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Population genetics and hydrodynamic modeling of larval dispersal dissociate contemporary patterns of connectivity from historical expansion into European shelf seas in the polychaete *Pectinaria koreni*

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Abstract

Using *Pectinaria koreni* as a biological model of larval dispersal, we coupled the analysis of differently evolving genetic markers (mitochondrial cytochrome oxidase I and four microsatellite loci) to hydrodynamic modeling of larval transport in the English Channel. To determine the influence of historical and contemporary processes on the genetic structure of our study populations, genetic relationships between English Channel, Irish Sea, and southern North Sea populations were assessed in relation to the long-term pattern of marine currents and to postglacial colonization pathways. Although significant, low level of overall nuclear genetic differentiation was best explained by the recent origin of populations within the study area and the retention of ancestral polymorphism. Both genetic data sets suggest that two ancestral gene pools contributed to the origin of our study populations, and secondary contacts occurred in the English Channel and southern North Sea as a result of two migration routes around the British Isles. Although Irish Sea and Belgium populations appeared more recently connected, populations of the eastern English Channel were more isolated. English Channel patterns of connectivity indicated high dispersal and gene flow along the French coast, from Normandy to the southern North Sea. Despite significant genetic differentiation between both coasts, migration model selection favored cross-channel gene flow and long-distance migration following the coastlines. Our results highlight the influence of postglacial colonization on genetic patterns in the English Channel, and indicate that contemporary mesoscale connectivity inferred by hydrodynamic modeling cannot, alone, explain the present genetic structure of populations in this area.

Understanding connectivity over different spatial and temporal scales is fundamental for conserving and managing the diversity of biological systems. In the marine environment, most species of benthic marine invertebrates with external fertilization are composed of geographically disjunct populations linked together by a dispersive larval stage. For species with such a lifestyle, the structure, dynamics, and ultimately the stability and persistence of populations are strongly dependent upon the success of the larval stage in reaching distant populations or in replenishing local genitor populations (Gaines and Bertness 1993; Caley et al. 1996; Botsford 2001). Factors affecting larval dispersal and the benthic recruitment phase include advective hydrodynamic processes caused by tide and wind-induced currents, oceanic boundaries (fronts and eddies), and long-term patterns of ocean currents, reproductive success, and the duration of the larval phase, and finally the behavior and physiological plasticity of larvae (Sponaugle et al. 2002). Significant mortality may occur at all stages of development from larvae to newly settled recruits and adults. Therefore, for dispersal to be effective in producing the next generation, larvae must survive in the

plankton, recruit onto suitable substrates, reach mature adulthood, and reproduce. Although the regulation of larval dispersal by physical circulation is of paramount importance, little is known because of the difficulty of accurately delineating breeding populations and measuring dispersal in the marine environment (but see Levin 2006). Hydrodynamic modeling studies of larval transport may provide means of recognizing patterns of larval movement and the dispersal potential of larvae (Barnay et al. 2003; Tilburg et al. 2005; Aiken et al. 2007). Nonetheless, quantifying the “effective” connectivity of marine populations requires additional indirect methods of assessment, such as population genetic tools, to validate these models.

Recent studies have shown that coupling genetics and fine-scale physical oceanographic modeling may clearly improve our understanding of larval dispersal and its effect on population dynamics (Gilg and Hilbish 2003; Hohenlohe 2004; Dupont et al. 2007). This approach, however, requires prior knowledge of the evolution of the populations in the study area. Indeed, although well-connected populations are always genetically homogeneous, the reverse is not always true. Such a genetic homogeneity may sometimes be linked to hidden historical effects of recent colonization, extremely large effective population sizes, and remnant ancestral polymorphisms. Associated with selective processes, historical effects may blur the effects of presently restricted gene flow (Fauvelot and Planes 2002) and could lead to erroneous predictions about

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the real connections among marine populations. Whereas classical nuclear markers such as allozymes may reveal historical patterns of genetic differentiation, mitochondrial deoxyribonucleic acid (mtDNA) variation is thought to better reflect more recent gene flow (Williams et al. 2002). Both markers differ in their temporal resolution of gene flow since allozymes exhibit four times the effective population size and show lower mutation rates than mtDNA. Both are also known to be under selection, which can complicate inferences, and mtDNA, despite being very informative, represents a single locus that cannot provide a full picture of events as reflected in the genome. In contrast, microsatellites, or short tandem repeats, have a significantly higher rate of mutation and are presumably neutral (but see Goldstein and Schlötterer 1999). Mutation events can therefore accumulate between divergent populations within shorter evolutionary periods, and in numbers sufficient to get a better representation of recent gene flow (Beaumont and Bruford 1999).

Although most genetic analyses fail to reveal significant levels of population differentiation for species with broad larval dispersal in the absence of biogeographical barriers (Palumbi 1994), a number of studies on benthopelagic species have reported genetic differentiation at relatively small spatial scales, independently of larval life span (Hedgecock 1986; David et al. 1997; Jolly et al. 2003). This is mainly due to environmental influences such as the fragmented nature of the habitat, oceanographic patterns promoting larval retention or larval behavior favoring homing, selective mortality of migrants, and the way propagules colonize new territories. Founder events, followed by rapid population growth and local adaptation upon colonization of new habitats, can also account for the discrepancy between high dispersal and reduced gene flow between adjacent and closely related populations. De Meester et al. (2002) propose that the monopolization of resources in a successfully established population results in the hindrance of gene flow by local adaptation and competitive superiority of resident genotypes. Particularly for species or populations presenting a short generation time, migration-drift equilibrium will be achieved faster. De Meester et al. (2002) also argue that regional patterns of genetic differentiation often reflect historical colonization of habitats, such as cases of secondary contacts, rather than contemporary gene flow. Similarly, widespread demographic instability caused by recent range expansions among recently established postglacial populations can result in a lack of genetic differentiation (Duvernell et al. 2008), which could easily be mistaken for extensive gene flow through dispersal. In any case, comparing patterns among multiple genetic markers provides a better picture of the temporal distribution of gene flow, which forms a stronger basis for any inferences made on the evolutionary drivers of population genetic structure.

At the scale of the English Channel, tidal residual currents and wind-induced currents are key factors controlling larval dispersal (Thiébaud et al. 1994; Ellien et al. 2000, 2004). In addition, the distribution of benthic populations is strongly dependent on the distribution of sediments (i.e., coarse to muddy fine sands), which in turn

is a function of local hydrodynamics. Since muddy fine sediments are restricted to bays and estuaries where local hydrodynamics are relatively weak, populations of soft sediment species such as the polychaete tubeworm *Pectinaria koreni* (Malmgren) exhibit a highly fragmented distribution. This species therefore constitutes an ideal biological model to study connectivity among disjunct and nonexploited marine populations. *P. koreni* is widely distributed in the northeast Atlantic (Holthe 1977). It is a semelparous species with a life span of 12–18 months (Elkaim and Irlinger 1987), a 2-week pelagic larval stage (Lambert et al. 1996), and a seasonal reproductive period that mostly takes place between April and June, but that can extend until September with several spawning events (Irlinger et al. 1991; Lagadeuc 1992b). Field studies and hydrodynamic two-dimensional (2-D) modeling of larval dispersal performed in the Baie de Seine (eastern English Channel) have highlighted the dominant role of wind-induced currents on the intra- and interannual patterns of larval dispersal, in relation to the variability of meteorological conditions over the species' larval life span (Lagadeuc 1992b; Ellien et al. 2000, 2004). Although larval exchanges may take place between neighboring populations to ensure replenishment, little is known about larval transport outside the boundaries of a given bay or estuary. Such events, although rare, may be sufficient enough to provide effective genetic connectivity across the English Channel since the exchange of only one effective migrant per generation may be sufficient to counterbalance genetic differentiation caused by drift or weak selection (Hartl and Clark 1989). On the contrary, larval retention or hydrodynamic barriers over many generations may set up significant levels of genetic structuring (Taylor and Hellberg 2003; Baums et al. 2006). Since indirect measures of gene flow incorporate thousands of generations of information, the analysis of differently evolving molecular markers with hydrodynamic modeling of larval dispersal may clearly help to capture the signatures of “contemporary vs. past” connectivity and “effective vs. potential” larval dispersal.

Both allozymes and a fragment of the mitochondrial cytochrome oxidase subunit I gene (mtCOI) revealed the existence of two potential cryptic species of *P. koreni*, one in the English Channel, North Sea, and Irish Sea (clade 1), the other in the eastern Atlantic (clade 2) (Jolly et al. 2005, 2006). Within clade 1, isolation by distance (IBD) between English Channel and Irish Sea populations at the mtCOI gene showed that, at this spatial scale, dispersal is constrained by geographic distance (Jolly et al. 2006). At the mesoscale of the English Channel, however, no evidence of IBD was observed. A lack of mitochondrial and nuclear (allozyme) genetic structure was also observed between both coasts of the eastern channel, despite strong hydrodynamic separation, which should favor isolation (Jolly et al. 2005). Other than balancing selection on loci, such genetic homogeneity is thought to be associated with either recent and progressive colonization of the English Channel within the last 10,000 yr, or with contemporary cross-channel larval fluxes. Thus, owing to their potential for selective neutrality and high mutation rates, microsat-

ellite markers may be better suited to examine contemporary gene flow and to correlate the degree of effective population genetic connectivity to patterns of potential larval dispersal predicted by hydrodynamic modeling.

