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

Handal, William; Szostek, Claire; Hold, Natalie; Andreello, Marco; Thiébaud, Eric; Ewan, Harney; Lefebvre, Gwendoline; Elodie, Borcier; Jolivet, Aurélie ; Nicolle, Amandine ; Boyé, Aurélien ; Foucher, Eric; Boudry, Pierre; Charrier, Grégory

Aquatic Conservation: Marine and Freshwater Ecosystems

DOI:
[10.1002/aqc.3316](https://doi.org/10.1002/aqc.3316)

Published: 31/10/2020

Peer reviewed version

[Cyswllt i'r cyhoeddiad / Link to publication](#)

Dyfyniad o'r fersiwn a gyhoeddwyd / Citation for published version (APA):

Handal, W., Szostek, C., Hold, N., Andreello, M., Thiébaud, E., Ewan, H., Lefebvre, G., Elodie, B., Jolivet, A., Nicolle, A., Boyé, A., Foucher, E., Boudry, P., & Charrier, G. (2020). New insights on the population genetic structure of the great scallop (*Pecten maximus*) in the English Channel coupling microsatellite data and demogenetic simulations. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 30(10), 1841-1853. <https://doi.org/10.1002/aqc.3316>

Hawliau Cyffredinol / General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal ?

Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Title:

New insights on the population genetic structure of the great scallop (*Pecten maximus*) in the English Channel coupling microsatellite data and ~~gene flow~~demo-genetic simulationsmodeling.

Handal, William (1), Szostek, Claire (2) Hold, Natalie (2,3), Andrello, Marco (4) Thiébaud, Eric (5) Harney, Ewan (1), Lefebvre, Gwendoline (1), Borcier, Elodie (1), Jolivet, Aurélie (9), Nicolle, Amandine (5,6) Boyé, Aurélien (1) Foucher, Eric (7) Boudry, Pierre (8) Charrier, Grégory (1)

Affiliation

- (1) Univ Brest, CNRS, IRD, Ifremer, LEMAR, Plouzané, France
- (2) School of Ocean Science, Bangor University, Askew Street, Menai Bridge, Isle of Anglesey, Wales UK
- (3) Environment Centre Wales, Molecular Ecology and Fisheries Genetics Laboratory, School of Biological Sciences, College of Natural Sciences, Bangor University, Bangor, UK
- (4) MARBEC, Univ. Montpellier, CNRS, Ifremer, IRD, Sète, France.
- (5) Sorbonne Université, CNRS, Station Biologique de Roscoff, UMR 7144, Adaptation et Diversité en Milieu Marin, Roscoff, France
- (6) ENSTA Bretagne, Pôle STIC/HOP, Brest France
- (7) Ifremer, Ctr Manche Mer-du Nord, Laboratoire de Ressources Halieutiques, Port en Bessin, France
- (8) Ifremer, Univ Brest, CNRS, IRD, LEMAR, Plouzané, France
- (9) TBM environment, Porte Océane, Auray, France

3 Abstract:

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

9 2. In this ~~study~~~~context~~, scallop~~s~~ samples were taken across the main fishing grounds along the French and
 10 English coasts of the English Channel (20 samples with temporal replicates for 3 sites, n = 895 individuals)
 11 and the population genetic structure was analysed ~~based~~~~using~~ on 13 microsatellite loci. By coupling
 12 empirical genetic data and genetic model~~l~~ing based on a bio-physical model simulating larval exchanges
 13 among stocks, a subtle genetic differentiation between south~~h~~-western English coast populations and the rest
 14 of the English Channel was revealed, which agreed with larval dispersal simulations.

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

19 **Keywords:** English Channel, gene flow, genetic modeling, genetic resources management, great
 20 scallop, low genetic structure, microsatellites.

Commented [MOU1]: The Discussion needs to develop thinking around what these results mean in terms of conservation/management developments. What should be protected etc ?

Commented [2]: Répondre à Microsoft Office User (06/09/2019, 19:48): "..."
 All answer to Pr J. Baxter comments are given in the word document.

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 bentho-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 ([25.10⁶ £ in United Kingdom \(Elliott & Holden, 2017\)](#)
42 [and 50.10⁶ 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).

Commented [MOU3]: I am not clear what is meant by this, please reword

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~~re~~ variations in the
62 reproductive success of scallop and in the origin of settlers (Nicolle et al., 2013, 2016).

Commented [MOU4]: It is a bit confusing having groups within a group, may be better to come with another terms for the spawning groups, maybe spawning populations ?

Commented [MOU5]: I am not clear what this means.

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.

