

## New insights on the population genetic structure of the great scallop (*Pecten maximus*) in the English Channel, coupling microsatellite data and demogenetic simulations

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### Abstract :

1. The great scallop (*Pecten maximus*) is a commercially important bivalve in Europe, particularly in the English Channel, where fisheries are managed at regional and local scales through the regulation of fishing effort. In the long term, knowledge about larval dispersal and gene flow between populations is essential to ensure proper stock management. Yet, previous population genetic studies have reported contradictory results.

2. In this study, scallop samples collected across the main fishing grounds along the French and English coasts of the English Channel (20 samples with temporal replicates for three sites, n = 1059 individuals), and the population genetic structure was analysed using 13 microsatellite loci. Coupling empirical genetic data with demogenetic modelling based on a biophysical model simulating larval exchanges among scallop beds revealed a subtle genetic differentiation between south-west English populations and the rest of the English Channel, which was consistent with larval dispersal simulations.

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3. The present study provides a step forward in the understanding of great scallop population biology in the English Channel, underlining the fact that even in a context of potentially high gene flow and recent divergence times since the end of the last glacial maximum, weak but significant spatial genetic structure can be identified at a regional scale.

**Keywords** : English Channel, gene flow, genetic modelling, genetic resources management, great scallop, low genetic structure, microsatellites

## 21 Introduction

22 Most **benthic** marine species are spatially distributed into fragmented populations that are generally  
23 interconnected by the dispersal of gametes, propagules, or individuals (Cowen & Sponaugle, 2009). The  
24 study of larval dispersal in the marine environment requires complementary approaches using both direct and  
25 indirect methods such as *in-situ* observation, microchemistry, biophysical modeling or molecular tools  
26 (Cowen & Sponaugle, 2009). Marine populations commonly display low levels of neutral genetic  
27 differentiation (e.g. Purcell, Cowen, Hughes, & Williams, 2006, but see Bilodeau, Felder, & Neigel, 2005).  
28 Nevertheless, the neutral population genetic structure results from the combined effect of genetic drift and  
29 gene flow, and weak genetic structure (if any) does not necessarily indicate a high degree of gene flow  
30 among populations (Whitlock & McCauley, 1998). For recent divergence times, since marine benthic  
31 invertebrates generally display large populations and therefore low genetic drift and supposed high dispersal  
32 rate, the migration-drift equilibrium is rarely reached (Waples, 1998). In the case of benthic-pelagic  
33 invertebrate species, combining larval dispersal modeling with population genetics, [through seascape](#)  
34 [genetics approaches \(Selkoe, Henzler, & Gaines, 2008\)](#), has proven relevant for understanding the role of  
35 oceanic currents in shaping the genetic diversity of populations (Foster et al., 2012; Galindo, Olson, &  
36 Palumbi, 2006).

37 The great scallop (*Pecten maximus* L.) is a bivalve belonging to the Pectinidae family which has a  
38 life cycle characterized by a 3-5-weeks dispersive planktonic larval phase followed by benthic juvenile and  
39 adult stages with a limited mobility (Nicolle, Dumas, Foveau, Foucher, & Thiébaud, 2013). This  
40 species is widely distributed along the North-east Atlantic coasts from Morocco to northern Norway and is  
41 an important commercial species in terms of landings ([25.10<sup>6</sup> £ in United Kingdom \(Elliott & Holden, 2017\)](#)  
42 [and 50.10<sup>6</sup> in France \(Les filières pêche et aquaculture, 2018\)](#)) and socio-economic values for European  
43 fisheries (Duncan, Brand, Strand, & Foucher, 2016). The main fishing grounds are located around the British  
44 Isles, along the eastern and western coast of Scotland, in the Irish Sea and in the English Channel (EC). In  
45 the EC, great scallop resources are **exploited** by different countries (United Kingdom, France,  
46 Ireland, Belgium and Netherlands) resulting in different management strategies (Duncan et al., 2016;  
47 Howarth & Stewart, 2014). In this respect, understanding the population genetic structure at the scale of the

48 whole EC is fundamental to ensure concordance~~adequacy~~ between biological processes~~and~~ stock  
49 management plans~~units~~ (e.g. Reiss, Hoarau, Dickey-Collas, & Wolff, 2009).

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50 Estimates of *P. maximus* larval connectivity between the main fishing grounds in the EC was  
51 provided by the development of a Lagrangian biophysical model that coupled a 3D hydrodynamic model and  
52 a biological submodel in a previous study (Nicolle et al., 2013, 2016). The biological submodel takes into  
53 account a temperature-dependent spawning time, a temperature-dependent planktonic larval duration, and  
54 larval behaviour. Model results highlighted the occurrence of three groups of highly connected scallop beds  
55 (Figure 1): (i) Eastern English Channel, (ii) Normano-Breton Gulf, (iii) South-western coast of England.  
56 According to the model, larval dispersal occurs mainly among neighbouring sites located less than 100 km  
57 away, while exchanges between the three groups are rare and weak. Within each group, two or three  
58 spawning units~~groups~~ act as source populations with high retention and self-recruitment rates while  
59 peripheral stocks act as sink populations with a low self-recruitment rate (Nicolle et al., 2016). Moreover in  
60 the model, the Bay of Brest, located at the tip of Brittany, was found to be partially isolated from the EC.  
61 Within a stock, year-to-year variations in environmental forcing are responsible for~~of~~ variations in the  
62 reproductive success of scallop and in the origin of settlers (Nicolle et al., 2013, 2016).

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63 In contrast, microsatellite-based population genetic studies of *P. maximus* showed contradictory  
64 results in the EC (Morvezen, Charrier, et al., 2016; Szostek, 2015). On the one hand, Szostek (2015)  
65 highlighted a lack of differentiation from Falmouth to the Sussex coast, but a significant differentiation  
66 between the stocks of the Bay of Seine and the rest of the eastern EC. On the other hand, Morvezen,  
67 Charrier, et al. (2016) did not report any significant differentiation between populations from Plymouth, the  
68 Bay of Saint Brieuc and the Bay of Seine. Consequently, the comparison of larval dispersal modelling and  
69 population genetic studies did not provide a clear picture of the population structure and connectivity  
70 patterns in this region. These discrepancies among-between studies may result from the small sample sizes  
71 (Szostek, 2015), or— from the use of different microsatellites markers and/or the limited number of EC  
72 scallop grounds sampled in both genetic studies (Morvezen, Charrier, et al., 2016; Szostek, 2015). A refined  
73 spatio-temporal sampling is therefore essential for a robust assessment of subtle population structure when  
74 low genetic differentiation is expected, as in the case for *P. maximus* in the EC.