The aim of the present work was to determine the relative influences of historical and contemporary processes on the genetic structure of *P. koreni* (clade 1) by comparing large-scale and mesoscale patterns of connectivity. One particular objective was to understand the role of larval dispersal on the contemporary population connectivity within the English Channel. Such knowledge can ultimately be extended to other commercially and ecologically important benthopelagic species with similar distributions and larval life span. For this purpose, we present allele frequency data at four highly polymorphic microsatellite loci for populations of the clade 1 of *P. koreni* distributed in the shelf seas around the British Isles. To separate the signatures of past and present gene flow, we compare our results with those obtained from two previous genetic studies based on lower mutating allozyme markers and the maternally inherited mtCOI gene (Jolly et al. 2005, 2006). Mesoscale patterns of population connectivity in the English Channel were then compared with the expected patterns of contemporary migration estimated using a recent 2-D hydrodynamic model (Bailly du Bois and Dumas 2005) and microsatellite-derived estimates of effective genetic differentiation and coalescent gene flow. This study provides a first attempt to relate simulated larval trajectories to patterns of genetic structure between putative “source” populations of *P. koreni* in the English Channel. It also provides a strong basis with which to test the likelihoods of different postglacial or contemporary migration scenarios.

Methods

Hydrodynamic modeling of larval dispersal potential—We modeled larval dispersal using the 2-D hydrodynamic Lagrangian model of the English Channel described by Bailly du Bois and Dumas (2005). Briefly, by solving an advection–diffusion–mortality equation, the model computes the transport, dilution, and mortality of particles under real tide and wind conditions in the English Channel, over timescales ranging from a week to several years. It assumes that turbulence due to tidal currents induces a rapid mixing of the entire water column, and that barotropic processes prevail over baroclinic ones in the channel dynamics (Pingree and Griffiths 1978). A mesh size of 1 km is used over the entire model domain, which covers the channel between 47°18'N and 56°20'N and between 6°28'W and 7°30'E. A preliminary calculation of instantaneous currents consisted of solving depth-integrated hydrodynamic equations using an alternative direction implicit finite difference method. By applying the “Lagrangian barycentric” method (Orbi and Salomon 1988; Salomon and Breton 1993; Breton and Salomon 1995), a database of residual currents was subsequently computed for some representative tidal conditions, assuming a spatially uniform wind stress. To compute larval dispersal, residual currents were then interpolated to real conditions

of tide and wind at the time of the simulation. Tidal amplitude was provided by the Service Hydrographique et Océanographique de la Marine (Brest). Average daily wind, assumed as representative of the entire model domain in the English Channel, was computed for the period 1980 to 2003 either from wind measurements performed by the weather station at the tip of Cape la Hague (Goury semaphore; MétéoFrance data) or by calculating the quadratic mean of the meteorological data from the European Centre for Medium-range Weather Forecast model. The coefficient of turbulent diffusion was calculated according to the empirically established Elder’s law, assuming a minimum value of $7.5 \text{ m}^2 \text{ s}^{-1}$. The model was qualitatively and quantitatively validated by comparing in situ distributions of dissolved radionuclide released from La Hague nuclear reprocessing plant with those simulated (Bailly du Bois and Dumas 2005).

The distribution of *P. koreni* is confined to muddy fine sands; thus the potential adult habitat was defined according to the distribution of superficial sediments (Larsonneur et al. 1982) and a compilation of historical records of this species in the English Channel (Fig. 1; Table 1). In this way, a total of 15 discrete potential source populations was delineated. The quantity of injected larvae for each population was calculated from estimates of adult densities and by assuming a sex ratio of 1:1 (Elkaïm and Irlinger 1987) and a mean female fecundity of 65,000 oocytes (Ellien et al. 2004) (see Table 1). *P. koreni* demes exhibit a very patchy distribution within its potential habitat (Thiébaud et al. 1997). However, to account for all possibilities, reproductive output was considered as evenly distributed for each population.

Larval dispersal was simulated over a period of 15 d, as estimated from in situ field observations in the eastern Baie de Seine (BS) (Lambert et al. 1996), with larvae considered as passive and neutrally buoyant particles. Although Lagadeuc (1992a) showed that larval behavior of *P. koreni* may alter the effects of currents on transport, Ellien et al. (2004) reported a broad agreement between simulated larval dispersal and field data in the Baie de Seine. These authors further suggested that such a depth-averaged model constitutes an efficient and robust tool to accurately predict larval dispersal distances and trajectories. Larval mortality was set to 0.06 d^{-1} , which corresponds to a low value among the range of mortality rates reported for marine invertebrate larvae (Rumrill 1990).

As larval dispersal of *P. koreni* was reported to be highly variable according to changes in seasonal and year-to-year variations in meteorological conditions, the temporal variability in local larval retention and in the strength and persistence of dispersal connections between populations was determined by simulating larval dispersal for each population at 528 different spawning dates. According to the extended reproductive period of *P. koreni*, larvae were released every week from April to August between 1980 and 2003. For each population, this procedure resulted in 22 release dates each year during 24 yr. A total of 528 connectivity matrices was then obtained. For each population and each release date, different parameters of settlement dynamics were calculated: (1) a retention rate

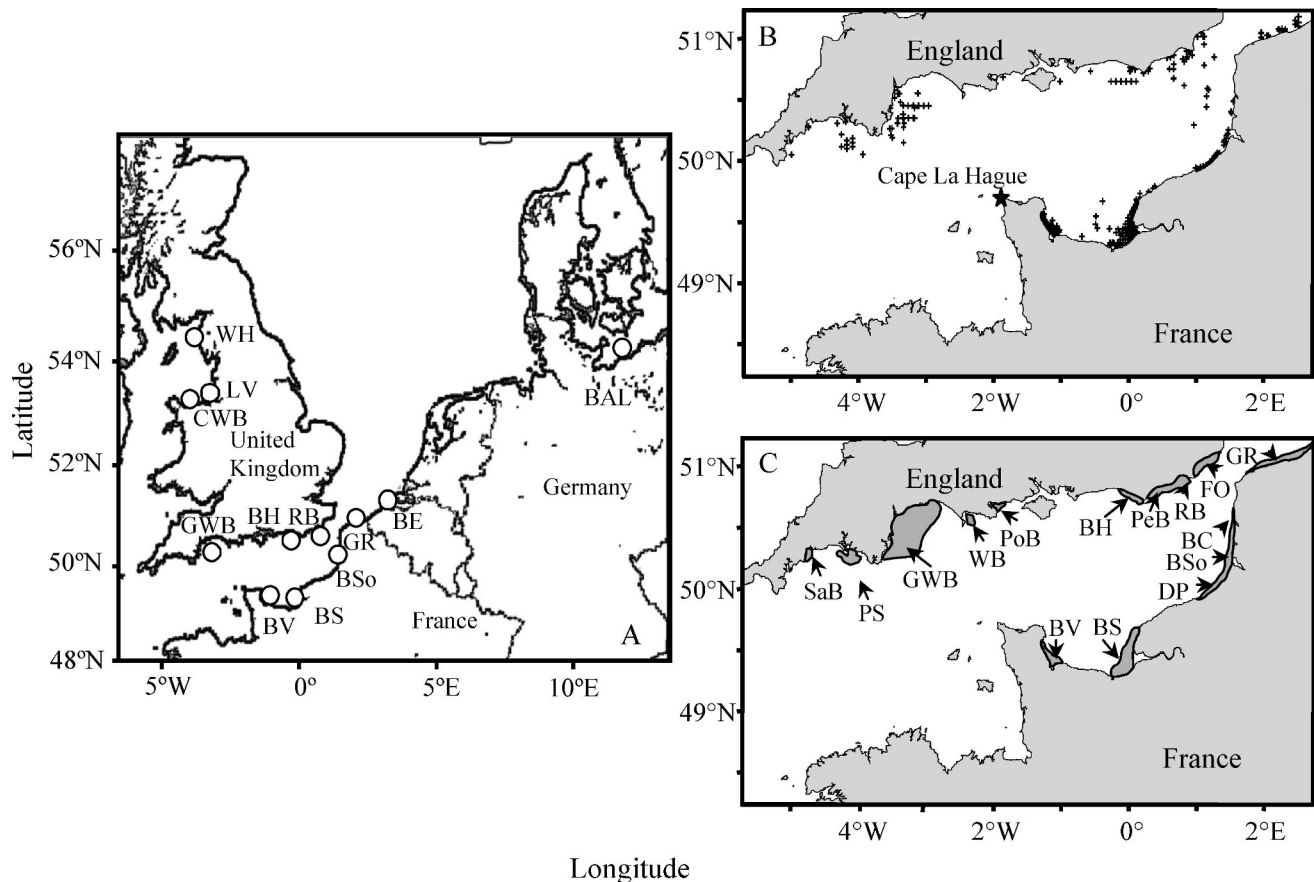


Fig. 1. *Pectinaria koreni* (clade 1). (A) Study area and locations of sampled populations for genetic analysis; (B) distribution of populations in the English Channel; (C) location of potential adult habitat and the 15 source populations used for modeling larval dispersal. Abbreviations for the study populations are the following: Baie des Veys (BV); eastern Baie de Seine (BS); Dieppe (DP); Baie de Somme (BSo); Baie de Canche (BC); Gravelines (GR); Folkestone (FO); Rye Bay (RB); Pevensey Bay (PB); Beachy Head (BH); Poole Bay (PoB); Weymouth Bay (WB); Great Western Bay (GWB); Plymouth Sound (PS); St. Austell Bay (SaB); Belgian coast (BE); Liverpool Bay (LV); Whitehaven (WH); Colwyn Bay (CWB); Baltic Sea (BAL).