Commented [MOU6]: There are two such references in the ref list, please identify which one. Please refer to the guidelines for authors that explain how to do this.

Commented [MOU7]: As above and all subsequent such references

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 scallops²
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 model~~l~~ing (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) (~~T~~able 1, ~~F~~igure 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 ground~~s~~ in this area. ~~— Sampling~~ ~~Sample~~ collection differed from Szostek (2015) ~~by~~~~with the~~
94 ~~inclusion of~~ an extensive sampling of the western English Channel ~~F~~rench 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%

Commented [MOU8]: This number is different to what is given in the Abstract

100 ~~Cetyltrimethylammonium bromide (of CTAB)~~, 1% Polyvinylpyrrolidone (PVP), 1.4 M of NaCl, 0.2 M of β -
101 Mercaptoethanol, 100 mM of Tris-HCl pH=8, and 3.75 μ l of Proteinase K (20mg.ml⁻¹). 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 μ 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 μ g. μ l⁻¹.

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 μ l
115 volume containing 1X green Go Taq flexi buffer (Promega), 1.5-2.0 mM MgCl₂, 0.2 μ M each dNTP, 0.2 μ M
116 universal primer (fluorescent), 0.2 μ M reverse primer, 0.02 μ M forward primer, 0.25 U Go Taq Flexi DNA
117 Polymerase (Promega), and 1 μ 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°C for 2
121 min, 72°C for 30 sec) x1, (94 °C for 30 sec, T_m + 1°C for 30 sec [-1°C per cycle until T_{mU} -3°C], 72°C for 30
122 sec) x 2-9 cycles, (94°C for 30 sec, T_{mU} -3°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](#)able 1).

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

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 (H_o) and expected (H_e) 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).

Formatted

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., 20178).

Commented [MOU9]: Check date, only 2018 in ref list

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

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 ~~M~~aterial ~~T~~able 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 ~~M~~aterial ~~T~~able 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 ~~homogeneous~~homogeneous 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 ~~F_{ST}~~ F_{ST} (Nei, 1973) using the function “fst.pairwise.monoecious” in MetaPopGen, the same weights being attributed to each population for ~~F_{ST}~~ F_{ST} calculations. All cohorts were pooled in each population in each replicate to calculate pairwise ~~F_{ST}~~ F_{ST} , and ~~these pairwise F_{ST}~~ 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), ~~this and~~ did not reveal any change in pairwise ~~F_{ST}~~ 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.

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, $p\text{-value} < 0.05$) (Figure 2). After FDR correction, two pairwise F_{ST} remained significant
 235 (MOR/GRA/MOR (F_{ST} = 0.0108, $p\text{-value} = 0.003 < 0.01$) and FAL/GRA (F_{ST} = 0.0084, $p\text{-value} =$
 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, $p\text{-value} \leq 0.003$).

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 ($p \leq 0.0054$) 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

Commented [10]: Je m'étais trompé concernant le seuil
pas 0.001 mais 0.01

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 ($F_{ST} = 0.0003$, Figure 4, grey dashed line) and EC nearly stabilized ($F_{ST} = 0.0003$, Figure 4, grey solid line) at 4000 years. Simulated pairwise 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 $F_{ST} = 0.004$). Mean pairwise 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 ($2.10^{-5} < \text{mean pairwise } F_{ST} < 10^{-4}$) (Figure 4). Besides the Bay of Brest, SWE showed the highest mean pairwise 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 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 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

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.,

Formatted

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, & Thiébaud, 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

Commented [MOU11]: It is a bit unclear how a small population of scallop can be thought of in terms of a spawning ground.

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 ~~F_{ST}~~ remained low in comparison to SWE genetic differentiation. However, the magnitude of ~~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 Gulf region, could largely affect larval transport, with gyres induced by capes acting as larval retention systems while gyres around islands acting as dissemination systems (Ménèsquen & Gohin, 2006). Larval connectivity is then expected to be important within the Normano-Breton Gulf 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 (Ménèsquen & Gohin, 2006) could contribute to isolate the Normano-Breton Gulf 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 underline~~ 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, Thiébaud, 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, Thiébaud, 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 Genetic 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).~~

Commented [MOU12]: This does not make sense

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

Commented [MOU13]: I do not understand what is being said here

Commented [14]: Répondre à Microsoft Office User (06/09/2019, 20:11): "..."
 I deleted the sentence which indeed was not clear.

Commented [MOU15]: Better not just to say this would be relevant, do it, even if you need to add some caveats

Commented [MOU16]: This is what makes it relevant to the journal, this is what needs to be done to develop the thinking around what management needs to be put in place to help conserve the scallop populations

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). Adaptive 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 -

Commented [17]: Reference à rajouter

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.