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75 In this context, the purpose of the present study was to ~~extensively~~ explore the empirical population  
76 structure of *P. maximus* at the scale of the EC ~~from-based on~~ an extensive sampling of most scallops<sup>2</sup>  
77 grounds. In addition, ~~P~~population structure was analysed through a multidisciplinary seascape genetics  
78 approach (Selkoe, Henzler, & Gaines, 2008) using previous results of coupling larval dispersal simulation  
79 obtained by Nicolle et al. (2016) as biological parameters implemented in ~~and the present demo-genetic~~  
80 model ~~population genetic modelling, with empirical population genetic data.~~ -The aim of this approach was  
81 to assess simulated spatial genetic structure in the metapopulation context described by Nicolle et al. (2016).  
82 Matches and mismatches between empirical and simulated genetic structure should informed about evolutive  
83 forces and potential bias driving observed empirical genetic structure. In this regard ~~addition~~, the study aimed  
84 at testing population structure patterns based on prior results from larval dispersal modelling (Nicolle et al.,  
85 2016).

## 86 **Material and Methods**

### 87 Sampling

88 A total of 1059 great scallops were sampled by dredging 20 sites ~~from 13~~ corresponding to  
89 commercially fished scallop beds located in the English Channel. Sample locations were based on the  
90 distribution of the main fishing grounds defined by Nicolle et al. (2016) (Table 1, Figure 1). Four fishing  
91 grounds were sampled two or three times to assess the year-to-year variability in the genetic structure. No  
92 sample was collected along the southern English coast between 4°W and 0° because of the absence of major  
93 fishing grounds in this area. ~~— Sampling~~ Sample collection differed from Szostek (2015) ~~by with the~~  
94 inclusion of an extensive sampling of the western English Channel French coast-line including also the Bay  
95 of Brest. A small piece of adductor muscle was collected ~~on from~~ each sampled individual and preserved in  
96 95% ethanol.

### 97 Microsatellite genotyping

98 DNA extraction was performed using a Cetyltrimethylammonium bromide (CTAB) method. About 200 mg  
99 of tissue were incubated overnight at 59°C in 750 µl of extraction buffer composed of 2%

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100 ~~Cetyltrimethylammonium bromide (of CTAB)~~, 1% Polyvinylpyrrolidone (PVP), 1.4 M of NaCl, 0.2 M of  $\beta$ -  
101 Mercaptoethanol, 100 mM of Tris-HCl pH=8, and 3.75  $\mu$ l of Proteinase K (20mg.ml<sup>-1</sup>). DNA was purified by  
102 the addition of one volume of Chloroform Isoamyl Alcohol 24:1 and the aqueous phase was collected after  
103 15 min of centrifugation at 4°C and 13000 rpm. This step was performed twice. Then, DNA was precipitated  
104 with 0.6 volume of isopropanol and centrifuged 30 min at 4°C and 13000 rpm. Pellets of DNA were washed  
105 twice with 75% of ethanol, centrifuged at 4°C and 13000 rpm during 5 min and suspended in 100  $\mu$ l of  
106 MilliQ water. DNA concentration was measured with a NanoDrop 8000 spectrophotometer (Thermo  
107 Scientific). Finally, all DNA samples were diluted to reach a concentration around 20  $\mu$ g. $\mu$ l<sup>-1</sup>.

108 Nineteen microsatellite markers were successfully amplified and optimized out of 23 previously  
109 published loci (Charrier, Morvezen, Calves, & Laroche, 2012; Morvezen, [Cornette](#), et al., 2013; Szostek,  
110 2015; Watts et al., 2005). The forward primer of each locus was tailed with a universal primer to reduce the  
111 genotyping costs (Schuelke, 2000). Four different universal primers were used, each of them labelled with a  
112 fluorescent dye (Supplementary material table 1). Moreover, a PIG-tail (5'-GTTTCTT) was added to the 5' -  
113 end of reverse primer to avoid genotyping errors due to excessive stutter peaks when needed (Brownstein,  
114 Carpten, & Smith, 1996). Each locus was amplified in a simplex polymerase chain reaction (PCR) in 10  $\mu$ l  
115 volume containing 1X green Go Taq flexi buffer (Promega), 1.5-2.0 mM MgCl<sub>2</sub>, 0.2  $\mu$ M each dNTP, 0.2  $\mu$ M  
116 universal primer (fluorescent), 0.2  $\mu$ M reverse primer, 0.02  $\mu$ M forward primer, 0.25 U Go Taq Flexi DNA  
117 Polymerase (Promega), and 1  $\mu$ l DNA template. PCRs were performed on a Thermocycler GeneAmp 9700  
118 (Applied Biosystem). A touchdown procedure was included in the thermal cycling regime to increase the  
119 stringency of the PCRs and, for each locus, annealing temperatures were set up according to the melting  
120 temperature of the primer pair ( $T_m$ ) and the tailed universal primer ( $T_{mU}$ ): (94°C for 3 min,  $T_m+2^\circ\text{C}$  for 2  
121 min, 72°C for 30 sec) x1, (94 °C for 30 sec,  $T_m + 1^\circ\text{C}$  for 30 sec [-1°C per cycle until  $T_{mU}-3^\circ\text{C}$ ], 72°C for 30  
122 sec) x 2-9 cycles, (94°C for 30 sec,  $T_{mU} -3^\circ\text{C}$  for 30 sec and 72°C for 30 sec) x 35-40 cycles, 72°C for 5  
123 min. Melting temperatures  $T_m$  and  $T_{mU}$  were calculated according to Marmur ~~&~~ [and](#) Doty (1962). The  
124 number of total cycles was adjusted between 35 and 45 cycles according to each locus (Supplementary  
125 [Material T](#)table 1).

126 The 19 amplified microsatellites were grouped into three panels. For each panel, 2  $\mu$ l of each  
127 amplified locus were mixed together, and 1.5  $\mu$ l of the mix was added to 10  $\mu$ l Hi-Di formamide and 0.15  $\mu$ l

128 GeneScan 500 LIZ size standard (Applied Biosystems). PCR products were denatured for 5 minutes at 95°C  
129 and immediately transferred on ice for 10 minutes, and then electrophoresed on an ABI-3130 capillary  
130 sequencer (Applied Biosystems). Electrophoregrams were analysed with Genmapper 4.0 (Applied  
131 Biosystems), and were scored independently by two people in order to minimize scoring errors. Individuals  
132 with more than 30% missing data were removed from the data set, resulting in 895 successfully genotyped  
133 individuals. The genotype data file was converted into the proper format for further data analyses with  
134 CREATE 1.37 (Coombs, Letcher, & Nislow, 2008).

