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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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.

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

Introduction

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

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

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

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

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

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

Material and Methods

Sampling

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

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Microsatellite genotyping

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

~~Cetyltrimethylammonium bromide (~~of CTAB~~)~~, 1% Polyvynilpyrolidone (PVP), 1.4 M of NaCl, 0.2 M of β-Mercaptoethanol, 100 mM of Tris-HCl pH=8, and 3.75 µl of Proteinase K (20mg.ml^{-1}). DNA was purified by the addition of one volume of Chloroform Isoamyl Alcohol 24:1 and the aqueous phase was collected after 15 min of centrifugation at 4°C and 13000 rpm. This step was performed twice. Then, DNA was precipitated with 0.6 volume of isopropanol and centrifuged 30 min at 4°C and 13000 rpm. Pellets of DNA were washed twice with 75% of ethanol, centrifuged at 4°C and 13000 rpm during 5 min and suspended in 100 µl of MilliQ water. DNA concentration was measured with a NanoDrop 8000 spectrophotometer (Thermo Scientific). Finally, all DNA samples were diluted to reach a concentration around 20 µg.µl^{-1}.

Nineteen microsatellite markers were successfully amplified and optimized out of 23 previously published loci (Charrier, Morvezen, Calves, & Laroche, 2012; Morvezen, Cornette, et al., 2013; Szostek, 2015; Watts et al., 2005). The forward primer of each locus was tailed with a universal primer to reduce the genotyping costs (Schuelke, 2000). Four different universal primers were used, each of them labelled with a fluorescent dye (Supplementary material table 1). Moreover, a PIG-tail (5'-GTTTCTT) was added to the 5' -end of reverse primer to avoid genotyping errors due to excessive stutter peaks when needed (Brownstein, Carpten, & Smith, 1996). Each locus was amplified in a simplex polymerase chain reaction (PCR) in 10 µl volume containing 1X green Go Taq flexi buffer (Promega), 1.5-2.0 mM $MgCl_2$, 0.2 µM each dNTP, 0.2 µM universal primer (fluorescent), 0.2 µM reverse primer, 0.02 µM forward primer, 0.25 U Go Taq Flexi DNA Polymerase (Promega), and 1 µL DNA template. PCRs were performed on a Thermocycler GeneAmp 9700 (Applied Biosystem). A touchdown procedure was included in the thermal cycling regime to increase the stringency of the PCRs and, for each locus, annealing temperatures were set up according to the melting temperature of the primer pair (T_m) and the tailed universal primer (T_{mU}): (94°C for 3 min, Tm+2°C for 2 min, 72°C for 30 sec) x1, (94 °C for 30 sec, Tm + 1°C for 30 sec [-1°C per cycle until T_{mU}-3°C], 72°C for 30 sec) x 2-9 cycles, (94°C for 30 sec, Tmu -3°C for 30 sec and 72°C for 30 sec) x 35-40 cycles, 72°C for 5 min. Melting temperatures T_m and T_{mU} were calculated according to Marmur ~~& ~~and Doty (1962). The number of total cycles was adjusted between 35 and 45 cycles according to each locus (Supplementary M~~m~~aterial T~~t~~able 1).

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

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

Data analysis

Within population diversity and marker quality

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

Population genetic structure

Global and pairwise population genetic differentiation were evaluated by estimating the Wright's statistics (F_{ST}) using the θ 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., 2018). 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

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

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

Results

Within-population genetic diversity

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

Population genetic structure

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

(BOB 2004, BOB 2015) with EEC samples (BOS 2012, BAS 2016) also showed significant values (~~*Fst*~~F_{ST} = 0.007-0.008, p-value < 0.05) (Figure 2). After FDR correction, two pairwise ~~*Fst*~~F_{ST} remained significant (~~MOR/~~GRA/MOR (~~*Fst*~~F_{ST} = 0.01~~08~~, p-value = 0.003~~< 0.01~~) and FAL/GRA (~~*Fst*~~F_{ST} = 0.00~~81~~, p-value = 0.008~~< 0.01~~). Populations belonging to the same groups did not show any significant differentiation, except in the western English Channel for GRA/MOR (~~*Fst*~~F_{ST} = 0.01, p-value ~~<~~= 0.00~~1~~3).