Acknowledgements

W. Handal was funded by a French doctoral research grant from the region Bretagne (50%) and the Université de Bretagne Occidentale (50%). The authors thank all people involved in sampling: Dominique Thomas, Victor Bouvard, Catherine Paul, Laurence Hegronmace, Ghislaine Hervieu, Olivier Gallet, André le

445 Gall, Pascal Delacourt, Bocher Gilles, Yves Verin, Dorothé Vincent, Rachid Amara, Desit Dominique,
 446 Rocher Guy, Jimmy Montreuil, Guy Montreuil, Kevin Webber, the Comité Départemental des Pêches
 447 Maritimes et des Elevages Marins du Finistère, the Comité Régional des Pêches Maritimes et des Elevages
 448 Marins de Normandie, the Parc naturel marin d'Iroise the diving service from the Station Biologique de
 449 Roscoff and Falfish.

450 ~~Cited~~References

451 Andrello, M., & Manel, S. (2015). MetaPopGen: an R package to simulate population genetics in
 452 large size metapopulations. *Molecular Ecology Resources*, 15(5), 1153-1162.
 453 Antao, T., Lopes, A., Lopes, R. J., Beja-Pereira, A., & Luikart, G. (2008). LOSITAN: A workbench
 454 to detect molecular adaptation based on a Fst-outlier method. *BMC Bioinformatics*, 9(1),
 455 323.
 456 Ayata, S.-D., Lazure, P., & Thiébaud, É. (2010). How does the connectivity between populations
 457 mediate range limits of marine invertebrates? A case study of larval dispersal between the
 458 Bay of Biscay and the English Channel (North-East Atlantic). *Progress in Oceanography*,
 459 87(1-4), 18-36.
 460 Beaumont, A. R., Morvan, C., Huelvan, S., Lucas, A., & Ansell, A. D. (1993). Genetics of
 461 indigenous and transplanted populations of *Pecten maximus*: no evidence for the existence
 462 of separate stocks. *Journal of Experimental Marine Biology and Ecology*, 169(1), 77-88.
 463 Belkhir, K., Borsa, P., Goudet, J., Chikhi, L., & Bonhomme, F. (1996-2004). GENETIX logiciel
 464 sous Windows™ pour la génétique des populations. Laboratoire Génome, Populations,
 465 Interactions CNRS UMR 5000, Université de Montpellier II, Montpellier (France)
 466 Benjamini, Y., & Yekutieli, D. (2001). The control of the false discovery rate in multiple testing
 467 under dependency. *The Annals of Statistics*, 29(4), 1165-1188.
 468 Beukers-Stewart, B., Vause, B., Mosley, M., Rossetti, H., & Brand, A. (2005). Benefits of closed
 469 area protection for a population of scallops. *Marine Ecology Progress Series*, 298, 189-204.
 470 Bilodeau, A. L., Felder, D. L., & Neigel, J. E. (2005). Population structure at two geographic scales
 471 in the burrowing crustacean callichirus islagrande (*decapoda, thalassinidea*): historical and
 472 contemporary barriers to planktonic dispersal. *Evolution*, 59(10), 2125-2138.
 473 Broquet, T., Viard, F., & Yearsley, J. M. (2013). Genetic drift and collective dispersal can result in
 474 chaotic genetic patchiness. *Evolution*, 67(6), 1660-1675.
 475 Brownstein, M. J., Carpten, J., & Smith, J. (1996). Modulation of non-templated nucleotide addition
 476 by Taq DNA Polymerase: Primer modifications that facilitate genotyping. *BioTechniques*,
 477 20(6), 1004-1010
 478 Calderón, I., Pita, L., Brusciotti, S., Palacín, C., & Turon, X. (2012). Time and space: genetic
 479 structure of the cohorts of the common sea urchin *Paracentrotus lividus* in Western
 480 Mediterranean. *Marine Biology*, 159(1), 187-197.
 481 Carvalho, G. R., & Hauser, L. (1994). Molecular genetics and the stock concept in fisheries.
 482 *Reviews in Fish Biology and Fisheries*, 4(3), 326-350.
 483 Charrier, G., Morvezen, R., Calves, I., & Laroche, J. (2012). Development of new microsatellite