(i.e., the ratio between the number of larvae retained within the source population and the number of injected larvae from this population), (2) a colonization rate (i.e., the ratio between the number of larvae transported to distant populations and the number of injected larvae from the source population), and (3) a self-recruitment rate (i.e., the ratio between the number of larvae retained within the source population and the total number of settlers received by this population). The frequency distributions of these parameters were drawn from the 528 discrete release dates and analyzed only for the seven *Pectinaria* populations of the English Channel sampled for genetic studies (see below). The average numbers of potential migrants among sites were calculated among all 15 populations.

Sampling for genetic analysis—A total of 824 individuals of *P. koreni* was collected from 11 populations of the English Channel, Irish Sea, and North Sea by dredging bays and estuaries (Fig. 1). Sampling was conducted (1) in March 2000 along the English and French coasts of the English Channel and North Sea (Gravelines, GR), (2) in July 2003 from the Belgian continental shelf (BE), and (3) in June 2004 from the Irish Sea. Additional samples from

the inner Baltic Sea (BAL; 54°11'N; 11°46'E) were obtained in May 2007. Most individuals collected came from one single position at a given locality. Samples from the eastern BS and from the Baie des Veys (BV) and Rye Bay (RB), however, consisted respectively of three and two discrete sampling sites. Despite considerable sampling effort, samples from the east coast of Wales and the Bristol Channel only consisted of two individuals (Jolly et al. 2006). Because of very high levels of genetic diversity, samples consisting of fewer than 60 individuals (collected from putative sink populations) were not used in statistical tests other than multivariate analyses.

Microsatellite genotyping—The individuals' genotypes were screened over four highly polymorphic microsatellite loci (PKG1, PKATGT1, PKATGT2, and PKATGT4) isolated by Weinmayr et al. (1999).

DNA was extracted using a 2% cetyl trimethyl ammonium bromide (CTAB) extraction procedure according to Jolly et al. (2003), whereas slightly different polymerase chain reaction (PCR) conditions were applied for the amplification of each microsatellite locus. Amplifications were carried out using a PTC200™ thermocycler (MJ

Table 1. *Pectinaria koreni* (clade 1). Population characteristics used for simulating larval transport in the English Channel. These parameters are derived from the distribution of muddy fine sediments in the English Channel (Larssonneur et al. 1982) and from a compilation of historical records (Holme 1950; Probert 1975; Desroy et al. 2003) and observations (L. Cabioch pers. comm.; F. Gentil and E. Thiébaud pers. obs.).

Population	Size of adult habitat (km ²)	Average adult density (individual m ⁻²)	Larval release
Baie des Veys (BV)	128	24.50	1.02×10 ¹⁴
Eastern Baie de Seine (BS)	448	32.92	4.79×10 ¹⁴
Dieppe (DP)	254	2.62	2.16×10 ¹³
Baie de Somme (BSO)	166	0.65	3.51×10 ¹²
Baie de Canche (BC)	224	0.52	3.79×10 ¹²
Gravelines (GR)	256	2.98	2.48×10 ¹³
St. Austell Bay (SaB)	16	0.11	5.72×10 ¹⁰
Plymouth Sound (PS)	16	0.15	7.80×10 ¹⁰
Great Western Bay (GWB)	1792	0.27	1.57×10 ¹³
Weymouth Bay (WB)	32	0.15	1.56×10 ¹¹
Poole Bay (PoB)	61	0.17	3.37×10 ¹¹
Beachy Head (BH)	128	1.04	4.33×10 ¹²
Pevensy Bay (PeB)	80	1.6	4.16×10 ¹²
Rye Bay (RB)	123	9.38	3.75×10 ¹³
Folkestone (FO)	64	3.89	8.09×10 ¹²

Research): (1) an initial denaturation step at 94°C for 4 min, (2) 38 cycles of denaturation at 94°C for 1 min, annealing for 40 s (PKATGT1-2-4 at 58°C and PKGT1 at 53°C) and elongation at 72°C for 50 s, and (3) a final elongation at 72°C for 10 min. PCR reactions were performed into a 10- μ L reaction volume consisting of 1 \times PCR buffer (supplied with polymerase enzyme); MgCl₂ at a concentration of 1.5 mmol L⁻¹ (PKGT1) or 2.2 mmol L⁻¹ (PKATGT1-2-4); 0.2 mmol L⁻¹ deoxynucleotide triphosphate; 0.4 μ mol L⁻¹ forward and reverse primers; 0.01 μ g μ L⁻¹ T4 gene 32 protein; 0.5 U of high-fidelity *Taq* polymerase (ABgene) (PKATGT1-2-4) or 0.5 U of Thermoprime Plus *Taq* polymerase (ABgene) (PKGT1); 1 μ L of a 50-ng CTAB-extracted genomic DNA. For each locus, one of the primers was labeled with IR²-700 or IR²-800 infrared fluorescent dye for genotyping. The PCR products were run on a 6% polyacrylamide and 7 mol L⁻¹ urea sequencing gel using an automated DNA sequencer (Li-Cor, model 4200™). For each microsatellite locus, alleles were labeled according to their size.

Statistical genetic analyses—Gene diversity as estimated by the observed (H_O) and expected (H_{NB} , Nei 1987) heterozygosities, the number of alleles per locus per population (N_O), and the allelic richness (R_S) were estimated using the FSTAT 2.9 software (Goudet 1995), which was also used to compare gene diversities between a priori-defined geographic groups. Standard deviations associated with gene diversity values were estimated using permutations in GENETIX 4.03 (Belkhir et al. 2004). Tests of genotypic disequilibrium between each pair of loci in each population were performed using Fisher's exact tests in GENEPOP 3.4 (Raymond and Rousset 1995). Devia-

tions from Hardy–Weinberg equilibrium were also examined for each population and each locus by calculating Wright's fixation index (F_{IS}) as estimated by F of Weir and Cockerham (1984) and testing its departure from zero by permuting genotypes within samples using GENETIX 4.03 software. Using the same software, the overall and pairwise values of genetic differentiation across samples and between localities were estimated by calculating Wright's statistics (F_{ST}) (Wright 1969) using θ of Weir and Cockerham (1984). All tests of genetic differentiation were performed with GENETIX 4.03 by permuting alleles between populations. The permutation approach implemented in this software was preferable to exact tests based on the identity in allelic distributions, because contingency tables produced from our highly polymorphic microsatellite loci gave a low number of observations in genotypic classes. On the basis of the results of the hydrodynamic circulation model, we calculated the significance levels for each pairwise value of genetic differentiation separately to avoid a type II error of rejecting significant results when these are true, due to excessive numbers of sample pairs. IBD over the whole studied area, and the English Channel only, was tested with 1000 permutations using a Mantel test implemented in GENEPOP 3.4 (Raymond and Rousset 1995). To search for specific genetic groupings among samples, a principal component analysis (PCA) was performed on both microsatellite genotype and non-singleton mtCOI haplotype frequencies (Jolly et al. 2006) using PCAGEN 1.2 (Goudet 1999). Differentiation between the observed groupings was tested with an analysis of molecular variance (AMOVA) using ARLEQUIN vs. 3 (Excoffier et al. 2005).

Markov Chain Monte Carlo (MCMC) simulations and migration model selection—We used the software MIGRATE-N version 3 (Beerli and Felsenstein 1999, 2001) to compare large-scale patterns of gene flow inferred from microsatellite loci with a similar previous analysis using the mtCOI gene (Jolly et al. 2006). Since the microsatellite data set does not fit a stepwise mutation model, and the level of polymorphism was highly fluctuating across loci, coalescent gene flow was simulated under an infinite allele model and mutation rates were calculated from the data for each locus.

At the scale of European shelf seas (macrospatial scale), we used our eight main populations and a full migration matrix using a random tree as start genealogy, with initial theta and migration values as start parameters generated from an F_{ST} -based calculation. We ran 10 short chains with 5×10^3 steps each, 10^5 sampled genealogies, and a burn-in phase of 10^4 generations, followed by three long chains with 5×10^4 steps, 10^6 sampled genealogies, and a burn-in phase of 10^4 generations. Parameter estimates were gained from a combination of three replicates.

At the mesoscale of the English Channel, we used the likelihood ratio test option and Akaike information criterion (AIC) implemented in MIGRATE-N to compare the expected pattern of larval transportation inferred from hydrodynamic modeling with the genetic data under different migration scenarios. To catch all the variability of

the system, however, it was important to include the small key intermediate Baie de Somme (BSO; $n = 12$) and distant Great Western Bay (GWB; $n = 14$) samples that had been discarded from analyses of genetic differentiation. To keep computations feasible, we grouped Beachy Head (BH; $n = 10$) with RB ($n = 90$) on the basis of geographical proximity along the south English coast in the eastern province, but kept separate GWB in the western province and BSO on the French coast in the eastern province. All models tested had a similar basic structure: all were restricted so that the only connections possible along the coastlines to and from GWB and BV were respectively with the group composed of RB and BH, and BS. Similarly, potential exchanges across the eastern English Channel were always allowed in the vicinity of the Dover Strait between BSO, RB, and GR. All parameters were free to vary.

We first estimated parameters for the following scenarios: (1) a stepping-stone model of migration (model A), expected to reflect actual dispersal on the basis of the hydrodynamic model, (2) a model of no cross-channel gene flow between BS and RB and no stepping-stone dispersal between BS and GR (model B), expected to reflect continuous gene flow along the coastlines, and (3) a model of cross-channel gene flow between BS and RB, more likely to reflect the signature of past migration, and stepping-stone dispersal between BS and GR (model C). Under these models we ran 10 short chains with 10^3 steps each, 2×10^4 sampled genealogies, and a burn-in phase of 10^4 generations, followed by three long chains with 10^4 steps, 5×10^5 sampled genealogies, and a burn-in phase of 10^4 generations. Parameter estimates were gained from a combination of five replicates. To get log-likelihoods comparable across the different simulations, we ran a final analysis, using the likelihood-ratio test option, with an unconstrained model of dispersal (model D) into which all our test models were nested. We ran 10 short chains with 10^3 steps each, 2×10^4 sampled genealogies, and a burn-in phase of 10^4 generations, followed by three long chains with 10^4 steps, 5×10^5 sampled genealogies, and a burn-in phase of 10^4 generations. Parameter estimates were gained from a combination of 10 replicates.

