions somewhere, as observed here in  
619Algeria, some sort of selection against hybrids must exist. It can still be  
620exogenous selection (Kruuk et al. 1999), but hybrids must perform poorly in both  
621habitats. Hybrids are the bridges used by neutral genes to flow across the barrier  
622and they either need to be produced in low proportion or to be all unfit for a  
623barrier to gene flow to have broad genomic effects (Barton and Bengtsson 1986).  
624Here, in the Algerian hybrid zone, this is indeed the case as we observed a strong  
625deficit of intermediate genotypes and strong departures from Hardy-Weinberg  
626and linkage equilibrium among physically unlinked loci (Figure 2). Finally, the  
627coarse-grained environment we simulated is not very likely. Although Atlantic  
628waters enter the Algerian current, Algerian waters are much more similar to other  
629Mediterranean waters than to Atlantic waters. Fine-grained habitat heterogeneity  
630was also far from evident between our sampling sites in Algeria as we sampled  
631very similar microsites: high-shore rocks protected from wave action by artificial  
632port breakwaters and with no evident influence of freshwater from nearby  
633estuaries. Taken altogether, we believe these arguments suggest intrinsic  
634reproductive isolation, maybe pre-zygotic given the apparent paucity of F1  
635hybrids, is a parsimonious evidence-based hypothesis that should be considered.

636Overall our results provide additional support for the coupling hypothesis, which  
637suggests that genetic breaks are often secondary contact semi-permeable  
638tension zones between heterogeneously differentiated genomes trapped by  
639physical barriers to dispersal or environmental boundaries (Bierne *et al*, 2011).

640Physical and environmental factors mostly explain the position of the genetic  
641breaks but the maintenance of genome-wide genetic differentiation is best  
642explained by reproductive isolation. Our model implies the differential coupling of  
643sister tension zones at two different geographic positions, at the AOF in the North  
644and at the GBB in the south. The abrupt genetic shift at the GBB is a new  
645observation in an understudied area. However, it fits well with the position of a  
646barrier to dispersal identified with oceanographic modelling in three recent  
647analyses (Andrello *et al*, 2015; Berline *et al*, 2014; Rossi *et al*, 2014). Note in  
648addition that these three hydrodynamic studies identified much more efficient  
649barriers to larval dispersal than the AOF within the Mediterranean Sea that are  
650not hotspots of genetic differentiation. Differential coupling of sister tension  
651zones can occur in coastal or river species living in linear landscapes with tree-  
652like reticulation that are not well-described by standard 1D or 2D stepping stone  
653models (Fourcade *et al*. 2013). For instance, some hybrid zones secondarily  
654trapped at the entrance of the Baltic Sea are likely to have produced sister hybrid  
655zones which have moved further north along the Norwegian coast to be trapped  
656somewhere in northern Scandinavia (e.g. in *Mytilus trossulus*, *Macoma balthica*,  
657*Gadus morhua*, *Platichthys flesus* and *Gammarus zaddachi*; reviewed in Bierne *et*  
658*al*, 2011). Recently the Baltic - North Sea contact zone between the strongly  
659divergent mussel species *Mytilus trossulus* and *M. edulis* has been investigated in  
660the southern coast area and was identified to be positioned well inside the Baltic  
661Sea in Germany (Stuckas *et al*. 2017) while it is localised in the Oresund in the  
662North (Väinölä and Hvilsom 1991).

663To conclude, the mosaic hybrid zone between Oran and Bejaia observed in *M.*  
664*galloprovincialis* mussels contributes to definitively refute the hypothesis that the  
665AOF itself generates a sufficiently strong barrier to dispersal to maintain genetic  
666differentiation in this species. It also opens the debate about the nature of the  
667genetic barrier, which is not necessarily related to differential adaptation to  
668Atlantic and Mediterranean waters but could imply intrinsic pre- or post-zygotic  
669reproductive isolation. The next step will be to conduct lab experiments (hybrid  
670crosses) and field studies (settlement and reproduction) to put the alternatives to  
671the test. Our results also call for new genetic studies along Algerian coasts in  
672other marine species. A few samples of sea bass from eastern Algeria proved to  
673be admixed between the Atlantic and Mediterranean lineages (Duraton *et al*.  
6742018), although we do not yet know the spatial variation of admixture  
675proportions in this system. Finally our study reveals how complex the interplay

676between connectivity (hydrography), environmental variation (seascape) and  
677reproductive isolation (including both extrinsic and intrinsic mechanisms) can be.  
678Without minimising the importance of hydrography and local selection, we  
679believe the excessive emphasis on oceanographic features in the interpretation  
680of the genetic structure in the sea sometimes results in an incomplete  
681understanding of the underlying processes explaining its origin and maintenance.