484 markers derived from expressed sequence tags for the great scallop (*Pecten maximus*).
 485 *Conservation Genetics Resources*, 4(4), 931-934.
 486 Chauvaud, L., Patry, Y., Jolivet, A., Cam, E., Le Goff, C., Strand, Ø., Charrier, G., Thébault, J., Lazure,
 487 P., Gotthard, K., and Clavier, J. (2012). Variation in size and growth of the great scallop *Pecten*
 488 *maximus* along a latitudinal gradient. *PLoS ONE*, 7(5), e37717.
 489 <https://doi.org/10.1371/journal.pone.0037717>
 490 Cochard, J. C., & Devauchelle, N. (1993). Spawning, fecundity and larval survival and growth in
 491 relation to controlled conditioning in native and transplanted populations of *Pecten maximus*
 492 (L.): evidence for the existence of separate stocks. *Journal of Experimental Marine Biology*
 493 *and Ecology*, 169(1), 41-56.
 494 Coombs, J. A., Letcher, B. H., & Nislow, K. H. (2008). Create: a software to create input files from
 495 diploid genotypic data for 52 genetic software programs. *Molecular Ecology Resources*,
 496 8(3), 578-580.
 497 Couceiro, L., Robuchon, M., Destombe, C., & Valero, M. (2013). Management and conservation of
 498 the kelp species *Laminaria digitata* : using genetic tools to explore the potential exporting
 499 role of the MPA “ Parc naturel marin d'Iroise ”. *Aquatic Living Resources*, 26(2), 197-205.
 500 Cowen, R. K., & Sponaugle, S. (2009). Larval dispersal and marine population connectivity. *Annual*
 501 *Review of Marine Science*, 1(1), 443-466.
 502 Dannewitz, J., Maes, G. E., Johansson, L., Wickstrom, H., Volckaert, F. A. M., & Jarvi, T. (2005).
 503 Panmixia in the European eel: a matter of time... *Proceedings of the Royal Society B:*
 504 *Biological Sciences*, 272(1568), 1129-1137.
 505 De Meeûs, T., Guegan, J.-F., & Teriokhin, A. T. (2009). MultiTest V.1.2, a program to binomially
 506 combine independent tests and performance comparison with other related methods on
 507 proportional data. *BMC Bioinformatics*, 10(1), 443.
 508 [Dauvin, J.C. \(2012\) Are the eastern and western basins of the English Channel two separate](#)
 509 [ecosystems? *Marine Pollution Bulletin* 64, 463–471.](#)
 510 Duncan, P. F., Brand, A. R., Strand, Ø., & Foucher, E. (2016). The European scallop fisheries for
 511 *Pecten maximus*, *Aequipecten opercularis*, *Chlamys islandica*, and *Mimachlamys varia*. In
 512 *Developments in Aquaculture and Fisheries Science* (Vol. 40, pp. 781-858). Elsevier.
 513 Dupont, L., Ellien, C., & Viard, F. (2007). Limits to gene flow in the slipper limpet *Crepidula*
 514 *fornicata* as revealed by microsatellite data and a larval dispersal model. *Marine Ecology*
 515 *Progress Series*, 349, 125-138.
 516 Ellien, C., Thiébaud, E., Dumas, F., Salomon, J.-C., & Nival, P. (2004). A modelling study of the
 517 respective role of hydrodynamic processes and larval mortality on larval dispersal and
 518 recruitment of benthic invertebrates: example of *Pectinaria koreni* (Annelida: Polychaeta) in
 519 the Bay of Seine (English Channel). *Journal of Plankton Research*, 26(2), 117-132.
 520 [Elliott, E. M., & Holden, J. \(2017\). *UK Sea Fisheries Statistics 2017*. 174.](#)
 521 Foster, N. L., Paris, C. B., Kool, J. T., Baums, I. B., Stevens, J. R., Sanchez, J. A., Bastidas, C.,
 522 Agudelo, C., Bush, P., Day, O., Ferrari, R., Gonzalez, P., Gore, S., Guppy, R., McCartney, M. A.,
 523 McCoy, C., Mendes, J., Srinivasan, A., Steiner, S., Vermeij, M. J. A., Weil, E., & Mumby, P. J.
 524 (2012). Connectivity of Caribbean coral populations: complementary insights from
 525 empirical and modelled gene flow. *Molecular Ecology*, 21(5), 1143-1157.
 526 Galindo, H. M., Olson, D. B., & Palumbi, S. R. (2006). Seascape genetics: a coupled
 527 oceanographic-genetic model predicts population structure of Caribbean corals. *Current*

528 *Biology*, 16(16), 1622-1626.

529 Gilg, M. R., & Hilibish, T. J. (2003). Patterns of larval dispersal and their effect on the maintenance
530 of a blue mussel hybrid zone in southwestern England. *Evolution*, 57, 1061-1077.