135 Data analysis

136 *Within population diversity and marker quality*

137 Allelic richness for each locus were calculated with  
138 FSTAT 2.9.3.2 (Goudet, 1995). The number of private alleles per locus was estimated with the R package  
139 poppr (Kamvar, Brooks, & Grünwald, 2015) and summed by sample. Observed ( $H_o$ ) and expected ( $H_e$ )  
140 heterozygosities and the Wright's fixation index ( $F_{IS}$ ) per locus were computed with GENETIX 4.05  
141 (Belkhir et al., 1996-2004). For each sample and for each locus, the significance of  $F_{IS}$  estimates (i.e.  
142 departure from 0) was tested using 10,000 permutations with GENETIX 4.05, and the correction for multiple  
143 testing was applied using the MultiTest V.1.2 (De Meeûs, Guegan, & Teriokhin, 2009) and the B-Y method  
144 (Benjamini & Yekutieli, 2001) respectively for populations and loci  $F_{IS}$ . Average null allele frequencies per  
145 sample was assessed with ML-NULFREQ (Kalinowski & Taper, 2006). Linkage disequilibrium was tested  
146 with GENEPOP 4.0.5 (Rousset, 2008) using default parameters (Dememorization number=10,000;  
147 batches=100; iterations=5,000). The occurrence of loci that may be under selection was explored using  
148 LOSITAN (50,000 simulations, stepwise mutation model, and 95% confidence intervals, (Antao, Lopes,  
149 Lopes, Beja-Pereira, & Luikart, 2008)). Finally, prior to further analyses, the data set was cleaned by  
150 removing all loci displaying significant departures from Hardy-Weinberg equilibrium (i.e.  $F_{IS}$   
151 significantly different from 0), null alleles, signatures of selection and/or linkage disequilibrium (one of the  
152 two linked loci was removed in that case). Filtering resulted in 13 markers. The statistical power for  
153 identifying genetic differentiation for this set of 13 markers was evaluated with POWSIM 4.1 (Ryman et al.,

2006) with  $N_e$  (effective population size) = 5,000 for 10,000 replicates. All genetic diversity statistics were calculated after filtering step for each sample overall conserved loci (Supplementary Material Table 2).

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#### Population genetic structure

Global and pairwise population genetic differentiation were evaluated by estimating the Wright's statistics ( $F_{ST}$ ) using the  $\theta$  of Weir & Cockerham (1984) with GENETIX 4.05. The significance of estimates was tested using 10,000 permutations of individuals among populations. PcoA was realised on pairwised  $F_{ST}$  matrix, using ape package (Paradis & Schliep, 2018), and was presented in Supplementary Material Figure 1.

For pairwise  $F_{ST}$ , false discovery rate (FDR) correction for multiple testing was applied using the B-Y method. Possible barriers to gene flow were investigated through a distance-based redundancy analysis on pairwise  $F_{ST}$  distances using the four groups of populations defined by (Nicolle et al., 2016) namely the Bay of Brest (BOB), the western English Channel (WEC), the south-western England (SWE) and the eastern English Channel (EEC) as explanatory variable and Cailliez's method to correct for negative eigenvalues (db-RDA; Legendre & Anderson, 1999), using the R package vegan (Oksanen et al., 2017).

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The global significance of the db-RDA was tested with 10,000 permutations. In addition, the influence of spatial coordinates of the populations (latitude and longitude) on their allele abundances was explored with a redundancy analysis (RDA). Prior to this analysis, Hellinger transformation (Legendre & Gallagher, 2001) was applied to allele abundances so that double zeros (the absence of an allele in two populations that are compared) were not considered as an indication of similarity among populations. Global significance and significance of each constrained axis were tested using 10,000 permutations.

#### ~~Demo-genetic simulations~~ Simulated genetic structure

The population genetic structure was simulated with the MetaPopGen (v. 006) R package (Andrello & Manel, 2015), that was chosen for its ability to model complex demographic scenarios, using the "sim.metapopgen.monoecious" function. Twenty-two populations across the EC were included in the analysis, based on those studied by Nicolle et al. (2016). Each population was composed of seven age-classes (Beukers-Stewart, Vause, Mosley, Rossetti, & Brand, 2005). Maximal population sizes ( $k_0$  in MetaPopGen) were inferred by multiplying the area covered by each population (Nicolle et al., 2016) with



180 the densities estimated by (Le Goff et al., 2017). However, given the very large population sizes ( $10^7$  to  $5.10^9$   
181 individuals), each of them was divided by 1000, in order to simplify computations and maintain the relative  
182 size of each population (Supplementary ~~M~~aterial ~~T~~able 23). The effective fecundity, i.e. the number of  
183 post settlement juveniles produced by a mature adult, was set to 70 according to the current knowledge of  
184 different life history traits of the great scallop (i.e. potential fecundity, fertilization rate, hatching rate, larval  
185 mortality rate, and recruits survival) (see Supplementary ~~M~~aterial ~~T~~able 43 for the detail of the  
186 computation). For effective fecundity computation, when the value of a biological trait (fertilization rate,  
187 hatching rate, larval mortality and recruits survival) was unknown for scallops, the mean value reported in  
188 the scientific literature for marine invertebrates was used. Even if some information was available on  
189 fecundity variability in the EC (Le Goff et al., 2017), the number of recruited larvae was kept  
190 ~~homogeneous~~homogeneous among fishing grounds. Survival was calculated according to the mortality  
191 function defined in Le Goff et al. (2017). The maximum recruitment capacity  $k_0$  was different for each  
192 population, constant through time and limited by population size. Mean values of connectivity among stocks  
193 was implemented as proposed by Nicolle et al. (2016) and was set constant through time. The initial allele  
194 frequencies were assigned randomly to populations given the unknown demographic history of scallop beds  
195 in the EC. Simulations were performed for 30 replicates over a period of 4,000 years, time for which sea  
196 level and hydrodynamics in the EC were supposed to be similar to present observations (Sturt, Garrow, &  
197 Bradley, 2013). Simulations considered a single locus with 13 alleles that corresponded to the mean number  
198 of alleles per locus encountered in the present data set (excluding the marker List15-13), and the mutation  
199 rate ~~per year~~ was set at  $10^{-6}$ . For each simulation replicate, the population genetic structure was assessed at  
200 time  $T = 4,000$  by calculating pairwise  ~~$F_{ST}$~~  $F_{ST}$  (Nei, 1973) using the function “fst.pairwise.monoecious” in  
201 MetaPopGen, the same weights being attributed to each population for  ~~$F_{ST}$~~  $F_{ST}$  calculations. All cohorts were  
202 pooled in each population in each replicate to calculate pairwise  ~~$F_{ST}$~~  $F_{ST}$ , and ~~these pairwise  $F_{ST}$~~  values were  
203 averaged across the 30 replicates. Sensitivity analyses were conducted for fecundity, mutation rate and  
204 population size, using mantel test (Oksanen et al., 2017), ~~this and~~ did not reveal any change in pairwise  
205  ~~$F_{ST}$~~  $F_{ST}$  (results not shown). Simulated and empirical genetic results were compared with a Procrustes  
206 analysis using the R package vegan (Oksanen et al., 2017); only the simulated populations that matched with  
207 the empirical sampling design (11 out of 22 simulated samples) were kept for this comparison.