682

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697

### 698**Conflict of Interest**

699The authors declare no conflict of interest.

700

### 701**Data Archiving**

702Sequence data have deposited in GenBank: accession numbers MK259098 -  
703MK259664

704Genotype data have been deposited in Dryad: doi:10.5061/dryad.m3t6p5g

705

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965

## 966**Titles and legends to figures**

967Table 1. Examples of marine hotspots of genetic differentiation.

968

969Figure 1. Sampling localities of *Mytilus galloprovincialis* in the north-eastern  
970Atlantic and the Mediterranean Sea. Proportion of individuals assigned to the  
971Atlantic cluster (in red), the Mediterranean cluster (in green) and unassigned (in  
972black), based on a DAPC analysis with the four loci (*COIII*, *Precol-D*, *EFbis* and  
973*EF2*). Sample names and their GPS positions are given in the supplementary  
974Table S1.

975

976Figure 2. *Mytilus galloprovincialis* Mediterranean allele frequencies at the four  
977semi-diagnostic loci analysed (*COIII*, *Precol-D*, *EFbis* and *EF2*) for (A) the 9  
978samples of the northern coastline and (B) the 14 samples of the southern  
979coastline. AOF: Almeria Oran Front, GBB: Gulf of Bejaïa Barrier. (C) Average  
980multilocus linkage disequilibrium (D, bold line, left axis) and Hardy-Weinberg  
981disequilibrium (Fis, dashed line, right axis) in samples of the northern coastline  
982and (D) samples of the southern coastline. Bar plot of the estimated ancestry  
983proportions (Q-values) estimated by STRUCTURE with the three nuclear markers  
984(*Precol-D*, *EFbis* and *EF2*) for (E) the samples of the northern coastline and (F) the  
985southern coastline.

986

987Figure 3. (A) Simulation output obtained with a bi-locus deterministic model with  
988selection against recombinant genotypes ( $s=0.1$ ) and a slight advantage of the  
989Mediterranean background ( $a=0.01$ ) in a 60 demes Y-shape stepping stone model  
990( $m=0.3$ ), including two weak barriers to gene flow ( $mbar=0.1$ ) between demes  
99120 and 21 (AOF) in the northern chain and between demes 40 and 41 (GBB) in

992the southern chain of demes, a contact between demes 50 and 51, and  
993unidirectional migration right to the AOF. Above: northern chain, below: southern  
994chain. The insert shows an output when migration was bidirectional between the  
995two chains. Clines are represented every 500 generations with a rainbow colour  
996code from orange to dark blue. Blue clines superimposed green clines in the  
997southern chain because they remain at the same position (trapping). (B)  
998Simulation with a contact between demes 10 and 11 and an advantage of the  
999Atlantic background ( $a=0.01$ ). Clines are represented every 500 generations with  
1000a rainbow colour code from orange to dark blue. Dark blue clines superimposed  
1001light blue and green clines because they remain at the same position (trapping).

1002

1003Figure 4. (A) A simulation output obtained at a neutral locus at a genetic map  
1004length of 1cM to one intrinsic incompatibility after 1000 generations, with the Y-  
1005shape bi-unidimensional stepping stone model, including two weak barriers to  
1006gene flow between demes 25 and 26 (AOF) in the northern chain and between  
1007demes 40 and 41 (GBB) in the southern chain of demes and unidirectional  
1008migration right to the AOF. (B) Proportion of Mediterranean ancestry under an  
1009admixture model (STRUCTURE Q-values). Geographic positions are rescaled so  
1010that Almeria superposes to Oran.