~~———~~The db-RDA showed that the four groups defined by Nicolle et al. (2016): "BOB", "WEC", "SWE" and "EEC", explained a weak but significant proportion (db-RDA, adjusted R^2 ~~=~~0.064~~6.4%~~, p = ~~<~~0.005~~1~~) of the variability of the pairwise ~~*Fst*~~F_{ST}. The main differences, materialized along the first db-RDA axis (p = 0.009~~<0.001~~), were found between ECC and SWE on one side and WEC and BOB on the other side. The s~~S~~econd axis (non-significant) distinguished samples from SWE and BOB from those of ECC and WEC (F~~f~~igure 3.a). Moreover, the geographic coordinates of the samples also explained a significant fraction (RDA, adjusted R^2 = 0.04~~.6%~~, p = ~~<~~0.004~~1~~) of the variance of the Hellinger-transformed genotype. Only the first RDA axis was significant (p =~~<~~ 0.005~~1~~) and underlined a gradient from the South-w~~W~~estern English coast to the French coast line. The Bay of Brest and Morlaix appeared in the middle of this gradient (Figure 3.b).

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

Simulated genetic structure

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

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

Discussion

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

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

Population genetic structure

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

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

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

According to empirical genetic data, pairwise F_{ST} comparisons suggested only a weak genetic structure along the French coast of the EC, between the Western and the Eastern basins supported mainly by MOR and GRA, and underlined by the db-RDA highlighting a weak significant structure between the WEC and EEC. WEC and EEC are considered as two differents systems in terms of biotic and abiotic characteristics (Dauvin, 2012). Significant genetic structure was reported for the slipper limpet *Crepidula fornicata* between both sides of Significant genetic structure was reported for the slipper

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limpet *Crepidula fornicata* between both sides of the Cotentin Peninsula (Dupont, Ellien, & Viard, 2007). Even if the Cotentin Peninsula behaves as a physical barrier limiting larval dispersal in *P. maximus* (Nicolle et al., 2013, 2016), low genetic drift due to high effective population sizes could increase the time needed for genetic divergence between WEC and EEC and maintain the two sites far from a migration-drift equilibrium. In addition, demo-genetic simulations revealed that even when an equilibrium is nearly reached, pairwise ~~*Fst*~~F_{ST} remained low in comparison to SWE genetic differentiation. However, the magnitude of ~~*Fst*~~F_{ST} should be interpreted carefully due to potential overestimation of the number of breeders implemented in the simulations and the uncertainty linked to initial allele frequencies.

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

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

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

Temporal genetic variation

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

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Implications for fisheries management

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

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

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

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Conclusion and perspectives

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

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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	**0,06***
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	**0,05***
6	Bay of Brest	BOB-2004	BOB	2004	23	4,43	0,50	**0,08*****
7	Camaret	CAM	BOB	2016	45	4,66	0,54	0,04
8	Morlaix	MOR	WEC	2016	46	4,57	0,53	**0,05*****
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	**0,04***
12	Granville	GRA	WEC	2017	41	4,53	0,51	**0,04*****
13	North Cotentin Peninsula	NCP	EEC	2016	48	4,59	0,55	**0,01***
14	Bay of Seine	BOS-2015	EEC	2015	45	4,59	0,52	**0,05*****
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	**0,04*****
19	Bassurelles	BAS-2017	EEC	2017	89	4,65	0,53	**0,06*****
20	Eastern English Channel	ECH	EEC	2017	47	4,66	0,54	**0,03*****

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_o 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 ~~*Fst*~~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 ~~*Fst*~~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 = ~~<~~0.00~~1~~9), global adjust R^2= 0.064. (b) Scores of samples on the axis 1 of the RDA (p = ~~<~~0.0~~0~~5~~1~~) 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 ~~*Fst*~~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 ~~*Fst*~~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 3~~2~~, table 4~~3~~).

Supplmentary 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, [MgCl2]: MgCl2 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:CGAAGGTTTGTGCTGTGAATC 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:GCGTGACAGTCGACCATTTC	240-290	No	57,9	35	0,2	1,5
PmNH70	P1	YY	F:AGTTGTGCTATTGAATGGGAAC R:ATGCACTGCTTGTCCACTTC	114-162	Yes	56,5	45	0,2	2
PmNH73	P1	DO	F:CATAGCGATGCAGGACAAGG R: ATTCCAATGTCTGCCGTCTG	203-253	Yes	57,3	40	0,2	1,5
PmNH11	P2	FAM	F: GCCATGGTCGGAAATCACC R: CAAACGCGCCAAGTCTACG	289-321	No	58,8	45	0,2	2
PmNH23	P2	YY	F:AAATGCCGTCAGCTTTCAG R:ACTGTACAAATCGGCCACG	238-283	No	54,5	40	0,2	2
LIST15-013	P2	M-13 Black	F:AATGATTTTCGTCTGTCCG R:AATATCTCAACAAGCGACC	259-523	No	52,4	40	0,2	2
PmGC05	P2	PET	F: AATTGTACTTTCAATCATAAACTGAG 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: GGGCTCATTTGTCGCATAGT 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:TCCCTTTGATTCAGGTTTGTC R:ATGATTTGGAATCGGCTTTG	310-350	No	53,2	35	0,2	2
LIST15-005	P3	PET	F:CAATAGTTCGTTCAGCGGCG R:CTCTTGGATGCTTGTGAGGG	260-329	Yes	59,4	35	0,1	1,5
LIST15-008b	P3	M-13 Blue	F:CTCTCACTTCCACTGTTGACC R:TGTTAGCACATTTTCTCCCCG	175-295	Yes	57,3	35	0,1	1,5
LIST15-012	P3	M-13 Black	F:CCTTACACACCTACCCTCC R:TTTGGGGGCGACATACTGC	180-250	No	58,8	35	0,2	1,5
PmRM020	P3	FAM	F: CCCTATTGGATGTCTTCAGCA R: CCGATGAGATGTGTTCGTGT	122-169	Yes	57,3	35	0,1	1,5
PmRM036	P3	YY	F: CTGCTTCGTCATCAAAAAC R: TCGAATACGCCCATATGATTC	285-328	Yes	52,4	35	0,2	1,5