Since better searches are always stronger when fewer parameters are estimated (P. Beerli pers. com.), we then refined our search to get more accurate estimates of the migration rate parameters of M_1 ($M_{BS \rightarrow GR}$ and $M_{GR \rightarrow BS}$) and M_2 ($M_{BS \rightarrow RB}$ and $M_{BS \rightarrow RB}$), and compared the likelihood of the resulting model E, under a full migration matrix model, with model D where all parameters $M_{j \rightarrow i}$ and associated θ were estimated concomitantly. Model E represents the average of the migration rates $M_{j \rightarrow i}$ (immigration rate m /mutation rate $m\mu$) and θ ($4N_e m\mu$) obtained separately under models B and C, where $4N_e$ is the effective population size at our diploid loci. The values for M_1 and M_2 for model E were recalculated using the above average migration matrix and average θ s as start parameters. All start parameters were held as constant, whereas estimates of M_1 , M_2 , and their associated θ -values (θ_{BS} , θ_{RB} , and θ_{GR}) were free to vary. We ran two long chains with 5×10^4 steps, 10^6 sampled genealogies, and a burn-in phase of 10^4 generations. Using the same search

strategy as previously used for model D, we ran a final analysis using the likelihood-ratio test option to compare models D and E with the summary of genealogies generated from the full migration matrix model.

Results

Modeled larval fluxes in the English Channel—For each simulated spawning event, a total of 4.18×10^{14} larvae were released in the English Channel. More than half of this larval pool (59.3%) died over a 2-week larval life span as a result of natural mortality, and the mean proportion of larvae transported outside the potential adult habitat was 32.4%. Thus, on average, only 8.3% of larvae settled on favorable substrate, with 7.8% retained within the source populations and only 0.5% exchanged among distant populations.

Simulated larval dispersal, however, exhibited considerable spatial and temporal variation. Mean larval retention rates were maximal in GWB (18.8%), and to a lesser extent in the eastern BS (9.5%) (Fig. 2). For the other populations, mean retention rates did not exceed 3.5% of released larvae. Although local hydrodynamic features, like the “Barfleur” gyre in BV, or spatial variation in residual current velocities, may be partly responsible for the variability in larval retention, the largest retention rates estimated in GWB and BS coincide with the largest areas of potentially favorable adult habitat. Intra- and interannual temporal variability in retention rate was also substantial in response to short-term variation in hydrodynamics due to varying meteorological conditions. The strongest temporal variability in retention rate was found within the populations of RB, BSO, and GR, with a coefficient of variation exceeding 80%. Although a significant number of larvae was generally retained locally, the retention rate was less than 1% among more than 40% of simulated spawning events for these three populations.

In addition to larval retention, the relative importance of local vs. external larval inputs was highly variable in space and time. Three different patterns emerged (Fig. 3). First, self recruitment was consistently high for BV, BS, and GWB, exceeding 95% in most simulated spawning events. Significant supply of settlers from distant populations occurred only very sporadically, and variation in local retention rates was the main cause of variation in primary settlement intensity. Second, for populations of GR and BH, self recruitment remained the main process involved in local population persistence over the long term, but larval supply from distant populations was more important than local supply in about 25% of simulated larval releases, which could play a significant role in the population dynamics of the species when retention rates are low. Third, for populations of BSO and RB, self-recruitment rates were highly variable in time, but averages reached 15.5% and 44.1%, respectively. This greater role of external larval supply on population dynamics could be related to the usually low retention of locally released larvae simulated at these sites.

Over several generations, all local *P. koreni* populations in the English Channel were connected at least to some of their

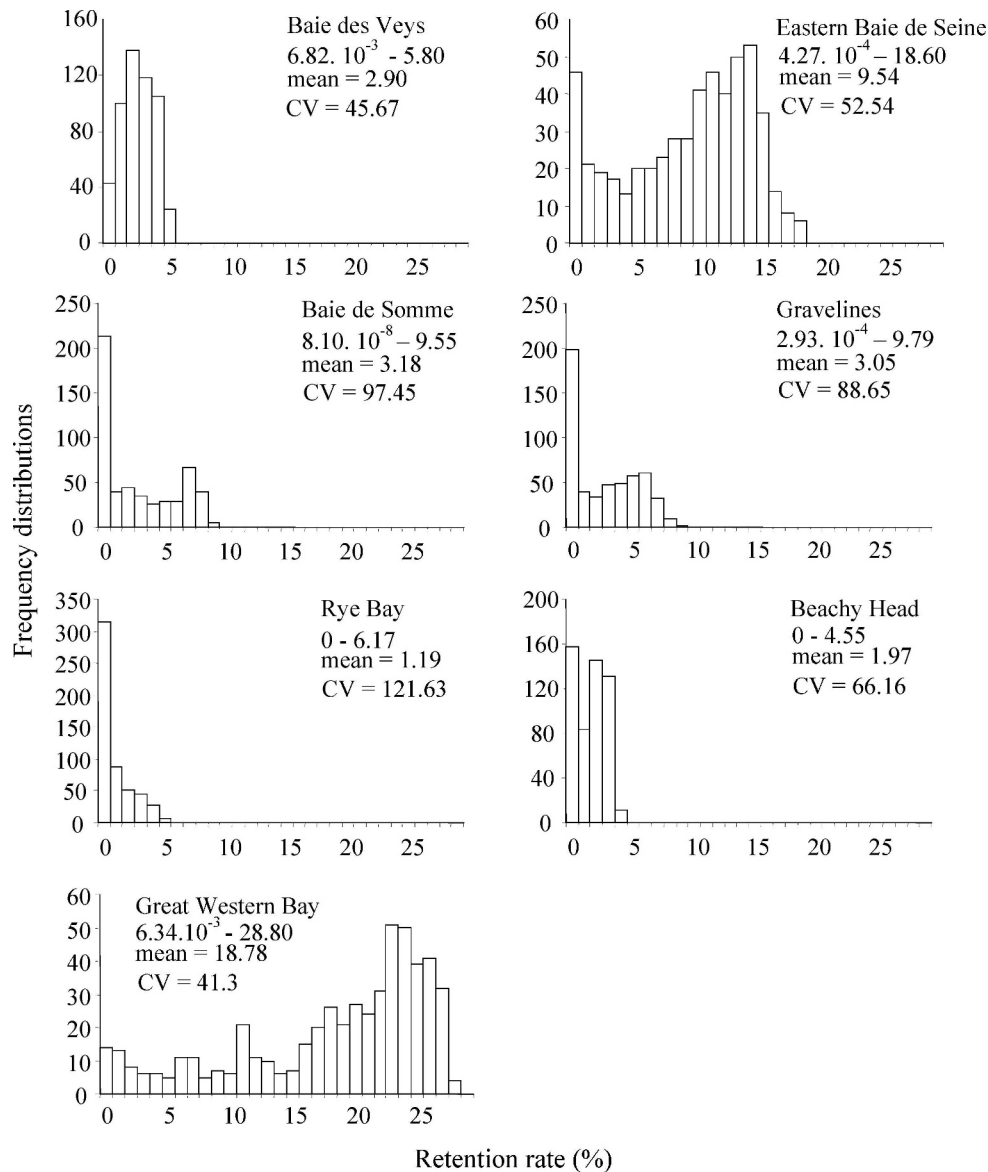


Fig. 2. *Pectinaria koreni* (clade 1). Frequency distributions of retention rates for the main populations in the English Channel on the basis of 528 connectivity matrices. The distribution for each population is characterized by the range in retention rate, its mean value, and its coefficient of variation (C.V.) (i.e., [standard deviation/mean] \times 100).

distant populations (Fig. 4A). Relatively strong connections (over 1% of the total number of larvae exchanged among the 15 populations) occurred mainly over short distances (1 km to 10 s of km), between very close populations distributed along the French or the eastern English coasts of the eastern channel. The number of connections was also maximal in these areas, with some populations like RB, BSo, or GR receiving larvae from up to five different populations. Larval exchanges tended to decrease with distances, suggesting a stepping-stone pattern of dispersal along the coastlines. For example, larvae released from BS are less and less connected to other populations along the French coasts of the channel as distances separating them increased: although mean exchanges between BS and Dieppe (DP) exceeded 10% of total exchanges, mean exchanges between the former and

GR represented less than 0.01% of total exchanges. Mainly asymmetric exchanges were observed from BS to GR, as tidal residual currents over the area are mainly oriented SW to NE. Cross-channel exchanges were restricted to the vicinity of the Dover Strait, although, despite short geographical distances between populations, exchanges remained generally weak since water mass transport in the strait is mainly channeled eastward, parallel to the coast. Connectivity between western and eastern provinces of the English Channel occurred very sporadically and only via BH and Poole Bay.