531 Goudet, J. (1995). FSTAT (Version 1.2): A computer program to calculate F-Statistics. *Journal of*
532 *Heredity*, 86(6), 485-486.

533 Hedgecock, D., & Pudovkin, A. I. (2011). Sweepstakes reproductive success in highly fecund
534 marine fish and shellfish: a review and commentary. *Bulletin of Marine Science*, 87(4),
535 971-1002.

536 Howarth, L. M., & Stewart, B. D. (2014). The dredge fishery for scallops in the United Kingdom
537 (UK): Effects on marine ecosystems and proposals for future management. Report to the
538 Sustainable Inshore Fisheries Trust. *Marine Ecosystem Management* (No. 5) (p. 54).
539 University of York, UK.

540 Jolly, M. T., Guyard, P., Ellien, C., Gentil, F., Viard, F., Thiébaud, E., & Jollivet, D. (2009).
541 Population genetics and hydrodynamic modeling of larval dispersal dissociate contemporary
542 patterns of connectivity from historical expansion into European shelf seas in the polychaete
543 *Pectinaria koreni*. *Limnology and Oceanography*, 54(6), 2089-2106.

544 Jolly, M. T., Thiébaud, E., Guyard, P., Gentil, F., & Jollivet, D. (2014). Meso-scale hydrodynamic
545 and reproductive asynchrony affects the source-sink metapopulation structure of the coastal
546 polychaete *Pectinaria koreni*. *Marine Biology*, 161(2), 367-382.

547 Jolly, M. T., Viard, F., Gentil, F., Thiébaud, E., & Jollivet, D. (2006). Comparative phylogeography
548 of two coastal polychaete tubeworms in the Northeast Atlantic supports shared history and
549 vicariant events: Comparative phylogeography of coastal tubeworms. *Molecular Ecology*,
550 15(7), 1841-1855.

551 Kalinowski, S. T., & Taper, M. L. (2006). Maximum likelihood estimation of the frequency of null
552 alleles at microsatellite loci. *Conservation Genetics*, 7(6), 991-995.

553 Kamvar, Z. N., Brooks, J. C., & Grünwald, N. J. (2015). Novel R tools for analysis of genome-wide
554 population genetic data with emphasis on clonality. *Frontiers in Genetics*, 6, 208.

555 Knutsen, H., Olsen, E. M., Jorde, P. E., Espeland, S. H., André, C., & Stenseth, N. C. (2011). Are
556 low but statistically significant levels of genetic differentiation in marine fishes 'biologically
557 meaningful'? A case study of coastal Atlantic cod. *Molecular Ecology*, 20(4), 768-783.

558 Lagadeuc, Y. (1992). Transport larvaire en Manche. Exemple de *Pectinaria koreni* (Malmgren),
559 annélide polychète, en Baie de Seine. *Océanologica Acta*, 15(4), 383-395.

560 Le Goff, C., Lavaud, R., Cugier, P., Jean, F., Flye-Sainte-Marie, J., Foucher, E., Desroy, N., Fias, S.,
561 Foveau, A. (2017). A coupled biophysical model for the distribution of the great scallop
562 *Pecten maximus* in the English Channel. *Journal of Marine Systems*, 167, 55-67.

563 [Les filières pêche et aquaculture Bilan 217. 2018. Données et bilans de FranceAgriMer.](#)

564 Lefebvre, A., Ellien, C., Davoult, D., Thiébaud, E., & Salomon, J. . (2003). Pelagic dispersal of the
565 brittle-star *Ophiotrix fragilis* larvae in a megatidal area (English Channel, France)
566 examined using an advection/diffusion model. *Estuarine, Coastal and Shelf Science*, 57(3),
567 421-433.

568 Legendre, P., & Anderson, M. J. (1999). Distance-based redundancy analysis: testing multispecies
569 responses in multifactorial ecological experiments. *Ecological Monographs*, 69(1), 1-24.

570 Legendre, P., & Gallagher, E. D. (2001). Ecologically meaningful transformations for ordination of
571 species data. *Oecologia*, 129(2), 271-280.

572 Lowe, W. H., & Allendorf, F. W. (2010). What can genetics tell us about population connectivity?:
573 genetic and demographic connectivity. *Molecular Ecology*, 19(15), 3038-3051.

574 Lubet, P., Devauchelle, N., Muzellec, M. L., Paulet, Y. M., & Dao, J. C. (1995). Reproduction of
575 *Pecten maximus* from different fisheries areas Rade de Brest, Baie de St Brieuc, Baie de
576 Seine. *Fisheries, Biology and Aquaculture of Pectinids*, 8, 22-29.