Supplmentary 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.

Populations	Statistics	PmNH59	PmNH60	PmNH62	PmNH70	PmRM002	PmNH73	List15013	PmNH11	PmNH23	PmRM053	PmRM057	PmRM072	PmGC05	List15-012	List15-04	List15-05	List15-08	PmRM02	PmRM036	Multi-locus
	Np	0,00	0,00	0,00	0,00	2,00	1,00	2,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	2,00
	Ar	4,297	2,824	4,151	-	8,33	-	-	-	-	2,495	8,283	3,635	-	6,188	1,998	8,577	-	2,405	2,655	4,65
FAL	H exp	0,72	0,40	0,65	0,07	0,87	0,17	0,94	0,17	0,29	0,27	0,89	0,64	0,86	0,81	0,14	0,88	0,33	0,27	0,24	0,54
N=48	H obs	0,70	0,40	0,70	0,02	0,86	0,11	0,97	0,10	0,33	0,31	0,89	0,63	0,80	0,72	0,06	0,80	0,24	0,31	0,24	0,54
	Fis	0,04	0,02	-0,07	**0,66*****	0,03	**0,35*****	-0,02	**0,4****	-0,15	-0,13	0,01	0,04	0,09	0,12	**0,56*****	0,11	**0,27****	-0,13	0,01	0,03
	Np	0,00	1,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1,00
	Ar	3,591	2,778	3,766	-	7,151	-	-	-	-	2,994	7,573	3,845	-	6,699	1,571	7,062	-	2,97	2,53	4,38
PLY	H exp	0,69	0,27	0,66	0,16	0,83	0,14	0,91	0,23	0,24	0,30	0,86	0,62	0,86	0,81	0,07	0,83	0,16	0,40	0,23	0,52
N=29	H obs	0,56	0,23	0,50	0,06	0,88	0,14	0,80	0,04	0,28	0,34	0,86	0,62	0,86	0,85	0,07	0,75	0,10	0,38	0,25	0,50
	Fis	0,21	0,18	0,26	**0,66*****	-0,03	-0,04	**0,14****	**0,84*****	-0,14	-0,12	0,01	0,02	0,01	-0,02	-0,01	0,12	**0,38****	0,06	-0,08	**0,06***
	Np	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
	Ar	4,031	2,136	4,295	-	8,541	-	-	-	-	2,495	7,226	4,646	-	6,691	1,308	8,674	-	2,423	1,977	4,54
SAL	H exp	0,68	0,27	0,72	0,09	0,89	0,13	0,90	0,14	0,23	0,25	0,85	0,71	0,87	0,82	0,04	0,88	0,20	0,26	0,14	0,52
N=42	H obs	0,76	0,27	0,76	0,03	0,87	0,07	1,00	0,09	0,26	0,24	0,85	0,74	0,67	0,90	0,04	0,87	0,17	0,29	0,15	0,54
	Fis	-0,11	0,02	-0,04	**0,66*****	0,03	**0,49*****	0,00	**0,36****	-0,10	0,08	0,01	-0,02	**0,26*****	-0,08	0,00	0,03	0,18	-0,12	-0,04	-0,02
	Np	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
	Ar	4,596	4,182	5	-	6,368	-	-	-	-	2,714	7,76	4,232	-	4,659	1,667	7,654	-	2,333	1,667	4,40
WLB	H exp	0,66	0,54	0,70	0,00	0,80	0,00	0,75	0,00	0,00	0,31	0,85	0,64	0,69	0,75	0,08	0,84	0,00	0,16	0,08	0,49
N=12	H obs	0,70	0,55	0,50	0,00	0,80	0,00	1,00	0,00	0,00	0,36	0,92	0,83	0,50	0,75	0,08	0,89	0,00	0,17	0,08	0,51
	Fis	-0,01	0,03	0,35	0,00	0,05	0,00	0,00	0,00	0,00	-0,13	-0,03	-0,26	**0,40*****	0,05	0,00	0,00	0,00	-0,02	0,00	0,02
	Np	0,00	0,00	0,00	0,00	0,00	0,00	1,00	0,00	0,00	1,00	0,00	0,00	0,00	0,00	0,00	0,00	2,00	0,00	0,00	1,00
	Ar	3,656	2,352	3,933	-	7,632	-	-	-	-	3,284	8,713	3,879	-	6,668	1,812	7,552	-	2,974	2,489	4,58
BOB-2015	H exp	0,68	0,39	0,69	0,07	0,85	0,25	0,94	0,17	0,28	0,53	0,89	0,65	0,85	0,82	0,10	0,86	0,13	0,33	0,21	0,56
N=46	H obs	0,72	0,40	0,69	0,07	0,73	0,23	0,84	0,14	0,28	0,54	0,84	0,65	0,74	0,80	0,09	0,80	0,05	0,33	0,16	0,54