## 208 Results

### 209 *Within-population genetic diversity*

210 The observed number of alleles per locus ranged from 5 to 32. An exceptionally high value of 93  
211 was found for the marker List15-13 ([Supplementary Material Table 2](#)). Neither linkage disequilibrium nor  
212 selection pressure were detected for any locus, except for PmNH11, which showed directional selection. The  
213 markers PmNH11, PmNH70, PmNH73, PmGC05, List15-13 and List15-08 showed at least eight significant  
214  $F_{IS}$  estimates out of 20 sampled populations ( $F_{IS} = [0.09-1]$ , p-value < 0.05) and null allele frequencies (>  
215 9%) were observed for markers PmNH70, PmNH73, PmNH11 and List15-08b ([Table 2 Supplementary  
216 Material Table 2](#)). Therefore, the markers PmNH11, PmNH70, PmNH73, PmGC05, List15-13 and List15-08  
217 were discarded ~~for~~ [from](#) further analyses. According to POWSIM, the reduced data set of 13 loci displayed  
218 the same statistical power as the original set of 19 loci ( $F_{ST} = 0.002$ ,  $\beta = 1$ ). Neither the heterozygosity  
219 ( $H_o = 0.50-0.57$ ), the allelic richness (4.38-4.82), nor the number of private alleles (0-2) showed major  
220 differences among population samples. Multi-locus  $F_{IS}$  estimates per population, using 13 microsatellites,  
221 ranged from 0 for BSB-2016 and BSB-2012 to 0.08 for BOB-2004. After multiple testing corrections 11  
222 samples showed significant heterozygote deficiencies ( $F_{IS} = 0.01-0.08$ , p-value < 0.05). [After post-  
223 filtering and quality control, the data set comprised 895 individuals from 20 sampling sites genotyped at 13  
224 microsatellites.](#)

### 225 *Population genetic structure*

226 The global  $F_{ST}$  estimate was low but significant ( $F_{ST} = 0.0013$ , p-value  $\equiv 0.02$ ). Pairwise  
227  $F_{ST}$  ranged from 0 to 0.013 (Figure 2). Before FDR correction, the highest proportions of significant  
228 pairwise  $F_{ST}$  were found between samples of the south-west England area (FAL and PLY, except for SAL  
229 and WLB, the two eastern samples) and samples of the WEC and EEC ( $F_{ST} = 0.005-0.009$ , p-value <  
230 0.05). Significant pairwise  $F_{ST}$  estimates were also observed between two Eastern English Channel  
231 samples (BOS 2012, BOS 2015) and two samples of the Western English Channel (MOR and BSB 2004)  
232 ( $F_{ST} = 0.006-0.011$ , p-value < 0.05) ([Supplementary Material Figure 1](#)). Comparison of the Bay of Brest

233 (BOB 2004, BOB 2015) with EEC samples (BOS 2012, BAS 2016) also showed significant values ( $F_{ST}$  =  
234 0.007-0.008,  $p$ -value  $< 0.05$ ) (Figure 2). After FDR correction, two pairwise  $F_{ST}$  remained significant  
235 (MOR/GRA/MOR ( $F_{ST}$  = 0.0108,  $p$ -value  $\leq 0.003 < 0.01$ ) and FAL/GRA ( $F_{ST}$  = 0.0084,  $p$ -value  $\leq$   
236 0.008  $< 0.01$ ). Populations belonging to the same groups did not show any significant differentiation, except  
237 in the western English Channel for GRA/MOR ( $F_{ST}$  = 0.01,  $p$ -value  $\leq 0.003$ ).

238 ——— The db-RDA showed that the four groups defined by Nicolle et al. (2016): “BOB”, “WEC”,  
239 “SWE” and “EEC”, explained a weak but significant proportion (db-RDA, adjusted  $R^2 = 0.0646$ ,  $p =$   
240  $< 0.0054$ ) of the variability of the pairwise  $F_{ST}$ . The main differences, materialized along the first db-RDA  
241 axis ( $p = 0.009 < 0.004$ ), were found between ECC and SWE on one side and WEC and BOB on the other  
242 side. The sSecond axis (non-significant) distinguished samples from SWE and BOB from those of ECC and  
243 WEC (Figure 3.a). Moreover, the geographic coordinates of the samples also explained a significant fraction  
244 (RDA, adjusted  $R^2 = 0.046$ ,  $p = < 0.0044$ ) of the variance of the Hellinger-transformed genotype. Only the  
245 first RDA axis was significant ( $p = < 0.0054$ ) and underlined a gradient from the South-wWestern English  
246 coast to the French coast line. The Bay of Brest and Morlaix appeared in the middle of this gradient (Figure  
247 3.b).

248 The patterns of genetic differentiation displayed some temporal variability that is particularly  
249 obvious when comparing temporal replicates in BOS and BSB. For instance, when considering pairwise  
250  $F_{ST}$  before FDR correction, BOS-2015 appeared different from PLY, contrary to BOS-2012, that appeared  
251 different from BOB-2015, BOB-2004, BSB-2004. The same observation applies to BSB samples, BSB-2004  
252 being the only BSB sample that presented significant  $F_{ST}$  estimate with FAL and BOS-2012. Sample of  
253 2004 for BSB and BOB appeared clearly differentiated in the pairwise  $F_{ST}$  matrix (Supplementary Material  
254 Figure 1).

### 255 *Simulated genetic structure*

256 After 4000 simulated years, the global  $F_{ST}$  value ( $F_{ST} = 0.0012$ ) did not reach equilibrium and  
257 was comparable to the global  $F_{ST}$  observed in the empirical data set (Figure 4, black solid line). The

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258 absence of equilibrium was driven by the Bay of Brest population, which is isolated from the others. When  
259 excluding the Bay of Brest, SWE reached a migration-drift equilibrium ( $F_{ST} = 0.0003$ , Figure 4, grey  
260 dashed line) and EC nearly stabilized ( $F_{ST} = 0.0003$ , Figure 4, grey solid line) at 4000 years. Simulated  
261 pairwise  $F_{ST}$  values among all populations were low and ranged from 0 to 0.005 (Figure 4). The Bay of  
262 Brest population was the most differentiated when compared to all other samples because of its relatively  
263 low population size and the assumed partial isolation of the Bay of Brest (mean pairwise  $F_{ST} = 0.004$ ).  
264 Mean pairwise  $F_{ST}$  values were higher between groups (SWE vs WEC:  $6.10^{-4}$ , SWE vs the EEC:  $4.5.10^{-4}$ ,  
265 and WEC vs ECC:  $2.10^{-4}$ ) than within groups ( $2.10^{-5} < \text{mean pairwise } F_{ST} < 10^{-4}$ ) (Figure 4). Besides the  
266 Bay of Brest, SWE showed the highest mean pairwise  $F_{ST}$  value. Simulated genetic differentiation  
267 between WEC and ECC were the lowest and were of the same order of magnitude as the mean pairwise  
268  $F_{ST}$  found within the WEC. The Morlaix sample appeared as the most genetically differentiated in the  
269 WEC. Procruste analysis between empirical and simulated pairwise  $F_{ST}$  matrix was not significant (p-  
270 value=0.52), meaning that patterns of empirical and simulated genetic differences were not similar.