Although local retention and self recruitment were the main processes involved in the dynamics of most local populations, not all populations played the same role in the meta-population dynamics at the scale of the eastern

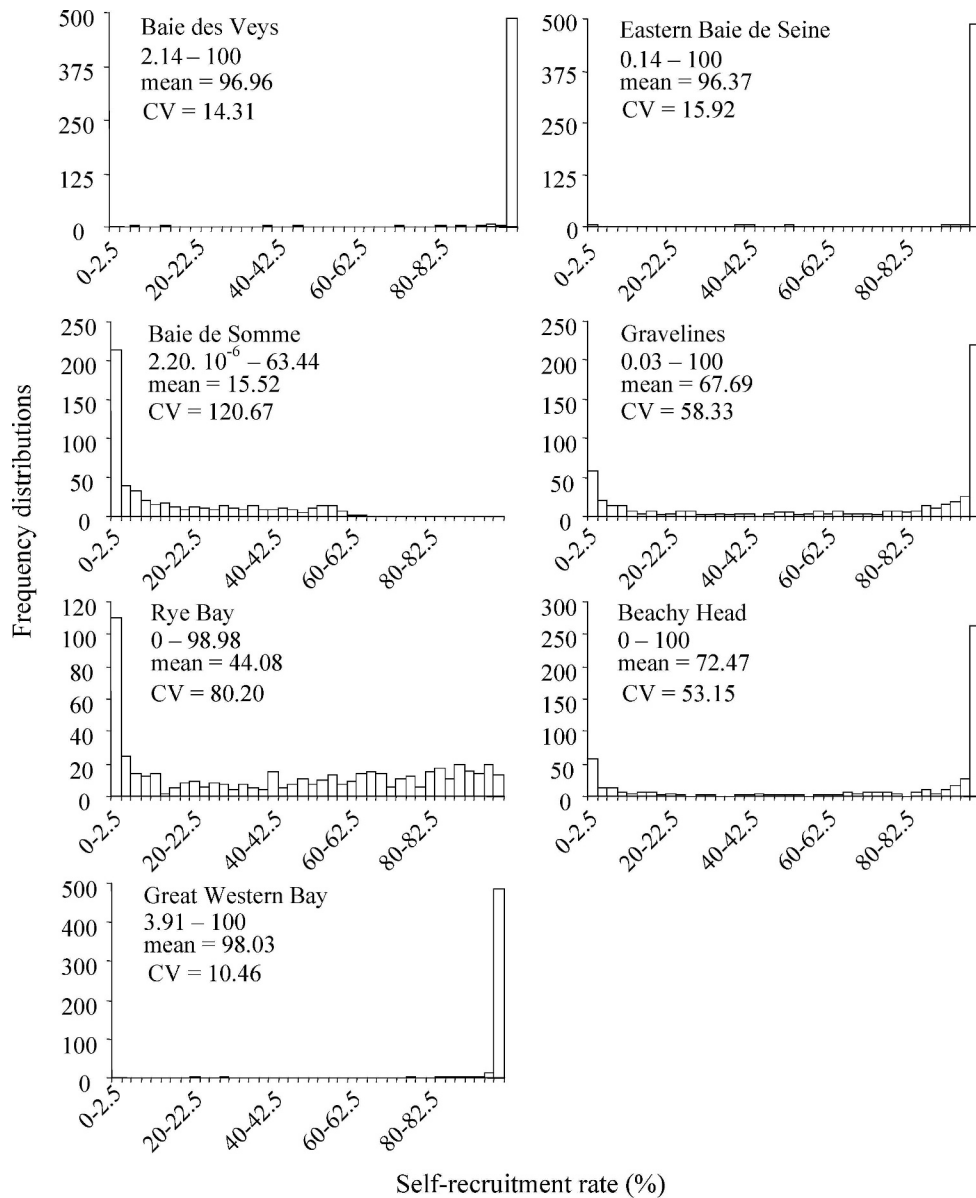


Fig. 3. *Pectinaria koreni* (clade 1). Frequency distributions of self-recruitment rates for the main populations in the English Channel on the basis of 528 connectivity matrices. The distribution for each population is characterized by the range in self-recruitment rate, its mean value, and its coefficient of variation (C.V.) (i.e., [standard deviation/mean] \times 100).

English Channel. According to its adult population size, its persistence due to a high retention rate, and its strong direct and indirect links with other populations, the BS population appears as one of the most stable source populations. Other populations with highly variable self-recruitment rates may on the contrary act as sinks or relay populations, because local population dynamics mostly rely on external larval imports. This is the case for BSo on the French coast and RB on the English coast.

Genetic diversity of P. koreni (clade 1)—There was no significant association of alleles between any of the four diploid loci. The four microsatellite loci exhibited very

high levels of polymorphism, ranging from 34 alleles at the locus PKATGT4 to 73 alleles at PKATGT2 (Table 2). Consequently, gene diversity values (H_{NB}) were also very high. All loci deviated significantly from Hardy–Weinberg proportions as revealed by the fixation index (F_{IS}), which reflected a pronounced heterozygote deficiency for all loci. These deficiency levels were nearly threefold lower for the less polymorphic locus PKATGT4 (34 alleles) compared with PKGT1 (42 alleles), whereas intermediate levels were recorded for two loci showing the highest number of alleles (PKATGT1, PKATGT2, see Table 2). High levels of heterozygote deficiencies are partly explained by the occurrence of null alleles, mainly because

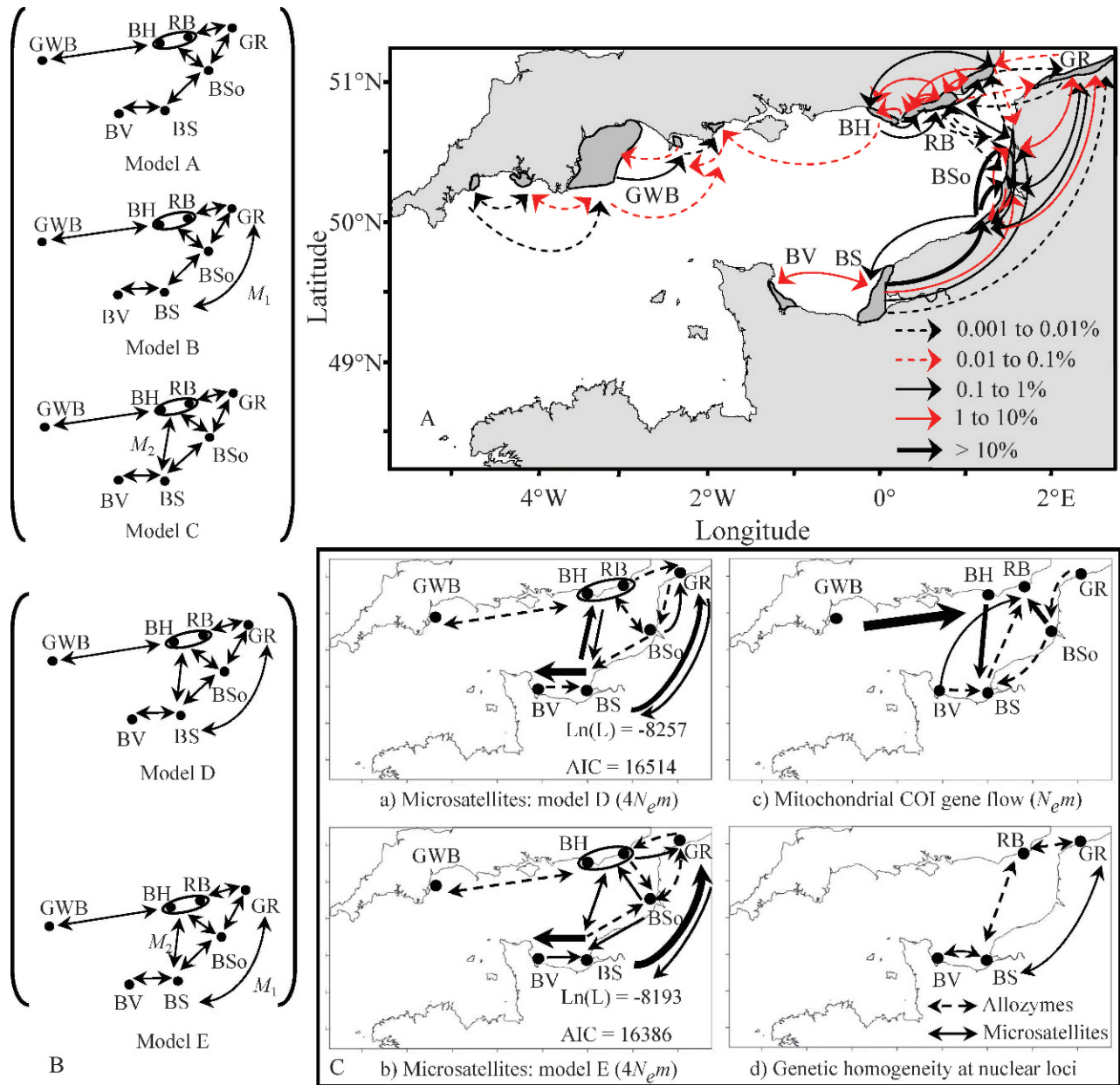


Fig. 4. *Pectinaria koreni* (clade 1). (A) Hydrodynamic modeling: mean larval fluxes on the basis of 528 connectivity matrices representing all possible spatial and temporal connections. Fluxes are expressed as a proportion of the total number of larvae exchanged among the 15 source populations. (B) Nested migration models compared under the microsatellite data set, using the likelihood-ratio test option implemented in MIGRATE-N (Beerli and Felsenstein 1999, 2001). Models A, B, and C, are nested into model D (cross-channel gene flow, no stepping-stone dispersal). Model E, which incorporates the migration rates M_1 and M_2 estimated, respectively, from model B and model C, was compared with model D under a full migration matrix. (C) Maps (a) and (b): gene flow patterns resulting from migration models D and E, with their associated log-likelihoods and AIC estimates. Map (c): the predominant pattern of gene flow in the English Channel inferred from the mtCOI gene (Jolly et al. 2006); the weights of the arrows are proportional to estimates of $N_e m$. Map (d): patterns of genetic homogeneity among eastern English Channel populations, as observed with allozymes (Jolly et al. 2005) and microsatellite loci.

a nonnegligible proportion of individuals did not amplify effectively at all loci. With such high degree of microsatellite polymorphism, we estimated that 75 individuals was the minimum sample size needed to retrieve 85% of the total genetic diversity across all loci. The three putative sink populations (i.e., GWB, BH, BSo) for which samples consisted of fewer than 15 individuals displayed

biased estimates of allelic richness (R_S) and gene diversity (H_{NB}). These populations, along with BAL, which consisted of 29 individuals, were discarded from pairwise analysis of genetic differentiation. They were, however, included in the PCA of nuclear data to estimate their genetic positioning in relation to potential source populations.