577 Marmur, J., & Doty, P. (1962). Determination of the base composition of deoxyribonucleic acid
578 from its thermal denaturation temperature. *Journal of Molecular Biology*, 5(1), 109-118.

579 Ménesguen, A., & Gohin, F. (2006). Observation and modelling of natural retention structures in the
580 English Channel. *Journal of Marine Systems*, 63(3-4), 244-256.

581 Morvezen, R., Boudry, P., Laroche, J., & Charrier, G. (2016). Stock enhancement or sea ranching?
582 Insights from monitoring the genetic diversity, relatedness and effective population size in a
583 seeded great scallop population (*Pecten maximus*). *Heredity*, 117(3), 142-148.

584 Morvezen, R., Charrier, G., Boudry, P., Chauvaud, L., Breton, F., Strand, Ø., & Laroche, J. (2016).
585 Genetic structure of a commercially exploited bivalve, the great scallop *Pecten maximus*,
586 along the European coasts. *Conservation Genetics*, 17(1), 57-67.

587 Morvezen, R., Cornette, F., Charrier, G., Guinand, B., Lapègue, S., Boudry, P., & Laroche, J. (2013).
588 Multiplex PCR sets of novel microsatellite loci for the great scallop *Pecten maximus* and
589 their application in parentage assignment. *Aquatic Living Resources*, 26(3), 207-213.

590 Nei, M. (1973). Analysis of gene diversity in subdivided populations. *Proceedings of the National*
591 *Academy of Sciences*, 70(12), 3321-3323.

592 Nicolle, A., Dumas, F., Foveau, A., Foucher, E., & Thiébaud, E. (2013). Modelling larval dispersal
593 of the king scallop (*Pecten maximus*) in the English Channel: examples from the bay of
594 Saint-Brieuc and the Bay of Seine. *Ocean Dynamics*, 63(6), 661-678.

595 Nicolle, A., Moitié, R., Ogor, J., Dumas, F., Foveau, A., Foucher, E., & Thiébaud, E. (2016).
596 Modelling larval dispersal of *Pecten maximus* in the English Channel: a tool for the spatial
597 management of the stocks. *ICES Journal of Marine Science: Journal Du Conseil*, fsw207.
598 <https://doi.org/10.1093/icesjms/fsw207>

599 Oksanen, J., Blanchet, G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin P. R.,
600 O'Hara R. B., Simpson, G. L., Solymos, P., Henry M. H., Stevens, M. H., Szoecs, E., and
601 Wagner, H. 2018. vegan: Community Ecology Package. R package version 2.5-3.
602 <https://CRAN.R-project.org/package=vegan>

603 Palsboll, P., Berube, M., & Allendorf, F. (2007). Identification of management units using
604 population genetic data. *Trends in Ecology & Evolution*, 22(1), 11-16.

605 [Paradis, E., & Schliep, K. \(2018\). ape 5.0: an environment for modern phylogenetics and](#)
606 [evolutionary analyses in R. *Bioinformatics*, 35, 526-528.](#)

607 Purcell, J. F. ., Cowen, R. K., Hughes, C. R., & Williams, D. A. (2006). Weak genetic structure
608 indicates strong dispersal limits: a tale of two coral reef fish. *Proceedings of the Royal*
609 *Society B: Biological Sciences*, 273(1593), 1483-1490.

610 Reiss, H., Hoarau, G., Dickey-Collas, M., & Wolff, W. J. (2009). Genetic population structure of
611 marine fish: mismatch between biological and fisheries management units. *Fish and*
612 *Fisheries*, 10(4), 361-395.

613 Rousset, F. (2008). genepop'007: a complete re-implementation of the genepop software for
614 Windows and Linux. *Molecular Ecology Resources*, 8(1), 103-106.

615 Ryman, N., Palm, S., André, C., Carvalho, G. R., Dahlgren, T. G., Jorde, P. E., Laikre, L., Larsson, L.

616 C., Palmé, A., & Ruzzante, D. E. (2006). Power for detecting genetic divergence: differences
617 between statistical methods and marker loci. *Molecular Ecology*, 15(8), 2031-2045.

618 Sanford, E., & Kelly, M. W. (2011). Local adaptation in marine invertebrates. *Annual Review of*
619 *Marine Science*, 3(1), 509-535.

620 Schuelke, M. (2000). An economic method for the fluorescent labeling of PCR fragments. *Nature*
621 *Biotechnology*, 18(2), 233-234.