## 271 Discussion

272 At the European scale, a clear genetic structure was reported between *P. maximus* samples  
273 from north Norway to Galicia; the Norwegian populations being differentiated from the other  
274 Atlantic populations (Morvezen, Charrier, et al., 2016, Vendrami et al., 2019). At the scale of the British  
275 Isles, no significant genetic structure has previously been detected regardless of the genetic markers  
276 employed (i.e. allozymes, mtDNA, microsatellite markers, SNPs) (Beaumont, Morvan, Huelvan, Lucas,  
277 & Ansell, 1993; Morvezen, Charrier, et al., 2016; Vendrami et al., 2017; Wilding, Beaumont, & Latchford,  
278 1999), apart in the Mulroy Bay (North of Ireland), suggesting that *P. maximus* forms a single panmictic  
279 population. Specific genetic differentiation of Mulroy Bay could results of restricted gene flow interactions  
280 with other populations associated to important restocking plan (Vendrami et al., 2019). Yet, at least two  
281 genetically differentiated groups of populations have been suspected in the EC using microsatellites  
282 (Szostek, 2015): one group including fishing grounds from Falmouth Bay to the Sussex coast, and a second  
283 group isolating the Cornwall and the Bay of Seine from the rest of the EC. The present study, which  
284 combined empirical genetic data and gene flow modelling based on previously published results of larval

285 dispersal and connectivity (Nicolle et al., 2016) led to the detection of a low but significant population  
286 genetic differentiation within the EC, and revealed different population structure patterns compared to those  
287 previously reported (Morvezen, Charrier, et al., 2016; Szostek, 2015).

### 288 *Population genetic structure*

289 Weak genetic differentiation within the EC was observed between the South-west  
290 England (SWE) coast and the rest of the EC, as underlined by pairwise  $F_{ST}$  estimates and the results of the  
291 RDA. This result is congruent with the larval dispersal model in this area (Nicolle et al., 2016) which showed  
292 a lack of larval connectivity between SWE and the rest of the EC. The same pattern was depicted for the  
293 brittlestar *Ophiothrix fragilis* in the EC (Lefebvre, Ellien, Davoult, Thiébaud, & Salomon, 2003). In  
294 particular, higher pairwise  $F_{ST}$  values estimated in the present study were observed between SWE samples  
295 located west of Start Point (FAL, PLY) and EC samples, in comparison to the samples east of Start Point  
296 (SAL, WLB) that were less differentiated from EC samples. This structure may be due to a reduction of gene  
297 flow on both side of Start Point induced by hydrodynamic features as  
298 suggested for blue mussels *Mytilus sp.* (Gilg & Hiblish, 2003). However no clear identification of genetic  
299 structure on both side of Start Point was observed in the present empirical genetic structure and the sampling  
300 design did not allow to explore this potential barrier to gene flow. Furthermore, simulated genetic structure  
301 was not observed in this area which could be  
302 explained by three hypotheses: (i) an incorrect  
303 estimation of population size leading to an over-representation of populations east of Start Point, (ii) the non-  
304 inclusion of populations from North Cornwall in simulations that could affect genetic diversity of samples  
305 between Land's End and Start Point, and (iii) a limitation of the biophysical model to properly simulate  
306 larval dispersal due to the complex nearshore hydrodynamics. The low empirical genetic differentiation  
307 observed between samples located east of Start Point and EEC is likely due to gene flow between  
308 these two areas but also probably to high  $N_e$ . Furthermore, genetic differentiation between western Start  
309 Point and EEC could results of an isolation by distance pattern As reported by Nicolle et al.,

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310 (2016), small populations of scallop along the southern English coast not considered as major spawning  
311 grounds could behave as relay populations and contribute to larval connectivity gene flow between SWE and  
312 EEC. Szostek (2015) also suggested that larvae could be easterly-advected eastwards from Lyme Bay to  
313 EEC. Remarkably, it appears that even in a species with a high potential for larval dispersal and that which  
314 displays recent divergence times (i.e since the last glacial maximum) (Vendrami et al., 2019), a weak fine  
315 scale genetic differentiation between west Start Point and the rest of the EC can be identified with refined  
316 sampling performed in this study. West Start Point appeared as a reproductive independent unit and could be  
317 considered as a management unit in the UK management policy.

318 The tip of Brittany is known to act as a barrier to larval dispersal (Ayata, Lazure, & ThiéBaut, 2010)  
319 and many marine species with a larval dispersal phase are genetically structured both sides of this region  
320 (Couceiro, Robuchon, Destombe, & Valero, 2013; Jolly, Viard, Gentil, ThiéBaut, & Jollivet, 2006). The  
321 isolation between scallops from the BOB and those from the EC is supported by simulations conducted in the  
322 present study on the basis of simulations of the larval dispersal (Nicolle et al., 2016), as well as by previous  
323 empirical population genetic data (Morvezen, Charrier, et al., 2016). In Morvezen, Charrier, et al. (2016), the  
324 Bay of Brest was significantly differentiated from both the Bay of Saint Brieuc ( $F_{ST} = 0.0061$ , p-value <  
325 0.05) and the Bay of Seine ( $F_{ST} = 0.009$ , p-value < 0.001). However, the empirical data collected in the  
326 present study did not show any significant genetic differentiation between the Bay of Brest and the Bay of  
327 Saint Brieuc or the Bay of Seine after FDR correction. However, Furthermore, relatively high  $F_{ST}$  estimates  
328 [ $F_{ST} = 0.003 - 0.008$ ] were recorded between BOB and the EEC. Refined sampling near the tip of Brittany  
329 associated with fine scale larval dispersal modelling are needed to better understand the possible barriers to  
330 larval connectivity that may isolate the Bay of Brest from the Ushant Sea and the Western English Channel.

331 According to empirical genetic data, pairwise  $F_{ST}$  comparisons suggested only a weak genetic  
332 structure along the French coast of the EC, between the Western and the Eastern basins supported mainly by  
333 MOR and GRA, and underlined by the db-RDA highlighting a weak significant structure between the  
334 WEC and EEC. WEC and EEC are considered as two different systems in terms of biotic and abiotic  
335 characteristics (Dauvin, 2012).

336 Significant genetic structure was reported for the slipper limpet *Crepidula fornicata* between both sides of  
337 Significant genetic structure was reported for the slipper

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338 limpet *Crepidula fornicata* between both sides of the Cotentin Peninsula (Dupont, Ellien, & Viard, 2007).  
339 Even if the Cotentin Peninsula behaves as a physical barrier limiting larval dispersal in *P. maximus* (Nicolle  
340 et al., 2013, 2016), low genetic drift due to high effective population sizes could increase the time needed for  
341 genetic divergence between WEC and EEC and maintain the two sites far from a migration-drift equilibrium.

342 In addition, demo-genetic simulations revealed that even when an equilibrium is nearly reached, pairwise  
343  $F_{ST}$  remained low in comparison to SWE genetic differentiation. However, the magnitude of  $F_{ST}$   
344 should be interpreted carefully due to potential overestimation of the number of breeders implemented in the  
345 simulations and the uncertainty linked to initial allele frequencies.