1011

1012Figure 5. (A) Simulation output obtained with a deterministic model with  
1013exogenous selection in a fine-grained environment between AOF and GBB in the  
1014southern coasts (in which habitat type was assigned randomly). Other  
1015parameters the same as previous figure. Thick line: selected locus, thin line:  
1016neutral locus after 1000 generations ( $r=1cM$ ) (B) Simulation output obtained with



1017a deterministic model with exogenous selection in a coarse-grained environment.

1018 Thick line: selected locus, thin line: neutral locus after 1000 generations ( $r=1\text{cM}$ ).

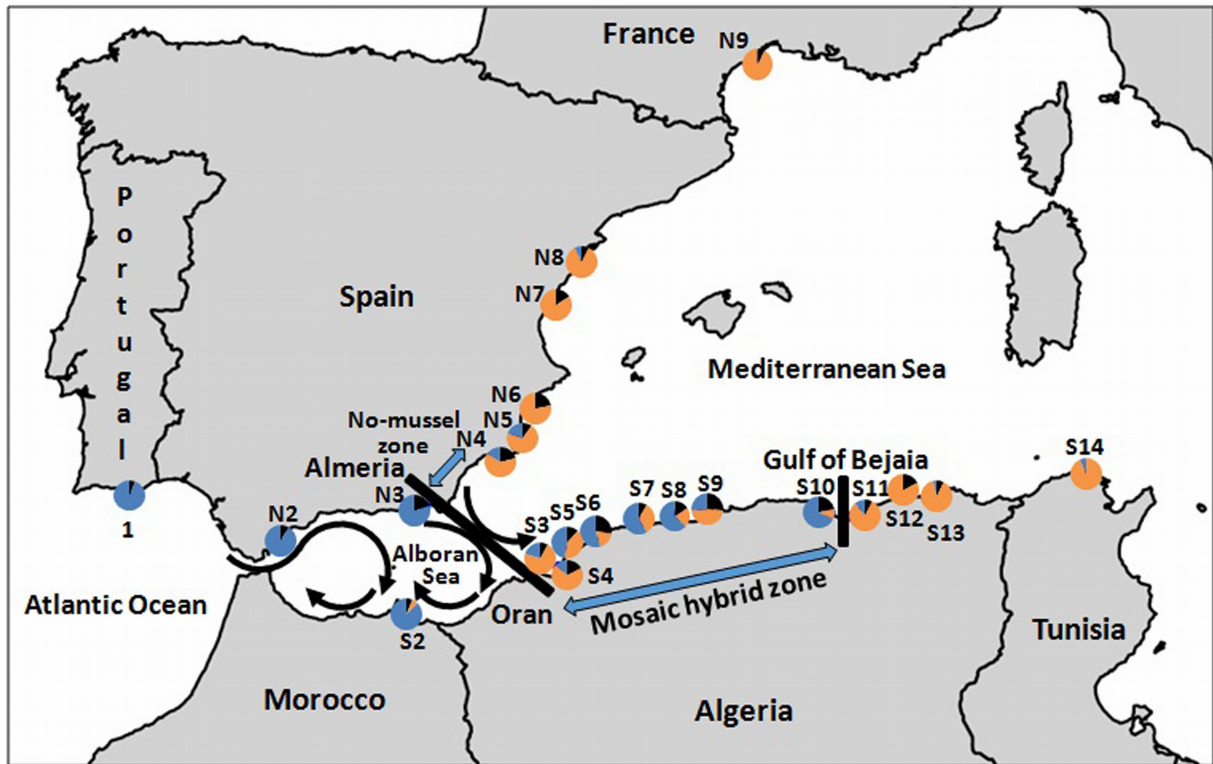
1019

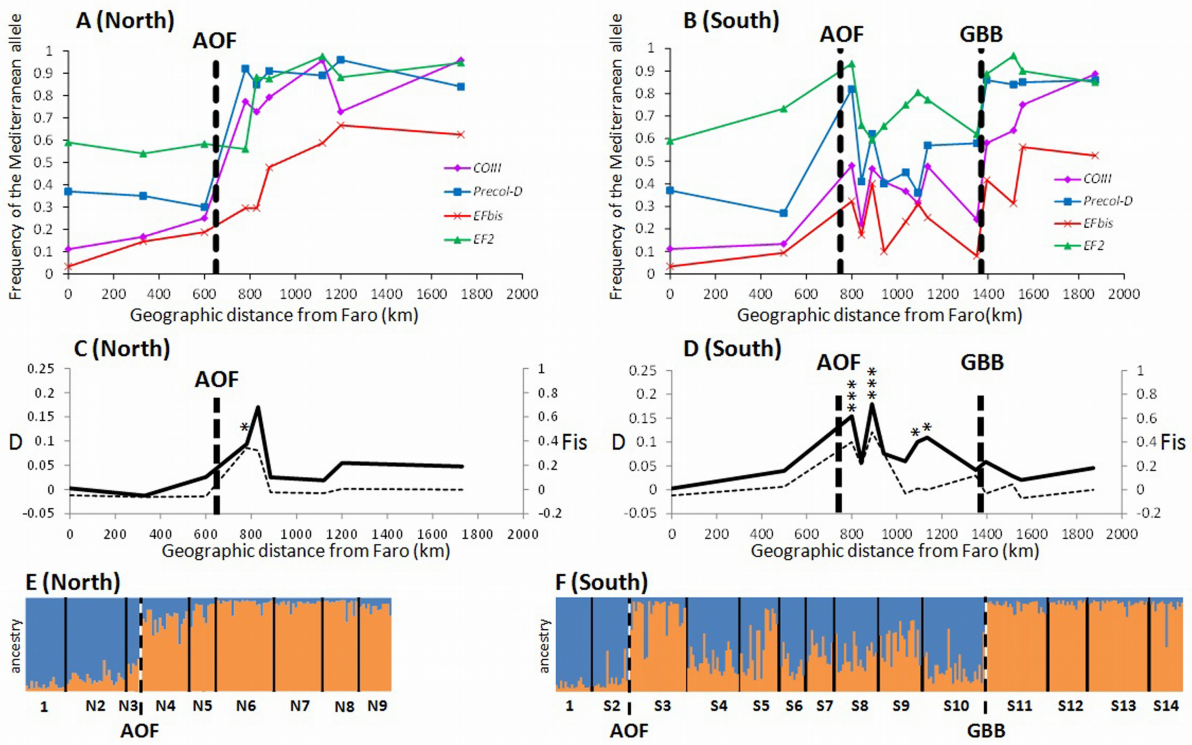
<b>Barrier to gene flow</b>	<b>Potential processes involved</b> <b>Vicariance (V)</b> <b>Temperature (T)</b> <b>Salinity (S)</b> <b>Hydrography (H)</b>	<b>References</b>
Øresund and Danish Belts	S	Johannesson and Andre (2006)
Almeria Oran Front	V, H, S, T	Paternello et al (2007), Galarza et al (2009)
Balearic Front	H	Galarza et al (2009)
Siculo - Tunisian Strait	V, H, S, T	Bahri Sfar et al (2000), Mejri et al (2009)
<b>Cape Cod (Massachusetts)</b>	V, H	McGovern & Hellberg (2003), Kelly et al. (2006), (Haney et al. 2007)
Cape Canaveral (Florida)	V, H, T	Reeb and Avise (1990), Avise et al (1992), Pelc et al. (2009)
Nova Scotia 44-45°N	T	Stanley et al. (2018)
Cape Mendocino (California)	C, H	Blanchette et al. 2008, Sivasundar & Palumbi (2010)
<b>Point Conception (California)</b>	V, H	Burton (1998), Cassone & Boulding (2006), Dawson (2001), Pelc et al. (2009).
Cape Agulhas (South Africa)	H	Evans et al. 2004, Teske et al (2014)
<b>30°S Chilean biogeographic break</b>	H	Brante et al (2012)