	Fis	-0,04	-0,02	0,01	-0,02	**0,16*****	0,09	**0,11*****	0,18	0,01	-0,01	0,06	0,00	**0,14****	0,04	0,18	0,08	**0,66*****	-0,01	**0,25****	**0,05***
	Np	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1,00	0,00	0,00	0,00
	Ar	4,748	1,976	3,892	-	6,702	-	-	-	-	3,308	7,457	3,908	-	6,907	1,696	8,798	-	2,335	1,444	4,43
BOB-2004	H exp	0,71	0,28	0,72	0,10	0,83	0,16	0,87	0,22	0,32	0,49	0,86	0,47	0,81	0,83	0,08	0,88	0,34	0,35	0,05	0,53
N=23	H obs	0,56	0,24	0,65	0,11	0,87	0,09	0,67	0,05	0,31	0,37	0,83	0,47	0,76	0,70	0,09	0,90	0,29	0,43	0,06	0,50
	Fis	0,23	0,17	0,11	-0,01	-0,03	**0,48*****	**0,26*****	**0,78*****	0,09	0,27	0,06	0,01	0,09	**0,19****	-0,01	-0,01	0,18	-0,23	0,00	**0,08*****
	Np	0,00	0,00	0,00	0,00	0,00	0,00	2,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1,00	0,00	0,00	0,00	1,00
	Ar	5,315	2,641	4,217	-	7,513	-	-	-	-	3,006	7,676	4,66	-	6,37	1,326	8,134	-	2,682	2,339	4,66
CAM	H exp	0,74	0,35	0,72	0,07	0,85	0,27	0,87	0,27	0,31	0,31	0,87	0,70	0,79	0,81	0,04	0,88	0,19	0,34	0,22	0,55
N=45	H obs	0,73	0,27	0,73	0,07	0,91	0,19	0,88	0,03	0,36	0,33	0,93	0,73	0,75	0,53	0,04	0,88	0,16	0,30	0,22	0,54
	Fis	0,03	0,25	0,00	-0,02	-0,06	**0,31****	0,00	**0,91*****	-0,15	-0,05	-0,06	-0,03	0,07	**0,35*****	-0,01	0,00	0,18	0,15	0,01	0,04
	Np	0,00	0,00	0,00	0,00	0,00	0,00	1,00	0,00	1,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1,00
	Ar	3,751	2,514	4,137	-	6,807	-	-	-	-	3,315	8,222	4,033	-	6,351	1,537	8,904	-	3,191	2,058	4,57
MOR	H exp	0,65	0,36	0,68	0,07	0,83	0,21	0,93	0,24	0,29	0,51	0,88	0,62	0,84	0,82	0,07	0,89	0,23	0,42	0,17	0,55
N=46	H obs	0,63	0,29	0,74	0,07	0,74	0,18	0,88	0,15	0,29	0,55	0,89	0,59	0,83	0,79	0,07	0,84	0,14	0,36	0,13	0,53
	Fis	0,04	0,23	-0,08	-0,02	0,12	0,15	0,06	**0,38****	0,02	-0,06	0,00	0,07	0,02	0,06	-0,02	0,06	**0,41*****	0,15	0,20	**0,05*****
	Np	0,00	0,00	0,00	2,00	0,00	0,00	4,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1,00	0,00	0,00	0,00	1,00
	Ar	3,798	2,616	4,503	-	7,204	-	-	-	-	3,106	8,758	3,956	-	7,105	2,043	8,491	-	2,834	2,27	4,72
BSB-2016	H exp	0,66	0,35	0,72	0,07	0,85	0,14	0,92	0,33	0,26	0,42	0,89	0,65	0,85	0,83	0,16	0,87	0,17	0,36	0,28	0,56
N=47	H obs	0,62	0,38	0,74	0,02	0,89	0,10	0,91	0,00	0,24	0,37	0,88	0,66	0,79	0,87	0,17	0,87	0,18	0,37	0,33	0,57
	Fis	0,08	-0,08	-0,02	**0,66*****	-0,03	**0,31****	0,02	**1*****	0,06	0,14	0,02	0,00	0,08	-0,03	-0,06	0,02	-0,05	-0,01	-0,16	0,00
	Np	0,00	0,00	0,00	0,00	0,00	0,00	1,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
	Ar	4,37	2,59	3,897	-	7,957	-	-	-	-	3,04	8,291	4,012	-	7,35	2,29	8,469	-	2,464	1,912	4,72
BSB-2012	H exp	0,71	0,31	0,67	0,02	0,86	0,24	0,92	0,18	0,24	0,39	0,88	0,67	0,85	0,84	0,22	0,88	0,25	0,32	0,16	0,55
N=47	H obs	0,72	0,36	0,70	0,02	0,73	0,24	0,94	0,15	0,27	0,43	0,93	0,70	0,70	0,80	0,24	0,86	0,18	0,30	0,17	0,55
	Fis	0,01	-0,16	-0,03	0,00	**0,16****	0,02	-0,01	0,18	-0,10	-0,09	-0,05	-0,04	**0,19*****	0,06	-0,09	0,04	**0,28*****	0,08	-0,07	0,00