346 In the WEC, the presence of important permanent gyres, in the Normano-Breton Gulf region, could  
347 largely affect larval transport, with gyres induced by capes acting as larval retention systems while gyres  
348 around islands acting as dissemination systems (Ménesguen & Gohin, 2006). Larval connectivity is then  
349 expected to be important within the Normano-Breton Gulf and, for instance, no genetic structure was  
350 detected for the slipper limpet *Crepidula fornicata* (Viard, Ellien, & Dupont, 2006). Conversely, the presence  
351 of retention zones generated by shoals and gyres around capes (Ménesguen & Gohin, 2006) could contribute  
352 to isolate the Normano-Breton Gulf from the rest of the WEC so that the significant genetic differentiation  
353 between the two most distant samples of the WEC (Morlaix vs. Granville) (Supplementary Material Figure  
354 1) may be due to reduced gene flow between extreme western and eastern part of the WEC. Even if panmixia  
355 seems to have been reached in WEC, deficit in heterozygotes observed for certain samples could underlined  
356 consanguinity favoured by incomplete panmixia during reproduction. As underlined by demo-genetic  
357 modelling, MOR appeared slightly genetically differentiated from other samples in the Normano Breton  
358 Gulf. Convergence of empirical and simulated genetic structure, stressed the possible genetics isolation of  
359 the Bay of Morlaix from closer fishing grounds.

360 In the EEC, the Bay of Seine did not appear differentiated from the other samples located in the  
361 EEC, neither with empirical or simulated data, in contrast to the results reported by Szostek (2015). Although  
362 the Bay of Seine has a mean retention rate of around 50% for *P. maximus*, larvae can disperse to the central  
363 EEC or eastward through the coastal river, with the magnitude of larval export depending on the  
364 hydroclimatic conditions, particularly wind (Nicolle et al., 2013, 2016). Similarly cross-channel gene flow  
365 and larval dispersal within the EEC were observed for the polychaete *Pectinaria koreni* with *in situ*

366 observations (Lagadeuc, 1992), larval dispersal modelling (Ellien, Thiébaud, Dumas, Salomon, & Nival,  
367 2004) or population genetic studies (Jolly et al., 2009).

### 368 **Temporal genetic variation**

369 Various sources of errors, such as genotyping errors, non-random sampling and varying alleles  
370 frequencies between cohorts could provide confounding results in a context of weak structuring (Knutsen et  
371 al., 2011; Waples, 1998). As ~~reported~~ ~~noticed~~ by Knutsen et al. (2011), even if samples do belong to the same  
372 panmictic unit, sampling different families could lead to undefined genetic structure that could affect the  
373 spatial signal of genetic differentiation. Therefore, assessing the temporal stability of genetic structure  
374 patterns by temporally replicating samples is of major importance to identify population units that are  
375 biologically meaningful (Dannewitz et al., 2005; Reiss et al., 2009). Comparisons of temporal replicates  
376 within the same site (BOB, BSB or BOS) did not show any significant differentiation. However,  
377 ~~comparisons of the~~ temporal replicates ~~of one location~~ from BOB, BSB and BOS, and particularly BOB-2004  
378 ~~and BSB-2004, displayed to other samples revealed some~~ temporal variability in spatial structuring patterns  
379 (eg BSB-2004/FAL:  $F_{ST} = 0.01$ ; BSB-2012/FAL:  $F_{ST} = 0.0004$ ; BSB-2016/FAL:  $F_{ST} = 0.004$ ). –Temporal  
380 genetic variability across cohorts is observed in many species of marine invertebrates (Calderón, Pita,  
381 Brusciotti, Palacín, & Turon, 2012; Jolly, Thiébaud, Guyard, Gentil, & Jollivet, 2014). Marine invertebrates  
382 can display unstructured genetic variability at small spatio-temporal scale, a pattern known as chaotic genetic  
383 patchiness (CGP) (Hedgcock & Pudovkin, 2011). Chaotic Genetic Patchiness can results from a strong  
384 variance in reproductive success (sweepstake hypotheses; Hedgcock & Pudovkin, 2011) ~~associated to~~ ~~and/or~~  
385 collective larval dispersal (Broquet, Viard, & Yearsley, 2013). The sampling scheme used in the present study  
386 does not allow to draw ~~any firm~~ conclusions about possible CGP in *P. maximus*. However, simulations of  
387 larval dispersal suggest that temporal fluctuations in hydrodynamic conditions during the scallop spawning  
388 period may result the settlement of larval pools of different origins in the same area which could contribute  
389 to CGP (Nicolle et al., 2013, 2016). ~~Finally, empirical and simulated genetic structure could results of~~  
390 ~~difficulty to estimated empirical weak genetic structure given multiple bias associated to sampling (Waples,~~  
391 ~~1998).~~

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392

### 393 **Implications for fisheries management.**

394 Results presented here provide novel information about the genetic structure of great scallop  
395 populations in the EC. In the  
396 presence of migration-drift disequilibrium, obtaining a clear delineation of populations through the  
397 evolutionary paradigm appears particularly subtle and challenging (Waples & Gaggiotti, 2006). While the  
398 identification of genetic stocks is crucial for the sustainable management of exploited species (Carvalho &  
399 Hauser, 1994), it seems important in a management context to make the distinction between gene flow and  
400 larval dispersal, i.e. between genetic and demographic connectivity. The lack of strong genetic differentiation  
401 depicted by both empirical and simulated data between the WEC and the EEC seems to result from  
402 few gene flow across the EC sufficient to homogenize genetic structure and/or low genetic  
403 drift combined with recent divergence. However, it is unlikely that the number of effective migrants  
404 contributing to the genetic homogeneity is enough to maintain demographic connectivity between  
405 the EEC and WEC (*sensu* Lowe & Allendorf (2010)). The genetic modelling shows that *P. maximus* genetic  
406 structure can be weak even if populations are completely isolated for several thousand years: the pairwise  
407  $F_{ST}$  between SWE and the EC sites are low (0.0004 – 0.001). The signal of weak genetic differentiation,  
408 through empirical and simulations results, could therefore suggest a complete isolation of scallop beds  
409 between the south-western coast of England and French coastline. It would be relevant to assess a genetic  
410 differentiation threshold for which demographically independent management units can be predicted as  
411 proposed by Palsboll, Berube, & Allendorf (2007). However, in the present study, the application of such  
412 threshold for the delimitation of management units was hampered by the uncertainty in the magnitude of  
413 simulated  $F_{ST}$ . Even if incertitude remained regarding precise  $F_{ST}$  values, demo-genetic modelling clearly  
414 illustrated that weak neutral genetic structure could be observed between main fishing grounds at fine scale,  
415 particularly on the northern Brittany coast. For instance, Morlaix appeared isolated in terms of gene flow and  
416 larval dispersal, underlining the need of rigorous management in order to maintain local fisheries and genetic  
417 diversity of this fishing grounds. Coupling a bio-physical and genetic model to an empirical genetic data set  
418 is a promising approach (Foster et al., 2012), as it could help defining sampling strategies for population

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419 genetic studies but also set up management strategies among fishing grounds for which strong assumption of  
420 demographic and genetic isolation exist. Nevertheless, but challenging issues remain to be addressed, such as  
421 the implementation of realistic biological parameters in demo-genetic modelling.