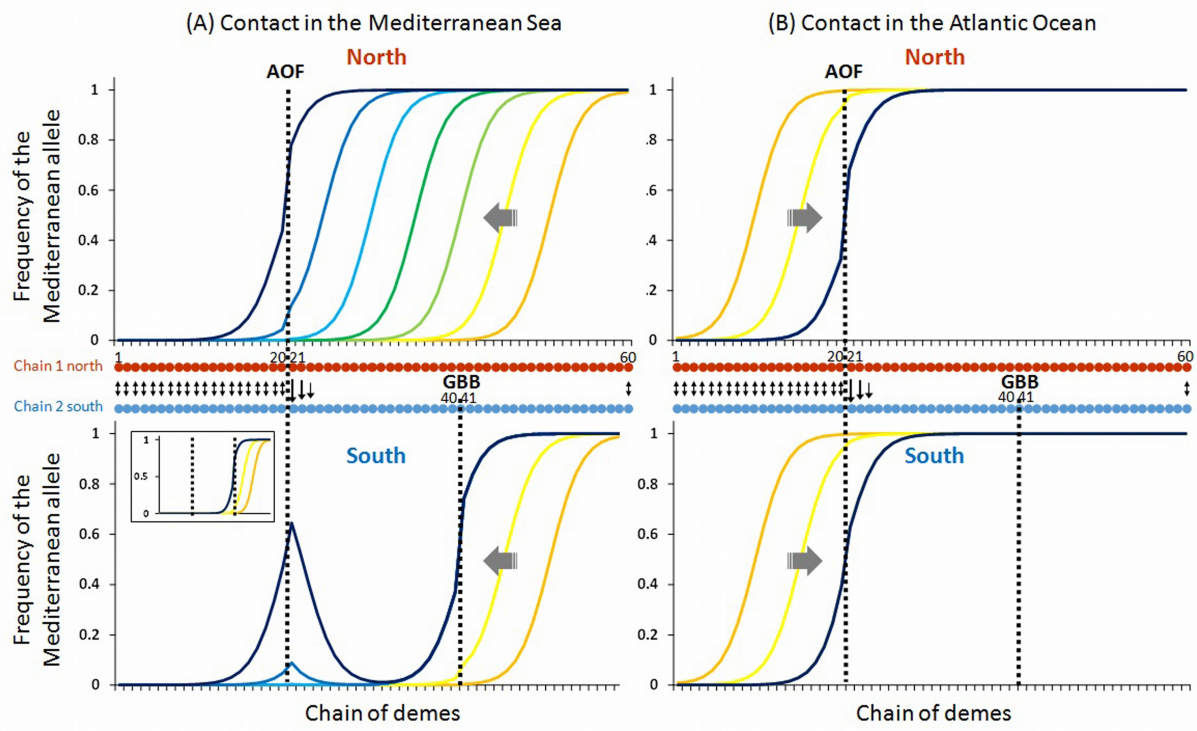
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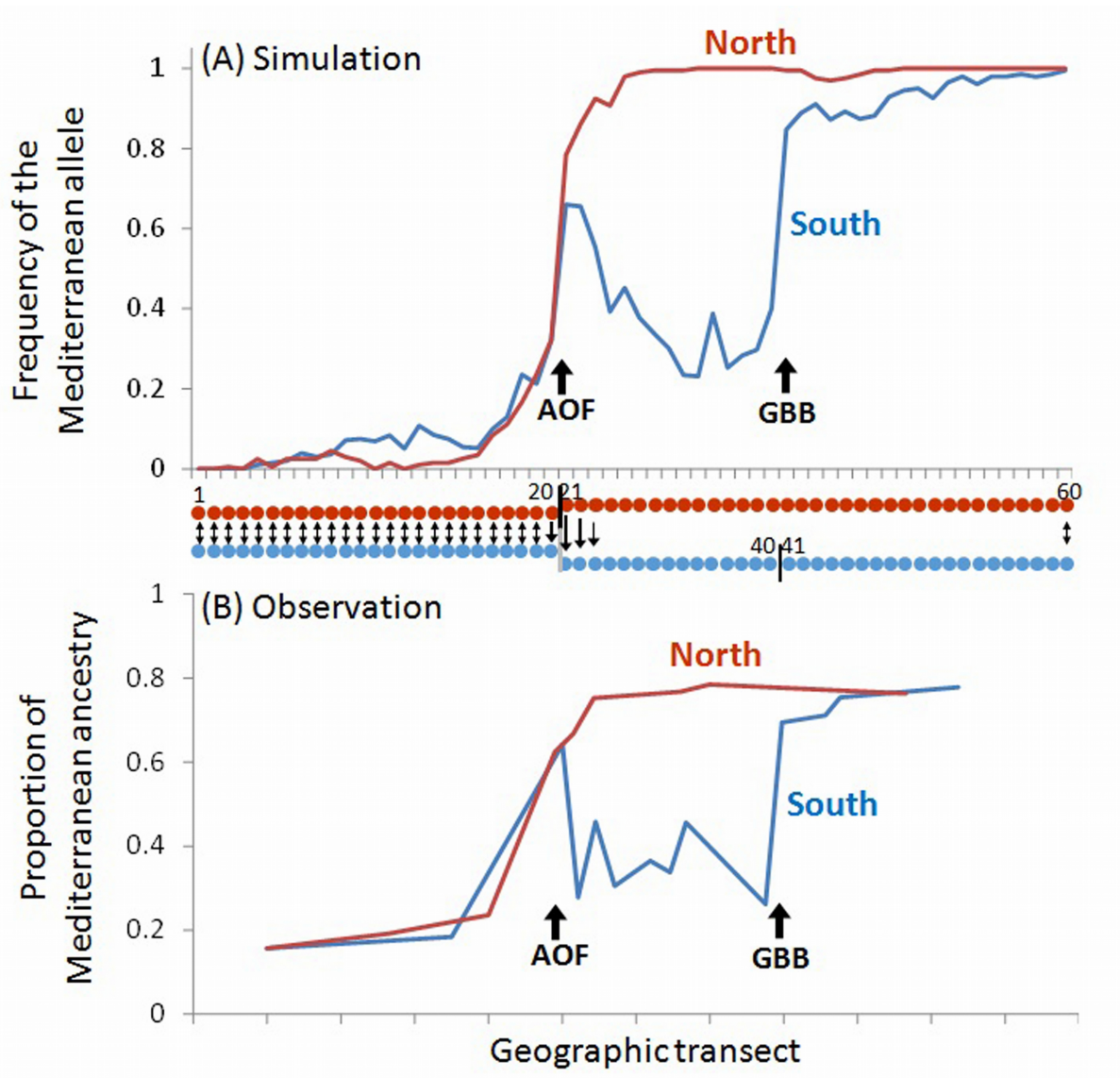