Table 2. *Pectinaria koreni* (clade 1). Expected (H_{NB}) and observed (H_O) heterozygosity for each microsatellite locus. Number of alleles (N_{ALL}); intrapopulation fixation index (F_{IS}) according to Weir and Cockerham (1984).

Locus	Length (base pairs) (range)	N_{ALL}	H_O	H_{NB}	F_{IS}
PKGT1	191–354 (164)	42	0.293	0.925	0.712***
PKATGT1	246–438 (193)	59	0.555	0.961	0.401***
PKATGT2	230–400 (171)	73	0.512	0.962	0.472***
PKATGT4	242–394 (153)	34	0.724	0.941	0.249***

*** $p < 0.001$.

Although levels of genetic diversity were high in all populations (Table 3), comparisons between a priori-separated groups on the basis of their geographic location (i.e., eastern English Channel—RB, BV, BS; Irish Sea—Whitehaven [WH], Liverpool [LV], Colwyn Bay [CWB]; southern North Sea—GR, BE) revealed significant differences in both gene diversity ($p = 0.042$) and allelic richness ($p = 0.041$). This was attributable to the Irish Sea group, which apart from showing the lowest heterozygote deficiencies ($F_{IS} = 0.387$; $p = 0.008$), was also genetically less diverse ($H_{NB} = 0.956$, $p = 0.003$; $R_S = 26.779$, $p = 0.012$).

Genetic structure of P. koreni (clade 1)—The PCA performed on non-singleton mtCOI haplotype frequencies clearly identified two geographically restricted groups of populations ($p = 0.021$), each representing an isolated gene pool that contributed to the origin of the study populations (Fig. 5A).

This pattern changes slightly when the PCA was performed on microsatellite data, but still revealed a significant overall genetic structure ($p = 0.001$) (Fig. 5B). Two slightly different main groups of populations emerge from the two analyses. The first (cluster 1) includes two populations from the Irish Sea (CWB and LV) and BE, from the Belgian continental shelf of the North Sea. The second (cluster 2) includes populations of the eastern English Channel (BV, BS, RB) together with GR, situated less than 65 km south of BE. The population of WH from the northeastern part of the Irish Sea occupies an intermediate position on the first significant factorial axis. WH is part of a third group (cluster 3) that includes GWB and BH, from the southern English coast. Samples from BAL appeared more closely related to cluster 1 than they were to cluster 2 or 3. An AMOVA performed after an a posteriori separation of the first two clusters of populations (clusters 1 and 2) resulted in a low but significant genetic differentiation among the two groups (fixation index, $F_{CT} = 0.004^*$, $p = 0.026$).

Globally, F_{ST} -based estimates of genetic differentiation were small but highly significant ($F_{ST} = 0.004$; $p < 0.001$) over the whole studied area. Although there was no significant correlation between pairwise matrices of genetic and geographic distances (Mantel test, $p = 0.099$), the highest levels of genetic differentiation were found between the most distant populations in both the Irish Sea and the eastern English Channel, respectively between WH and CWB and between RB and BV ($F_{ST} = 0.01^{***}$ and $F_{ST} =$

0.004^{**} , respectively; Table 4). Irish Sea populations generally appeared to be more structured (overall $F_{ST} = 0.006^{***}$) than those in the eastern English Channel (overall $F_{ST} = 0.002^*$), although this difference was not significant ($p = 0.142$). In the eastern English Channel, BS and BV together with BS and GR were especially well connected ($F_{ST} = 0.000$; Table 4) and, judging from the significance levels, gene flow between RB and BS and between GR and RB appeared to be only slightly restricted ($F_{ST} = 0.002^*$). As reflected by the AMOVA performed previously, pairwise estimates of genetic differentiation indicated that the population from BE was genetically more similar to populations from the Irish Sea ($0.0004 < F_{ST} < 0.004^*$) than to those from the eastern English Channel ($0.003^{**} < F_{ST} < 0.007^{***}$).

Coalescent gene flow and migration model selection—Figure 6 depicts the macroscale pattern of connectivity using estimates of the migration rate parameter M ($4N_e m/\theta$). This parameter is a better representation of the importance of immigration over mutation in bringing new variants into the population. M was strongest among the eastern English Channel, especially between BS and RB ($M_{BS \rightarrow RB} = 4.43$ and $M_{RB \rightarrow BS} = 3.84$, with $\theta_{BS} = 6.436$ and $\theta_{RB} = 4.468$) and between BS and BV ($M_{BS \rightarrow BV} = 3.84$ and $M_{BV \rightarrow BS} = 4.40$, with $\theta_{BV} = 4.362$). However, relatively strong and symmetric rates are observed along the continental coastlines between the Baie de Seine (BS and BV) and North Sea populations (GR and BE), where $M_{BS \rightarrow GR} = 3$ and $M_{BE \rightarrow BS} = 3.15$ (with $\theta_{GR} = 4.49$ and $\theta_{BE} = 3.885$). These migration rates were similar in magnitude and symmetry to those observed between the North Sea and the Irish Sea populations of CWB and LV ($M_{GR \rightarrow LV} = 3.01$ and $M_{CWB \rightarrow BE} = 3.63$; $\theta_{LV} = 4.789$ and $\theta_{CWB} = 4.632$). Migration rates to and from WH, however, were much weaker, but it is interesting to note that the rate parameter M was stronger with BE ($M_{BE \rightarrow WH} = 2.81$) and that both populations had the smallest θ ($\theta_{BE} = 3.885$ and $\theta_{WH} = 3.518$). In contrast with the mtCOI gene (Jolly et al. 2006), the nuclear microsatellite loci depicted a different but complementary picture of the colonization pathways around the British Isles, with more predominant Irish Sea and North Sea connections, as opposed to the ones between Irish Sea and English Channel populations.

At the mesospatial scale of the English Channel, the comparison of the log-likelihood values for each of our test models (models A, B, and C; see Fig. 4B) was carried out under the restricted model D. The likelihood-ratio test

Table 3. *Pectinaria koreni* (clade 1). Genetic diversity and heterozygosity (standard error) at microsatellite loci for each well-sampled population. *n*, number of individuals; *N_O*, average number of alleles; *H_O*, observed heterozygosity; *H_{NB}*, nonbiased expected heterozygosity; *R_S*, multilocus average allelic richness based on a minimum sample size of 20 diploid individuals. Sample locations: eastern Baie de Seine (BS), Baie des Veys (BV), Rye Bay (RB), Gravelines (GR), Belgium (BE), Liverpool (LV), Whitehaven (WH), Colwyn Bay (CWB).

	English Channel			North Sea		Irish Sea		
	BS	BV	RB	GR	BE	LV	WH	CWB
<i>n</i>	227	70	134	90	74	61	61	71
<i>N_O</i>	42	33	38	33	31	28	31	31
<i>H_O</i>	0.4699 (0.1826)	0.4772 (0.1838)	0.5059 (0.2116)	0.5224 (0.2381)	0.5514 (0.2263)	0.5852 (0.2215)	0.5407 (0.1506)	0.6299 (0.1574)
<i>H_{NB}</i>	0.9604 (0.0165)	0.9604 (0.0143)	0.9597 (0.0124)	0.9542 (0.0189)	0.9562 (0.0168)	0.9535 (0.0151)	0.9518 (0.0230)	0.9522 (0.0215)
<i>R_S</i>	22.11	21.95	21.65	20.85	20.63	19.93	20.81	20.29

clearly rejected the stepping-stone model of dispersal expected from our hydrodynamic modeling (model A; $\ln[L]_{\text{test}} = -10,038$, $\text{AIC} = 20,088$). Rather, model selection criteria preferred the model of cross-channel exchanges, expected from the hypothesis of past gene flow (model C; $\ln[L]_{\text{test}} = -3478$, $\text{AIC} = 6968$; $p < 0.001$) instead of model B ($\ln[L]_{\text{test}} = -3593$, $\text{AIC} = 7198$), expected to reflect continuous gene flow between BS and GR. Under a full migration matrix, the likelihood-ratio test selected model E (Fig. 4C map b; $\ln[L]_{\text{test}} = -8193$, $\text{AIC} = 16,386$; $\text{df} = 36$, $p < 0.001$) over model D ($\ln[L]_{\text{test}} = -8257$, $\text{AIC} = 16,514$), under which cross-channel exchanges from BS to RB were greater ($4N_e m = 31$ compared with $4N_e m = 23.8$ in model E) and gene flow from BS to GR was weaker ($4N_e m = 30$ as opposed to $4N_e m = 41.6$ in model E). In addition, under the preferred model E, exchanges in the vicinity of the Dover Strait were increased, for example from BSo to RB ($4N_e m = 21.6$ compared with $4N_e m = 11.5$ in model D) and from RB to GR ($4N_e m = 20$ compared with $4N_e m = 10.3$ for model D). In both models, however, migration rates between RB and GWB were always more restricted ($10.5 < 4N_e m < 16.7$) compared with those along the French coast, where BS was always a large source of migrants for BV ($62 < 4N_e m < 71$) and for GR. Model E can be compared with the pattern of genetic differentiation given by microsatellites (Fig. 4C map d), with genetic homogeneity between BS and BV on one side and BS and GR on the other. By contrast, both allozymes (Fig. 4C map d) and the mtCOI gene (Fig. 4C map c) favored cross-channel exchanges and very limited connectivity along the French coast.