622 Selkoe, K. A., Henzler, C. M., & Gaines, S. D. (2008). Seascape genetics and the spatial ecology of
623 marine populations. *Fish and Fisheries*, 9(4), 363-377.

624 Sturt, F., Garrow, D., & Bradley, S. (2013). New models of North West European Holocene
625 palaeogeography and inundation. *Journal of Archaeological Science*, 40(11), 3963-3976.

626 Szostek, C. L. (2015). Population characteristics and environmental interactions of the king scallop
627 fishery in the English Channel. (PhD thesis). Bangor University, Wales.

628 Vendrami, D. L. J., Telesca, L., Weigand, H., Weiss, M., Fawcett, K., Lehman, K., Clark, M. S.,
629 Leese, F., McMinn, C., Moore, H., & Hoffman, J. I. (2017). RAD sequencing resolves fine-
630 scale population structure in a benthic invertebrate: implications for understanding
631 phenotypic plasticity. *Royal Society Open Science*, 4(2), 160548.

632 Vendrami, D. L. J., De Noia, M., Telesca, L., Handal, W., Charrier, G., Boudry, P., Eberhart-Philips,
633 L., & Hoffman, J. I. (2019). RAD sequencing sheds new light on the genetic structure and
634 local adaptation of European scallops and resolves their demographic histories. *Scientific*
635 *Reports*, 9(1). <https://doi.org/10.1038/s41598-019-43939-4>

636 Viard, F., Ellien, C., & Dupont, L. (2006). Dispersal ability and invasion success of *Crepidula*
637 *forficata* in a single gulf: insights from genetic markers and larval-dispersal model.
638 *Helgoland Marine Research*, 60(2), 144-152.

639 Waples, R. S. (1998). Separating the wheat from the chaff: patterns of genetic differentiation in high
640 gene flow species. *Journal of Heredity*, 89(5), 438-450.

641 Waples, Robin S., & Gaggiotti, O. (2006). What is a population? An empirical evaluation of some
642 genetic methods for identifying the number of gene pools and their degree of connectivity
643 *Molecular Ecology*, 15(6), 1419-1439.

644 Watts, P. C., Mallanaphy, P. J., McCarthy, C., Beukers-Stewart, B. D., Mosley, M. W. J., Brand, A.
645 R., & Saccheri, I. J. (2005). Polymorphic microsatellite loci isolated from the great scallop,
646 *Pecten maximus* (Bivalvia: Pectinidae). *Molecular Ecology Notes*, 5(4), 902-904.

647 Weir, B. S., & Cockerham, C. C. (1984). Estimating F-Statistics for the analysis of population
648 structure. *Evolution*, 38(6), 1358.

649 Whitlock, M. C., & McCauley, D. E. (1998). Indirect measures of gene flow and migration:
650 $F_{ST} \approx 1/(4Nm+1)$. *Heredity*, 82(2), 9.

651 Wilding, C. S., Beaumont, A. R., & Latchford, J. W. (1999). Are *Pecten maximus* and *Pecten*
652 *jacobaeus* different species? *Journal of the Marine Biological Association of the United*
653 *Kingdom*, 4.

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_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, [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: CGTCGAGGGAAAAAGTGAAAT	79-175	Yes	57,3	35	0,2	1,5
PmNH59	P1	YY	F:CGAAGTTTGTGCTGTGAATC 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:GCGTGACAGTCGACATTTT	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:AAATGCCCTCAGCTTTTACG 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: AATTGTACTTTCATCATAAACTGAG 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: GGGCTCATTTGTGCGCATAGT 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:TCCCTTTGATTACAGTTTGTG R:ATGATTTGGAATCGGCTTTG	310-350	No	53,2	35	0,2	2
LIST15-005	P3	PET	F:CAATAGTTCGTTTACGCGCG 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:CCTTACACACCTACCTCC R:TTTGGGGGCGACATACTGC	180-250	No	58,8	35	0,2	1,5
PmRM020	P3	FAM	F: CCCTATTGGATGTCTTCAGCA R: CCGATGAGATGTGTTCTGTG	122-169	Yes	57,3	35	0,1	1,5
PmRM036	P3	YY	F: CTGCTTCGTATCAAAAAAC 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.