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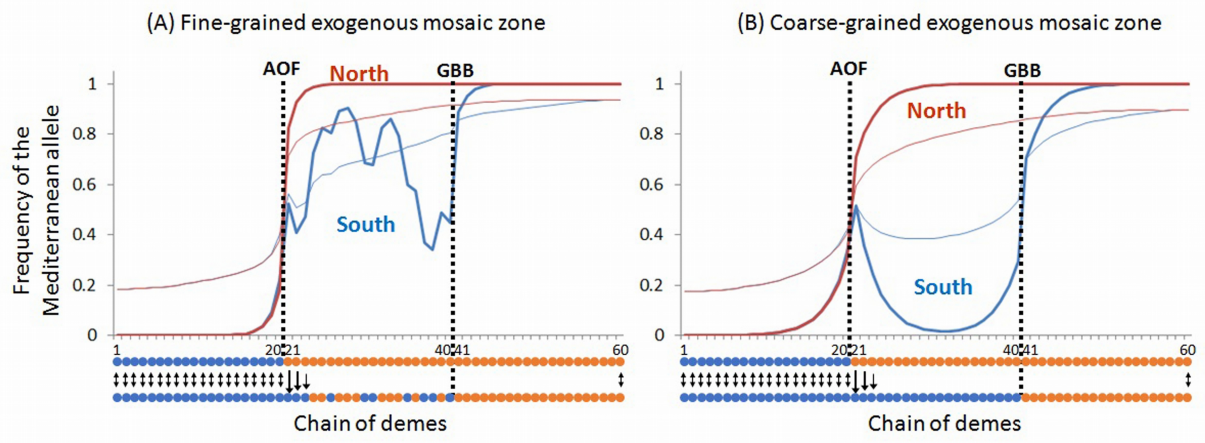
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