	Np	0,00	0,00	0,00	0,00	1,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1,00	0,00	0,00	1,00	0,00	0,00	2,00
	Ar	3,978	2,88	2,999	-	8,025	-	-	-	-	3,16	8,103	3,56	-	6,855	2,195	7,464	-	2,628	2,798	4,55
BSB-2004	H exp	0,66	0,40	0,66	0,05	0,83	0,14	0,85	0,22	0,49	0,41	0,86	0,45	0,78	0,81	0,18	0,84	0,28	0,37	0,35	0,56
N=20	H obs	0,75	0,50	0,68	0,05	0,80	0,15	0,53	0,15	0,50	0,35	0,95	0,50	0,72	0,50	0,20	0,80	0,26	0,35	0,29	0,55
	Fis	-0,11	-0,23	-0,01	0,00	0,07	-0,04	**0,40*****	**0,34****	0,01	0,17	-0,07	-0,10	0,11	**0,40*****	-0,06	0,08	0,10	0,07	0,18	**0,04***
	Np	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1,00	0,00	0,00	0,00	0,00	0,00	1,00
	Ar	3,72	2,165	4,897	-	7,674	-	-	-	-	2,955	8,276	4,329	-	6,067	1,549	8,004	-	2,108	2,674	4,53
GRA	H exp	0,66	0,25	0,75	0,11	0,85	0,16	0,94	0,15	0,17	0,39	0,88	0,67	0,84	0,79	0,07	0,87	0,05	0,24	0,25	0,53
N=41	H obs	0,73	0,22	0,85	0,11	0,78	0,10	0,94	0,05	0,13	0,39	0,92	0,71	0,82	0,55	0,07	0,82	0,05	0,28	0,18	0,51
	Fis	-0,08	0,13	-0,13	-0,03	0,10	**0,40****	0,02	**0,65*****	0,24	0,01	-0,04	-0,05	0,03	**0,32****	-0,02	0,07	-0,01	-0,13	**0,31****	**0,04*****
	Np	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1,00	0,00	0,00	0,00	1,00	0,00	0,00	0,00	0,00	1,00	0,00	0,00	1,00
	Ar	3,771	2,671	4,27	-	7,934	-	-	-	-	2,948	8,34	4,636	-	6,361	2,039	7,41	-	2,913	1,831	4,59
NCP	H exp	0,67	0,36	0,72	0,07	0,88	0,21	0,89	0,12	0,37	0,35	0,89	0,68	0,85	0,79	0,14	0,85	0,23	0,30	0,12	0,55
N=48	H obs	0,74	0,33	0,79	0,02	0,89	0,10	0,88	0,13	0,38	0,35	**0,79***	0,60	0,79	0,74	0,15	0,91	0,13	0,31	0,13	0,55
	Fis	-0,09	0,10	-0,09	**0,66*****	0,00	**0,54*****	0,02	-0,05	-0,01	0,01	0,11737	0,13	0,09	0,06	-0,04	-0,06	**0,47*****	-0,05	-0,04	**0,01***
	Np	0,00	0,00	0,00	0,00	0,00	0,00	1,00	2,00	0,00	0,00	1,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1,00	2,00
	Ar	3,609	2,167	4,113	-	7,749	-	-	-	-	3,107	7,749	4,47	-	7,151	1,533	8,27	-	2,602	2,583	4,59
BOS-2015	H exp	0,61	0,33	0,70	0,13	0,86	0,28	0,90	0,28	0,25	0,37	0,86	0,69	0,87	0,83	0,07	0,88	0,13	0,35	0,26	0,54
N=45	H obs	0,53	0,31	0,79	0,05	0,82	0,18	0,83	0,11	0,28	0,32	0,82	0,68	0,87	0,80	0,07	0,79	0,14	0,30	0,29	0,52
	Fis	0,14	0,07	-0,13	**0,66*****	0,06	**0,36*****	0,09	**0,63*****	-0,10	0,14	0,07	0,03	0,01	0,04	-0,01	0,11	-0,03	0,18	-0,10	**0,05*****
	Np	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
	Ar	3,979	2,045	4,954	-	8,305	-	-	-	-	2,864	8,287	4,353	-	7,995	1,773	7,523	-	3,488	2,318	4,82
BOS-2012	H exp	0,67	0,21	0,75	0,05	0,88	0,19	0,92	0,10	0,28	0,31	0,88	0,73	0,86	0,86	0,10	0,85	0,11	0,41	0,20	0,55
N=47	H obs	0,68	0,21	0,79	0,05	0,85	0,11	0,92	0,02	0,28	0,24	0,85	0,70	0,84	0,91	0,11	0,85	0,11	0,43	0,19	0,55
	Fis	-0,01	0,01	-0,04	-0,01	0,05	**0,4*****	0,02	**0,79*****	0,02	0,23	0,05	0,05	0,04	-0,05	-0,03	0,01	-0,03	-0,03	0,03721	0,02