422 Finally, recent studies emphasized the existence of local adaptation among marine species having  
423 high dispersive life stage (Conover et al., 2006, Sanford and Kelly, 2011). Adaptive origins of phenotypic  
424 variation should be of primary interest in a context of management and enhancement. -Among *P. maximus*  
425 fishing grounds in the EC were observed -

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## 426 **Conclusion and perspectives**

427 Multidisciplinary approaches are crucial to assess population delineation in a context of low  
428 and chaotic genetic structure. By coupling bio-physical and genetic modelling approaches and empirical  
429 genetic data obtained from an extensive spatio-temporal sampling, the genetic differentiation of the *P.*  
430 *maximus* populations located along the South-western coast of England was explored, and  
431 weak genetic differentiation were assumed for the Bay of Brest, and between WEC  
432 and EEC. Nevertheless, temporal variability should be further explored, and the hypothesis of chaotic genetic  
433 patchiness should be investigated. A hierarchical sampling among cohorts across multiple years would be  
434 particularly relevant to address the effect of inter-annual genetic variability in a context of weak genetic  
435 structure (see for example (Morvezen, Boudry, Laroche, & Charrier, 2016), in the context of *P. maximus*  
436 population enhancement). Finally, local adaptation processes among main fishing grounds of the EC should  
437 be investigated, given phenotype variation for which genetic determinism is assumed.  
438 Future fine scale population genetic studies dealing with stock management and combining multiple  
439 Future fine scale population genetic studies dealing with stock management and combining multiple  
440 approaches appeared necessary for future management support.

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449 Roscoff and Falfish.

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### Tables

Table 1: List of the population samples analysed in the present study with sampling number reference on figure 1, sampling name, sampling code and geographic regions precised as following SWE: south western English coast, BOB: Bay of Brest, WEC: western English Channel, EEC: eastern English Channel. Year refers to the sampling year and Analysed ind refers to the number of analysed individual per population. Diversity index presented are computed among 13 loci retained after quality control. Ar: Allelic richness based on minimum sample size of 8 individuals (PmNH23 being discarded from the dataset for Ar). Ho: observed heterozygosities. *Fis* estimates (Bold values = significance tested with 10,000 permutations: \* p-value < 0.05, \*\* p-value < 0.01, \*\*\* p-value < 0.001 after multiple testing correction).

Sampling Number	Sampling name	Sampling code	Geographic Region	Year	Analysed ind	Ar	Ho	Fis
1	Falmouth	FAL	SWE	2016	48	4,65	0,54	0,03
2	Plymouth	PLY	SWE	2004	29	4,38	0,50	<b>0,06*</b>
3	Salcombe	SAL	SWE	2017	42	4,54	0,54	-0,02
4	West Lyme Bay	WLB	SWE	2017	12	4,40	0,51	0,02
5	Bay of Brest	BOB-2015	BOB	2015	46	4,58	0,54	<b>0,05*</b>
6	Bay of Brest	BOB-2004	BOB	2004	23	4,43	0,50	<b>0,08***</b>
7	Camaret	CAM	BOB	2016	45	4,66	0,54	0,04
8	Morlaix	MOR	WEC	2016	46	4,57	0,53	<b>0,05***</b>
9	Bay of Saint Brieuc	BSB-2016	WEC	2016	47	4,72	0,57	0,00
10	Bay of Saint Brieuc	BSB-2012	WEC	2012	47	4,72	0,55	0,00
11	Bay of Saint Brieuc	BSB-2004	WEC	2004	20	4,55	0,55	<b>0,04*</b>
12	Granville	GRA	WEC	2017	41	4,53	0,51	<b>0,04***</b>
13	North Cotentin Peninsula	NCP	EEC	2016	48	4,59	0,55	<b>0,01*</b>
14	Bay of Seine	BOS-2015	EEC	2015	45	4,59	0,52	<b>0,05***</b>
15	Bay of Seine	BOS-2012	EEC	2012	47	4,82	0,55	0,02
16	Bay of Seine	BOS-2004	EEC	2004	33	4,54	0,55	-0,01
17	Dieppe	DIE	EEC	2016	46	4,68	0,55	0,01
18	Bassurelles	BAS-2016	EEC	2016	94	4,55	0,53	<b>0,04***</b>
19	Bassurelles	BAS-2017	EEC	2017	89	4,65	0,53	<b>0,06***</b>
20	Eastern English Channel	ECH	EEC	2017	47	4,66	0,54	<b>0,03***</b>



### Figures Legends

Figure 1: Sampling map, 1 (FAL), 2 (PLY), 3 (SAL), 4 (WLB), 5 (BOB-2015), 6 (BOB-2004), 7 (CAM), 8 (MOR), 9 (BSB-2016), 10 (BSB-2012), 11 (BSB-2004), 12 (GRA), 13 (NCP), 14 (BOS-2015), 15 (BOS-2012), 16 (BOS-2004), 17 (DIE), 18 (BAS-2016), 19 (BAS-2017), 20 (ECH). ~~Samples 1 to 4: south western coast of England. Samples 5 to 7: Bay of Brest. Samples 9 to 12: Normano-Breton Gulf. Samples 13 to 20: eastern English Channel.~~ Scallop symbols represent each sampling site included in the population genetics modeling, and their size is proportional to the population size assumed in the simulations (cf  $K_0$  supplementary material table 2). Shade of grey corresponds to local retention rate and links between nodes correspond to larval dispersal (Nicolle et al., 2016). ~~Letters correspond to metapopulation groups defined by Nicoll et al. (2016): A (sout western coast of England: samples 1 to 4), B (eastern English Channel: samples 13 to 20), C (Normano-Breton Gulf : samples 9 to 12) and D (the Bay of Brest: samples 5 to 7)~~

Figure 2: Above the diagonal: estimated pairwise  $F_{ST}$ , with significance tested using 10,000 permutations (\* $p < 0.05$ , \*\* $p < 0.01$  before FDR correction). Under the diagonal: p-values \* $p < 0.05$  after FDR correction. Negatives values are set to 0.

Figure 3: (a) Plot of the db-RDA on  $F_{ST}$  matrix using geographic regions (EEC: eastern English Channel, WEC: western English Channel, BOB: Bay of Brest, SWE: south western England) as explanatory variable and using Cailliez's method (\*\* $p = < 0.0049$ ), global adjust  $R^2 = 0.064$ . (b) Scores of samples on the axis 1 of the RDA ( $p = < 0.0054$ ) constrained by the spatial coordinates of the populations (latitude and longitude) response variables are allele abundances with Hellinger transformation. Global adjust  $R^2 = 0.046$ .

Figure 4: Pairwise  $F_{ST}$  simulated with MetaPopGen for each population used in genetic modeling (the Bay of Brest exhibited values ranging from 0.003 to 0.005, with a mean of 0.004. These high values were therefore not represented to facilitate readability). Black sample are shared between empirical and simulated sampling, grey samples are only present in simulated sampling. SWE: south western English coast. WEC: western English Channel. EEC: eastern English Channel. In the bottom-right corner: Evolution across time of global mean  $F_{ST}$ . Black-solid-line: all samples, Grey-dashed-line: all SWE samples and Grey-solid-line: all samples (SWE and Bay of Brest samples excluded).