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-focus
FAL N=48	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	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	
	Heap		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	
	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	
	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
PLY N=29	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	1.00	
	Ar		3.591	2.778	3.766	-	7.151	-	-	-	2.994	7.573	3.945	-	6.689	1.571	7.062	-	2.97	2.53	4.38	
	Heap		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	
	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	
	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	0.86***
SAL N=42	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	
	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	
	Heap		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	
	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	
	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	0.01	
WLB N=12	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	
	Ar		4.586	4.182	5	-	6.368	-	-	-	2.714	7.76	4.232	-	4.659	1.667	7.654	-	2.333	1.667	4.40	
	Heap		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	
	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	
	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	
BOB-2015 N=46	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	2.00	0.00	1.00	
	Ar		3.669	2.952	3.933	-	7.632	-	-	-	3.094	8.713	3.979	-	6.688	1.812	7.552	-	2.974	2.469	4.58	
	Heap		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	0.16	
	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	
	Fis		-0.04	-0.02	0.01	-0.02	0.16***	0.00	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***
BOB-2004 N=23	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	
	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	
	Heap		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	
	H obs		0.56	0.24	0.65	0.11	0.87	0.09	0.87	0.05	0.31	0.37	0.83	0.47	0.76	0.70	0.09	0.90	0.29	0.43	0.06	
	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	0.88***
CAM N=45	Np		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	0.00	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	-	2.882	2.339	4.66	
	Heap		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	
	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	
	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
MOR N=46	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	1.00	
	Ar		3.751	2.514	4.137	-	6.807	-	-	-	3.315	8.222	4.033	-	6.351	1.537	8.904	-	1.919	2.058	4.57	
	Heap		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	
	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	
	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	0.65***
BSB-2016 N=47	Np		0.00	0.00	0.00	2.00	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		3.798	2.616	4.503	-	7.204	-	-	-	3.106	8.758	3.956	-	7.105	2.043	8.491	-	2.834	2.27	4.72	
	Heap		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	
	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	
	Fis		0.08	-0.08	-0.02	0.66***	-0.03	0.31***	0.02	***	0.06	0.14	0.02	0.00	0.08	-0.03	0.06	-0.02	-0.05	-0.01	-0.16	0.00
BSB-2012 N=47	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	
	Ar		4.37	2.59	3.897	-	7.957	-	-	-	3.04	8.201	4.012	-	7.35	2.29	8.469	-	2.464	1.912	4.72	
	Heap		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	
	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	
	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
BSB-2004 N=20	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	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	
	Heap		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	0.16	0.84	0.28	0.37	0.35	
	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	
	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	0.84***
GRA N=41	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	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	
	Heap		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	
	H obs</																					

Migration (Nicolle et al., 2016)

Capacity (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
-------	--------	--------	--------	--------	--------	--------	--------	-------	------	-------	-------	-------	-------	--------	--------	---------	--------	------	------	--------	-------	--------

Survival probability (Le Goff et al. 2017)

Survival probability (Le Goff et al. 2017)

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 <i>et al.</i> , 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		

Eckman J. E. (1996). Closing the larval loop: linking larval ecology to the population dynamics of marine benthic invertebrates. *Journal of Experimental Marine Biology and Ecology*, 200, 207-237.

Paulet Y. M., & Fifas S. (1989). Etude de la fécondité potentielle de la coquille Saint-Jacques *Pecten maximus* en baie de Saint-Brieuc. *Haliotis*, 19, 275-285.

Paulet Y. M., Dorange G., Cochard J.C., & Le Pennec M. (1992). Reproduction et recrutement chez *Pecten maximus* L. *Annales de l'Institut Océanographique, Paris*, 68, 45-64.

Rumrill S.S. (1990). Natural mortality of marine invertebrate larvae. *Ophelia*, 32, 163-198.

Thorson, G. (1961). Length of pelagic larval life in marine bottom invertebrates as related to larval transport by ocean currents. In: *Sears, M., Ed., Oceanography*, 67, 455-474.

Thouzeau G. (1991). Déterminisme du pré-recrutement de *Pecten maximus* (L.) en baie de Saint Brieuc : processus régulateurs de l'abondance, de la survie et de la croissance des post-larves et juvéniles. *Aquatic Living Resources*, 4, 77-99.

654
655 **S**
656 **u**
657 **p**
658 **p**
659 **l**
660 **e**
661 **m**
662 **e**
663 **n**
664 **t**
665 **a**
666 **r**
667 **y**
668
669 **M**
670 **a**
671 **t**
672 **e**
673 **r**
674 **i**
675 **a**
676 **l**
677
678 **F**
679 **i**
680 **g**
681 **u**
682 **r**
683 **e**
684
685 **l**
686 **:**
687
688 **P**
689 **c**
690 **o**
691 **A**
692
693 **r**
694 **S**
695 **a**
696 **l**
697 **i**
698 **s**
699 **e**