	Np	0,00	0,00	0,00	0,00	0,00	0,00	2,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	2,00	1,00	0,00	0,00	2,00
	Ar	3,439	1,99	3,68	-	8,215	-	-	-	-	2,357	8,158	4,697	-	7,113	2,252	8,115	-	2,218	2,189	4,54
BOS-2004	H exp	0,60	0,34	0,67	0,13	0,88	0,21	0,93	0,10	0,20	0,24	0,88	0,70	0,81	0,84	0,20	0,86	0,15	0,32	0,23	0,53
N=33	H obs	0,64	0,31	0,78	0,07	0,88	0,23	0,80	0,00	0,22	0,24	0,91	0,76	0,56	0,73	0,21	0,90	0,16	0,30	0,26	0,55
	Fis	-0,05	0,10	-0,16	**0,48*****	0,01	-0,06	**0,16*****	**1*****	-0,07	0,02	-0,02	-0,07	**0,33****	**0,15****	-0,07	-0,03	-0,03	0,07	-0,11	-0,01
	Np	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
	Ar	3,478	2,319	4,605	-	7,437	-	-	-	-	3,379	8,553	4,436	-	6,708	1,829	8,501	-	2,908	2,045	4,68
DIE	H exp	0,65	0,40	0,74	0,03	0,86	0,27	0,92	0,21	0,24	0,45	0,89	0,70	0,86	0,83	0,11	0,87	0,19	0,30	0,16	0,55
N=46	H obs	0,59	0,40	0,81	0,03	0,78	0,16	0,83	0,13	0,24	0,44	0,91	0,76	0,85	0,84	0,11	0,85	0,18	0,24	0,18	0,55
	Fis	0,11	0,02	-0,09	0,00	0,10	**0,41*****	**0,12****	**0,38****	-0,02	0,02	-0,01	-0,07	0,03	-0,01	-0,03	0,04	0,07	0,19	-0,06	0,01
	Np	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1,00	0,00	0,00	0,00	1,00
	Ar	3,992	2,759	4,304	-	8,028	-	-	-	-	2,922	7,866	4,432	-	6,028	1,494	7,836	-	2,411	2,528	4,55
BAS-2016	H exp	0,68	0,36	0,71	0,11	0,87	0,26	0,91	0,11	0,26	0,38	0,88	0,72	0,87	0,80	0,06	0,87	0,17	0,31	0,25	0,55
N=94	H obs	0,67	0,34	0,77	0,02	0,78	0,17	0,84	0,12	0,28	0,33	0,90	0,66	0,79	0,73	0,07	0,80	0,10	0,34	0,22	0,53
	Fis	0,02	0,05	0,08	**0,79*****	**0,12****	**0,37*****	**0,09****	0,06	0,07	0,12	0,02	0,08	**0,10****	0,09	0,02	0,08	**0,44*****	0,11	0,13	**0,04*****
	Np	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
	Ar	3,83	2,472	4,273	-	7,927	-	-	-	-	3,13	7,854	4,636	-	6,909	1,957	7,699	-	2,959	2,177	4,65
BAS-2017	H exp	0,65	0,34	0,71	0,07	0,88	0,19	0,91	0,14	0,30	0,43	0,88	0,72	0,86	0,84	0,13	0,86	0,21	0,38	0,18	0,56
N=89	H obs	0,51	0,35	0,69	0,02	0,82	0,14	0,84	0,09	0,29	0,35	0,88	0,83	0,73	0,80	0,13	0,81	0,16	0,30	0,14	0,53
	Fis	**0,22*****	0,01	0,03	**0,66*****	0,07	**0,29*****	**0,09****	**0,37*****	0,01	**0,19****	0,00	0,15	**0,16*****	0,05	0,04	0,06	**0,25*****	**0,22****	**0,20****	**0,06*****
	Np	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	1,00	0,00	1,00	0,00	0,00	0,00	2,00
	Ar	4,618	2,657	4,451	-	8,314	-	-	-	-	2,578	7,592	4,48	-	6,85	1,483	8,193	-	2,443	2,238	4,66
ECH	H exp	0,70	0,38	0,71	0,04	0,88	0,25	0,91	0,23	0,37	0,37	0,86	0,72	0,85	0,82	0,06	0,88	0,15	0,23	0,18	0,55
N=47	H obs	0,67	0,38	0,79	0,05	0,83	0,23	0,87	0,12	0,34	0,32	0,72	0,85	0,74	0,79	0,06	0,89	0,13	0,21	0,20	0,54
	Fis	0,06	0,01	-0,10	-0,01	0,07	0,10	0,06	**0,48*****	0,10	0,14	**0,17****	-0,17	**0,13***	0,05	-0,01	0,00	0,11	0,09	-0,06	**0,03*****
Null allele frequencies		0,03	0,03	0,01	0,18	0,03	0,18	0,04	0,23	0,05	0,03	0,01	0,01	0,05	0,05	0,01	0,02	0,09	0,03	0,03	