Different simulations undertaken under a full matrix model, whether at the macroscale (two simulations) or the mesoscale of the English Channel (two simulations), with constant or variable mutation rates among loci, always gave very similar estimates of θ , with BS presenting the highest population size ($6.16 < \theta_{\text{BS}} < 6.44$). All the other populations of the English Channel presented lower average estimates, all ranging from $\theta_{\text{GR}} = 4.43$ to $\theta_{\text{RB}} = 4.92$, apart from GWB in the western province, which presented the lowest ($\theta_{\text{GWB}} = 3.67$). Overall, compared with the eastern English Channel ($\theta_{\text{AVG}} = 5.18$), both the

North Sea ($\theta_{\text{AVG}} = 4.16$) and the Irish Sea ($\theta_{\text{AVG}} = 4.31$) had more reduced population sizes.

Discussion

According to the published haplotype network (Jolly et al. 2005, 2006), historical admixture of ancestral haplotypes and the retention of ancestral polymorphism may have resulted in a large-scale Wahlund effect among populations of *P. koreni* (clade 1). This historical effect is not apparent from the allozyme loci where there were no large deviations of genotype frequencies from those expected under Hardy–Weinberg equilibrium. Most likely, a state of panmixia was reached shortly after the secondary admixture. It is therefore most likely that the high levels of intrapopulation differentiation (F_{IS}) observed here at the microsatellite loci are caused by the presence of null alleles. Interestingly, the less polymorphic (34 alleles) microsatellite locus PKATGT4 had the lowest F_{IS} values, albeit significant, and along with PKGT1 (42 alleles) exhibited the greatest differentiation among populations. In contrast, the other two more polymorphic loci (73 and 59 alleles) contributed the least to the overall levels of genetic differentiation. Values of F_{ST} may be depressed at high heterozygosities for a range of population structures and demographic histories (Beaumont and Nichols 1996), and loci that show unusually high levels of genetic differentiation are often assumed to be subject to selection. Whereas specifically testing for these effects would require a high number of loci, using cluster analyses and the available data for each population, we did not detect any evidence for spatially varying selection.

Despite the contrasting temporal resolution of mitochondrial and nuclear gene loci, both showed clear genetic structuring of populations at the scale of the whole study area (Irish Sea, English Channel, and southern North Sea). The amount of nuclear genetic differentiation, however, is weak, with low values of pairwise genetic differentiation even when these are significant. This may be partly explained by the fact that *P. koreni* has discrete generations and populations, even with considerable census sizes, that experience extinction–recolonization dynamics on an annual basis (Eagle 1973, 1975; Lambert 1991). These

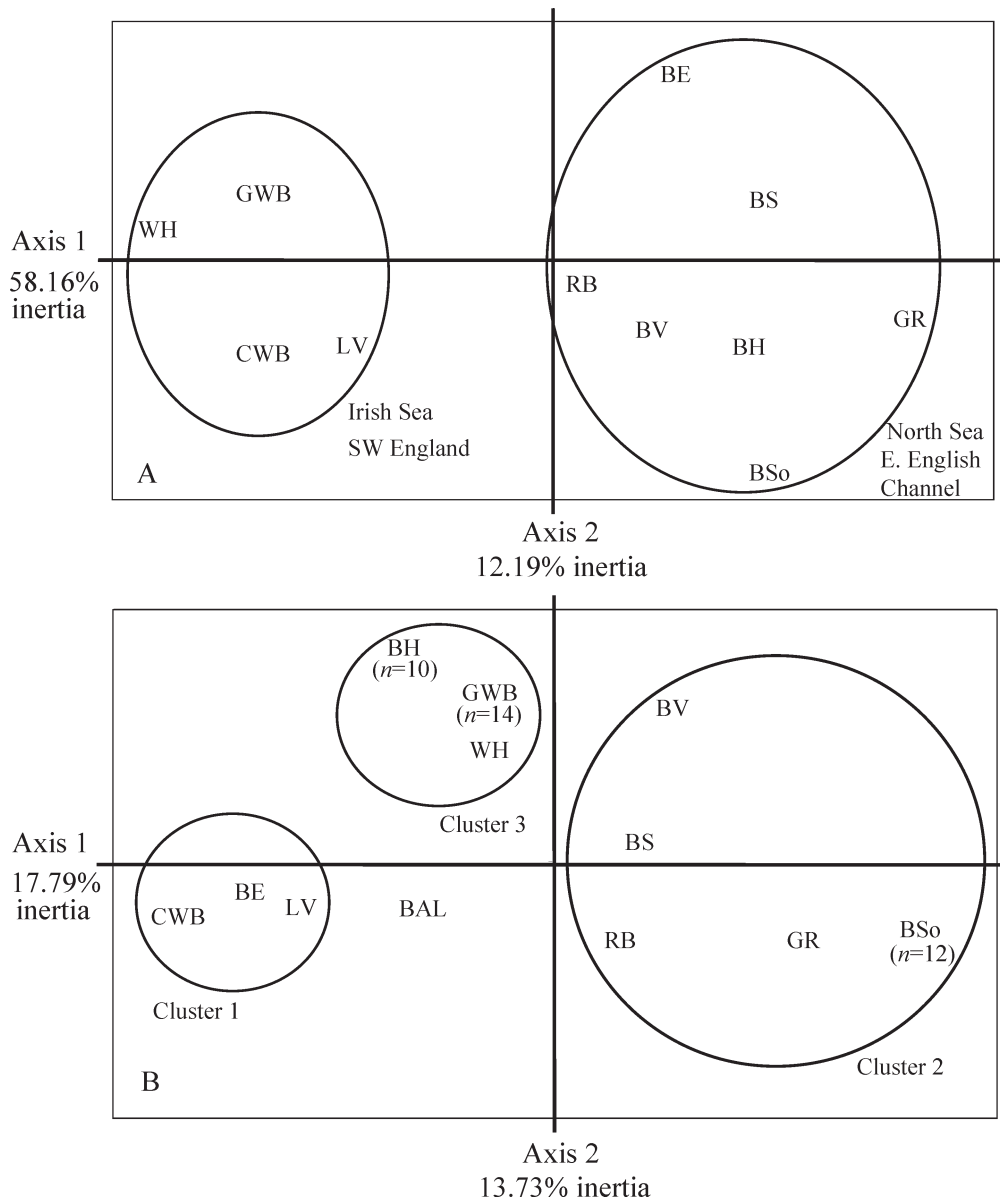


Fig. 5. *Pectinaria koreni* (clade 1). Principal component analyses (PCA) obtained from allelic frequencies at (A) non-singleton mtCOI haplotypes and (B) four microsatellite loci, using PCA-Gen 1.2 (Goudet 1999). Irish Sea: WH, CWB, LV; western English Channel: GWB; eastern English Channel: BV, RB, BS, BH, BSo; southern North Sea: BE, GR; Baltic Sea: BAL.

characteristics are reflected in the considerable amount of genetic variation found among all well-sampled populations. Although the effective population size is expected to be four times greater in the case of nuclear markers, our data sets indicate that weak levels of genetic differentiation may be also associated with both the retention of ancestral polymorphism and post-Pleistocene expansion of *P. koreni* (clade 1) into European shelf seas. More specifically, historically driven patterns of gene flow associated with the progressive colonization of the seas surrounding the British Isles (within the last 10 to 12,000 years according to postglacial estimates of sea level rise, Lambeck 1997; Renssen and Vandenberghe 2003) may have masked contemporary patterns of gene flow among more recently established populations. Hydrodynamic modeling of po-

tential larval trajectories and coalescent gene flow analyses enabled us to address this issue in the English Channel, but first, some interesting points need to be discussed in relation to the postglacial colonization of *P. koreni* clade 1 and the present-day long-term pattern of marine currents around the British Isles.

mtDNA and microsatellite loci reveal large-scale complementary histories—Using non-singleton mtDNA haplotype frequencies from published sequences (Jolly et al. 2006) we identified two historical gene pools that contributed to the origin of contemporary populations. The PCA clearly highlighted the geographic partitioning of all populations. The analysis also demonstrated the existence of post-Pleistocene connections between the Irish Sea and the

Table 4. *Pectinaria koreni* (clade 1). Above diagonal: significant pairwise F_{ST} -values from Weir and Cockerham (1984) at microsatellite loci. Below diagonal: p -values associated test of significance performed with GENETIX 4.02 (Belkhir et al. 2004) with 1000 permutations. Each test was carried out independently for separate pairwise combinations of populations. n , number of individuals genotyped.

	English Channel			North Sea		Irish Sea		
	BS	BV	RB	GR	BE	LV	WH	CWB
n	227	70	134	90	74	61	61	71
BS	—	0.000	0.002*	0.000	0.003**	0.003*	0.003*	0.004**
BV	0.362	—	0.004**	0.006***	0.007***	0.008***	0.004*	0.008***
RB	0.012	0.005	—	0.002*	0.004**	0.004**	0.007***	0.006***
GR	0.443	0.000	0.036	—	0.007***	0.007**	0.007**	0.010***
BE	0.008	0.000	0.009	0.000	—	0.004*	0.003	0.000
LV	0.040	0.000	0.003	0.001	0.021	—	0.005*	0.002
WH	0.018	0.027	0.000	0.001	0.073	0.023	—	0.010***
CWB	0.001	0.000	0.000	0.000	0.415	0.126	0.000	—

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

southwest English coast, and historical population expansion in the eastern English Channel and the southern North Sea. Unfortunately, sampling is still insufficient to give a precise answer to the historical distribution of the two source populations or historical gene pools. Were they both present along the Atlantic coasts of Ireland and the western approach of the English Channel, or did one historically

occupy an area of the North Sea situated along the north coast of Scotland?