### **Supplementary material**

The following supplementary material contains information about : (i) loci used in the present study (table 1), [\(ii\) genetic diversity per loci and per sample \(table2\)](#) and (iii) biological parameters implemented in genetic modeling (table [32](#), table [43](#)).

**Supplementary material table 1:** List of loci dispatched in three panels, with their assigned fluorochrome and primer sequences. Range of sizes: range of observed alleles. Pig-tail: whether a Pig-tail was used or not (No effect of Pig tail on stuttering was observed for PmNH73 and List15-008b). Tm: melting temperature, assessed according to Marmur & Doty (1962). Cycles: Number of PCR cycles applied. [R]: Reverse concentration of the reverse primer, [MgCl<sub>2</sub>]: MgCl<sub>2</sub> concentration in the PCR.

Locus	Panel	Fluorochrome	Primers	range of sizes	Pig tail	Tm	Cycles	[R]	MgCl2
PmRM002	P1	PET	F: GTGACAATGTGTCCACCTGC R: CGTCGAGGGAAAAGTGAAGT	79-175	Yes	57,3	35	0,2	1,5
PmNH59	P1	YY	F:CGAAGGTTGTGCTGTGAATC R:CCAGCAATGACATCCGATCG	260-300	Yes	57,9	35	0,2	1,5
PmNH60	P1	FAM	F:TTGTACAAATGCTGGCGTGG R:TCTACTCTGGCAGATCATGGG	175-216	Yes	55,9	35	0,2	1,5
PmNH62	P1	PET	F:GGGACCACTGTAAACAATGTG R:GGTGACAGTCGACCATTTC	240-290	No	57,9	35	0,2	1,5
PmNH70	P1	YY	F:AGTTGTGCTATTGAATGGGAAC R:ATGCACTGCTTGTCCAATTC	114-162	Yes	56,5	45	0,2	2
PmNH73	P1	DO	F:CATAGCGATGCAGGACAAGG R:ATCCAATGTCTGCCGTCTG	203-253	Yes	57,3	40	0,2	1,5
PmNH11	P2	FAM	F: GCCATGTCGGAAATCACC R: CAAACGGCCCAAGTCTACG	289-321	No	58,8	45	0,2	2
PmNH23	P2	YY	F:AAATGCCCTCAGCTTTTACG R:ACTGTACAAATCGGCCACG	238-283	No	54,5	40	0,2	2
LIST15-013	P2	M-13 Black	F:AATGATTTTCGTCTGTCCG R:AAATATCTCAACAAGCGACC	259-523	No	52,4	40	0,2	2
PmGC05	P2	PET	F: AATTGTACTTCAATCATAAACTGAG R: ACAGTAATCTAGGAAACACAATG	200-280	Yes	55,3	35	0,2	2
PmRM053	P2	PET	F: CCTTGTGACATGACGCTCTG R: GGAACGCAACCGATTAGAAG	151-179	No	57,3	35	0,2	1,5
PmRM057	P2	DO	F: GGGCTCATTGTGCGATAGT R: ATGGTTAGGTGAGACGCCAT	120-192	No	57,3	35	0,2	1,5
PmRM072	P2	FAM	F: GGCATTGCAGAGACCTATCC R: TCAATCGATCGCTAATCACTACA	102-158	Yes	57,1	35	0,2	2
LIST15-004	P3	M-13 Black	F:TCCCTTTGATTGAGGTTTGTG R:ATGATTTGGAATCGGCTTTG	310-350	No	53,2	35	0,2	2
LIST15-005	P3	PET	F:CAATAGTTCGTTGAGCGGG R:CTCTTGGATGCTTGTGAGGG	260-329	Yes	59,4	35	0,1	1,5
LIST15-008b	P3	M-13 Blue	F:CTCTCACTTCCACTGTTGACC R:TGTTAGCACATTTTCTCCCG	175-295	Yes	57,3	35	0,1	1,5
LIST15-012	P3	M-13 Black	F:CCTTACACACTACCTCC R:TTTGGGGCGACATACTGC	180-250	No	58,8	35	0,2	1,5
PmRM020	P3	FAM	F: CCCTATTGGATGTCTTACGCA R: CCGATGAGATGTTCGTGT	122-169	Yes	57,3	35	0,1	1,5
PmRM036	P3	YY	F: CTGCTTGTATCAAAAAC R: TCGAATACGCCCATATGATTC	285-328	Yes	52,4	35	0,2	1,5

**Supplementary material table 2:** Table of parameters of genetic diversity per locus and per population. Np: Number of private alleles, Ar: Allelic richness based on minimum sample size of 8 individuals (PmNH23 being discarded from the dataset for Ar), expected (Hexp) and observed (Hobs) heterozygosities,  $F_{IS}$  estimates (Bold values = significance tested with 10,000 permutations: \* p-value < 0.05,\*\* p-value <0.01, \*\*\* p-value<0.001 after multiple testing correction). Multi-locus: Multilocus diversity parameters without the six discarded loci.





Supplementary material table 43: Details of estimation for effective fecundity.

Biological traits	Mean value	References
Potential fecundity	21. 10 <sup>6</sup>	Paulet and Fifas, 1989
Fertilization rate	0.25	Eckman, 1996
Hatching rate	0.25	Paulet et al., 1992
rate of mortality	0.25	Rumrill, 1990
Planktonic larval duration	30 days	Nicolle <i>et al.</i> , 2013
Survival of recruits	0.1	Thorson 1960
Number of recruits (effective fecundity) = 21. 10 <sup>6</sup> x 0.25 x 0.25 x exp(-0.25x30) x 0.1 = 72.6		

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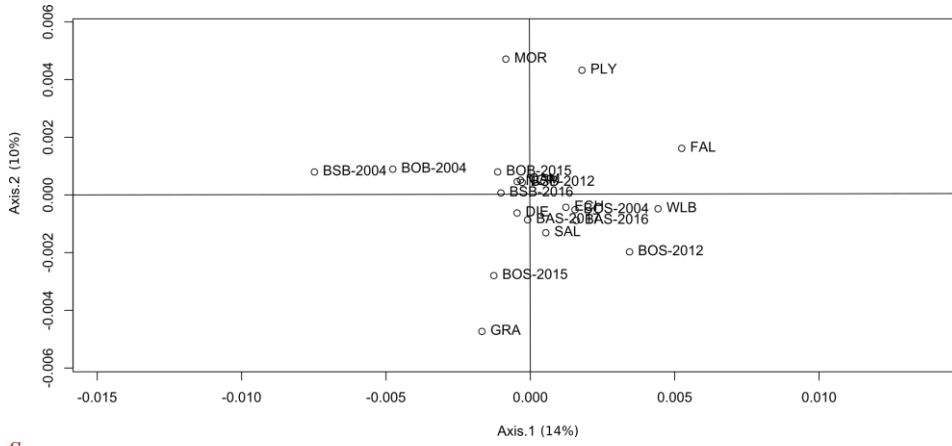
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