Supplementary material table 3: Parameters implemented in MetaPopGen simulations. Migration corresponds to the larval dispersal simulated by Nicolle et al., 2016. Columns are populations receiving larval, lines are populations emitting larval. Capacity (k0) is the maximal population size per population. Fecundity corresponds to the effective fecundity for male and female. Survival probability are calculated for each age-classes and are set identical among populations

Migration (Nicolle et al., 2016)

	Antifer	Vergoyer	Greenwich	Dieppes	Birxham	Brighton	Eastbourne	Falmouth	Morlaix/Lanion	Cherbourg	Plymouth	Bay of Brest	Rye Bay	SE Jersey	Saint Brieuc	Bay of Seine	Saint Malo/ Chausey	Celtic North	Celtic South	Plymouth	Jersey	Weymouth
Antifer	0.092	0.032	0.001	0.193	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.015	0.000	0.000	0.000	0.000	0.000	0.000
Vergoyer	0.000	0.021	0.001	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Greenwich	0.001	0.017	0.131	0.000	0.000	0.025	0.029	0.000	0.000	0.000	0.000	0.000	0.009	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Dieppes	0.000	0.121	0.000	0.186	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Birxham	0.000	0.000	0.000	0.000	0.207	0.000	0.000	0.001	0.000	0.000	0.035	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.004	0.000	0.077
Brighton	0.000	0.003	0.008	0.000	0.000	0.012	0.003	0.000	0.000	0.000	0.000	0.000	0.040	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Eastbourne	0.000	0.016	0.060	0.000	0.000	0.014	0.012	0.000	0.000	0.000	0.000	0.000	0.042	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Falmouth	0.000	0.000	0.000	0.000	0.002	0.000	0.000	0.002	0.000	0.000	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.029	0.000	0.000
Morlaix/Lanion	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.013	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.015	0.000
Cherbourg	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.034	0.000	0.000	0.000	0.001	0.000	0.049	0.006	0.000	0.000	0.000	0.008	0.000
Plymouth	0.000	0.000	0.000	0.000	0.048	0.000	0.000	0.004	0.000	0.000	0.028	0.000	0.000	0.000	0.000	0.000	0.000	0.006	0.000	0.035	0.000	0.001
Bay of Brest	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.000	0.000	0.368	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Rye Bay	0.000	0.011	0.011	0.000	0.000	0.001	0.003	0.000	0.000	0.000	0.000	0.000	0.003	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
SE Jersey	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.016	0.000	0.000	0.000	0.024	0.000	0.000	0.078	0.000	0.000	0.000	0.036	0.000
Saint Brieuc	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.000	0.000	0.000	0.000	0.001	0.315	0.000	0.061	0.000	0.000	0.000	0.009	0.000
Bay of Seine	0.065	0.000	0.000	0.006	0.000	0.000	0.000	0.000	0.000	0.003	0.000	0.000	0.000	0.000	0.000	0.424	0.000	0.000	0.000	0.000	0.000	0.000
Saint Malo/ Chausey	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.004	0.000	0.000	0.000	0.061	0.030	0.000	0.160	0.000	0.000	0.000	0.011	0.000
Celtic North	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.226	0.019	0.004	0.000	0.000
Celtic South	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.019	0.238	0.000	0.000	0.000
Plymouth	0.000	0.000	0.000	0.000	0.009	0.000	0.000	0.000	0.000	0.000	0.014	0.000	0.000	0.000	0.000	0.000	0.000	0.011	0.000	0.088	0.000	0.000
Jersey	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.013	0.000	0.000	0.000	0.002	0.006	0.000	0.022	0.000	0.000	0.000	0.139	0.000
Weymouth	0.000	0.000	0.000	0.000	0.039	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.186

Capactity (Nicolle et al., 2016, Le Goff et al., 2017)

k_0	460136	352441	281996	490262	323774	155715	111740	15951	6969	56420	75388	65219	28868	234936	563661	2474010	281830	5632	1288	307116	43754	414672

Fecondity (Supplementary material 3)

$\varphi_{0,F,M}$ for 1-year old	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
$\varphi_{0,F,M}$ for 2+ / 1-year old	70	70	70	70	70	70	70	70	70	70	70	70	70	70	70	70	70	70	70	70	70	70

Survival probability (Le Goff et al., 2017)

σ_{age1}	0.76	0.76	0.76	0.76	0.76	0.76	0.76	0.76	0.76	0.76	0.76	0.76	0.76	0.76	0.76	0.76	0.76	0.76	0.76	0.76	0.76	0.76
σ_{age2}	0.88	0.88	0.88	0.88	0.88	0.88	0.88	0.88	0.88	0.88	0.88	0.88	0.88	0.88	0.88	0.88	0.88	0.88	0.88	0.88	0.88	0.88
σ_{age3}	0.92	0.92	0.92	0.92	0.92	0.92	0.92	0.92	0.92	0.92	0.92	0.92	0.92	0.92	0.92	0.92	0.92	0.92	0.92	0.92	0.92	0.92
σ_{age4}	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95
σ_{age5}	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95
σ_{age6}	0.96	0.96	0.96	0.96	0.96	0.96	0.96	0.96	0.96	0.96	0.96	0.96	0.96	0.96	0.96	0.96	0.96	0.96	0.96	0.96	0.96	0.96
σ_{age7}	0.96	0.96	0.96	0.96	0.96	0.96	0.96	0.96	0.96	0.96	0.96	0.96	0.96	0.96	0.96	0.96	0.96	0.96	0.96	0.96	0.96	0.96

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

Biological traits	Mean value	References
Potential fecundity	21. 10^6	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 *et al.*, 2013
Survival of recruits	0.1	Thorson 1960
Number of recruits (effective fecundity) = 21. 10^6 x 0.25 x 0.25 x exp(-0.25x30) x 0.1 = 72.6		

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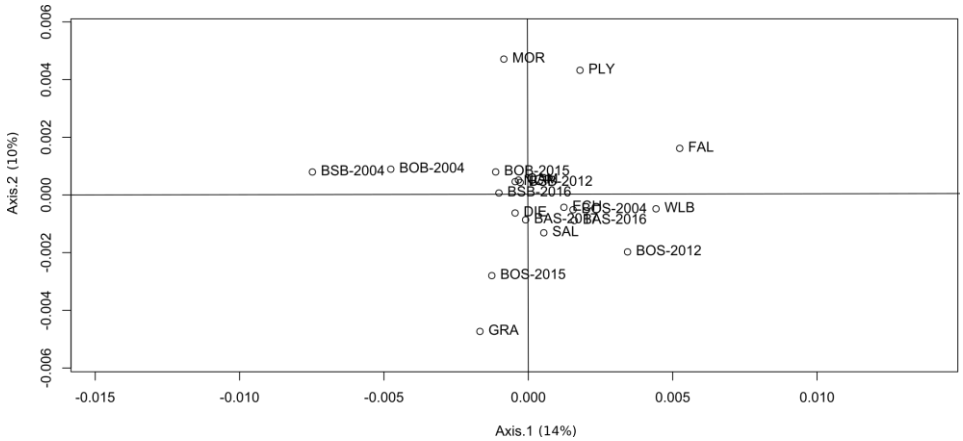

Supplementary Material Figure 1: PcoA results