On the basis of the distribution of non-singleton haplotypes, the population of BH belongs to the eastern English Channel group, but coalescent simulations using the complete mitochondrial data set (Jolly et al. 2006) clearly depicted strong ancestral gene flow from the Irish Sea to the western English Channel (GWB), and from the western to the eastern province (BH). In contrast, gene flow between the Irish Sea and the southern North Sea was much weaker. These patterns, combined with the fact that both southern North Sea populations had mitochondrial signatures similar to eastern English Channel populations, suggest that one historical source population contributed to the establishment of all contemporary populations of the eastern English Channel and southern North Sea at a time when a shoreline must have still existed across the central part of the North Sea. This bridge would have effectively separated the southern from the northern part of the North Sea around 8700 yr ago (Smith 1989). Several narrow passes or gorges linking the eastern English Channel to the southern and central North Sea were subsequently widened during sea level rise into what is now the Dover Strait, after which dispersal further north was facilitated by the onset of modern water circulation.

On the basis of the microsatellite markers, concordance exists with the clustering pattern exhibited by the mtCOI gene for populations of the eastern English Channel (except BH), Irish Sea (CWB, LV), and Solway Firth–western English Channel (WH, GWB). However, microsatellites are markers with high mutation rates and although similarities exist with mtDNA, the nuclear data described a more recent history of secondary contact and restriction to gene flow in the eastern English Channel and the southern North Sea. For example, samples from the southern English coast (GWB and BH) and Solway Firth (WH) were positioned intermediately with respect to the other Irish Sea and eastern English Channel populations, which suggests historical contact between western (GWB) and eastern provinces (BH) of the channel. The positioning of the BAL samples also suggests a composite origin for this population, associated with postglacial expansion of the

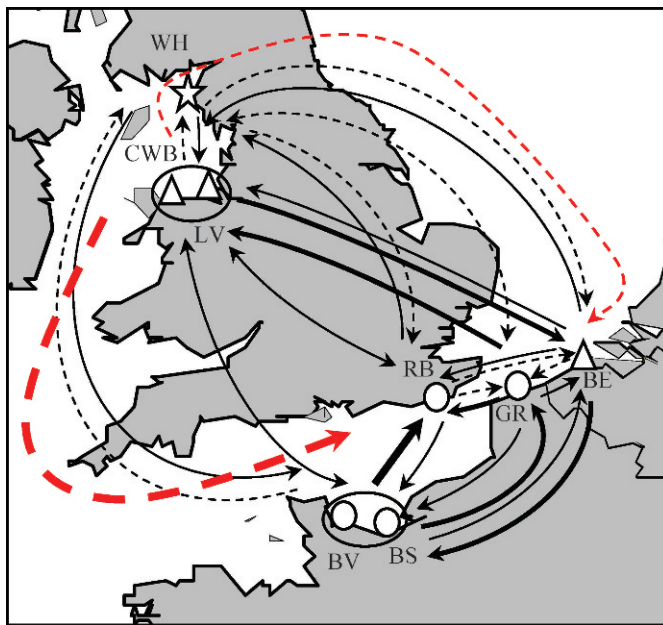


Fig. 6. *Pectinaria koreni* (clade 1). Map representing the scaled migration rate parameter M (immigration rate m /mutation rate μ) obtained from a full matrix model of connectivity in MIGRATE-N (Beerli and Felsenstein 1999, 2001). For a better representation, only the strongest fluxes to and from the CWB-LV group and the BS-BV group are shown. Triangles, bullets, and stars represent respectively clusters 1, 2, and 3 of the principal component analysis (PCA) on the basis of microsatellite allele frequencies. The major directions and strengths in gene flow inferred from the mtCOI gene (Jolly et al. 2006) are illustrated by red arrows proportional to migration rates ($N_e m$).

two ancestral gene pools identified in the Irish Sea and the eastern English Channel.

Our analyses also clearly indicate secondary contact in the southern bight of the North Sea between historical source populations that diverged at mitochondrial and nuclear DNA, a result that agrees well with other reported cases of secondary contact in the same area (see Derycke et al. 2008). *P. koreni* would have had ample time to colonize the North Sea after the Younger Dryas cold phase (13,000–11,000 yr ago) and before the formation of the Dover Strait (around 8000 yr ago), at which time both the English Channel and the Irish Sea were partly open to the Atlantic (Renssen and Vandenberghe 2003). If ancestral gene flow (Jolly et al. 2006) was predominantly oriented from the Irish Sea to the western English Channel (GWB), and from the western toward the eastern province, both coalescent simulations and the positioning of the Belgian population (BE) in the PCA indicate a separate and possibly temporally distinct pathway directed from the Irish Sea to the southern part of the North Sea via the unsampled Scottish and eastern English coasts (Fig. 7). In addition, the strength of the signal in the PCA may suggest a high frequency of long-distance dispersal during postglacial expansion into the southern North Sea, which can be explained by the setting up of Holocene marine currents. A similar explanation was given by Colson and Hughes (2007) for the lack of IBD in the predatory gastropod *Nucella lapillus* in the East Atlantic. On a more contemporary note, we can observe that the long-term influx of water coming in through the Dover Strait is much weaker than that brought in by Atlantic water into the northern part of the North Sea (Turrell 1992; Fig. 7). In addition, the distribution of the ^{137}Cs released from Sellafield nuclear reprocessing plant (Irish Sea) also demonstrates significant transport into the North Sea.

On the basis of contemporary oceanographic patterns, we could argue for more recent dispersal along the eastern coast of Scotland and England, setting up gene flow through many generations. What might be more surprising, however, are the levels of genetic differentiation observed among southern North Sea populations. Populations of *P. koreni* are continuously distributed from the north coast of France up to the Dutch coast (Van Hoey et al. 2005). In addition, the predominant flow through the Dover Strait is from west to east (Fig. 7) and the water flowing out of the English Channel into the North Sea follows the Belgian and Dutch coasts up to Denmark (Breton and Salomon 1995; Bailly du Bois and Dumas 2005). Gene flow is therefore expected between French and Belgian populations, although this may have taken the form of differential introgression of nuclear and mitochondrial markers. There may also be either a strong reproductive asynchrony and differential selection between individuals of GR and BE, or a dampening of larval exchanges during the reproductive period of *P. koreni* since net fluxes in the vicinity of the Dover Strait may be close to zero in spring (Turrell et al. 1992). In addition, Van Hoey et al. (2005) proposed that the important changes observed along the Belgian continental shelf in the composition of the *Abra alba* community, to which *P. koreni* is one of the top 10 representatives,

may be at least partly explained by the specific hydrodynamic conditions in the English Channel (flood-dominated currents) and the southern bight of the North Sea (ebb-dominated currents), thereby creating hydrological conditions favoring little larval exchange.

In general, the large-scale comparison of genetic data with the long-term pattern of marine currents around the British Isles agrees well in recognizing patterns that correspond to past gene flow and secondary contact zones. Not only are the predominant fluxes revealed by mtDNA oriented differently from those predicted by hydrodynamic models of water circulation, but gene flow between the Irish Sea and the southern English coast, or for that matter between the Irish Sea and the southern North Sea, is very improbable without the presence of intermediate populations. Likewise, gene flow inferred from microsatellites between the western and the eastern provinces of the English Channel would require extreme wind conditions in the light of our simulated larval transport, suggesting that they mostly reflect postglacial colonization pathways. Nonetheless, at the mesoscale of the eastern English Channel (including GR), both population genetic differentiation indices and the migration model selection procedure used tended to agree with hydrodynamic simulations of potential larval transport.

Correlation between gene exchanges and modeled larval transport in the English Channel—According to the hydrodynamic modeling, over several generations, all local *P. koreni* populations in the English Channel were connected at least to some of their distant populations. Nevertheless, both coalescent gene flow simulations and hydrodynamic modeling of larval transport demonstrated limited exchanges across the central province of the English Channel, compared with other potential exchanges. For example, most populations in the eastern English Channel are well connected through larval dispersal along both the English and French coastlines. In particular, considerable gene flow was predicted by the circulation model between BS and BV, and between BS and GR, and no genetic differentiation was observed. First, this reveals that both BS and BV are tightly connected even if they are both extremely self-sustainable. Second, previous studies on natural populations of *Ostrea edulis* (Launey et al. 2002) and the invasive *Crepidula fornicata* (Dupont et al. 2003) show genetic homogeneity along the same 230-km stretch of coastline separating BS from GR. Conversely, small but significant genetic differentiation occurs among populations from both coasts (i.e., the pairs RB-GR and RB-BS), a result consistent with predictions based on the hydrodynamic model. Interestingly, previous work on enzyme loci reported no genetic differentiation between the same populations, but significant genetic differentiation along the coastline between BS and GR ($F_{ST} = 0.019^{**}$; $p < 0.01$; Jolly et al. 2005). Keeping in mind that selective postlarval and winter mortalities may induce significant levels of genetic differentiation among connected adult populations, cross-channel gene flow as illustrated between BS and RB are for the moment best explained by past gene flow, now largely restricted to the coastlines. However, a stepwise

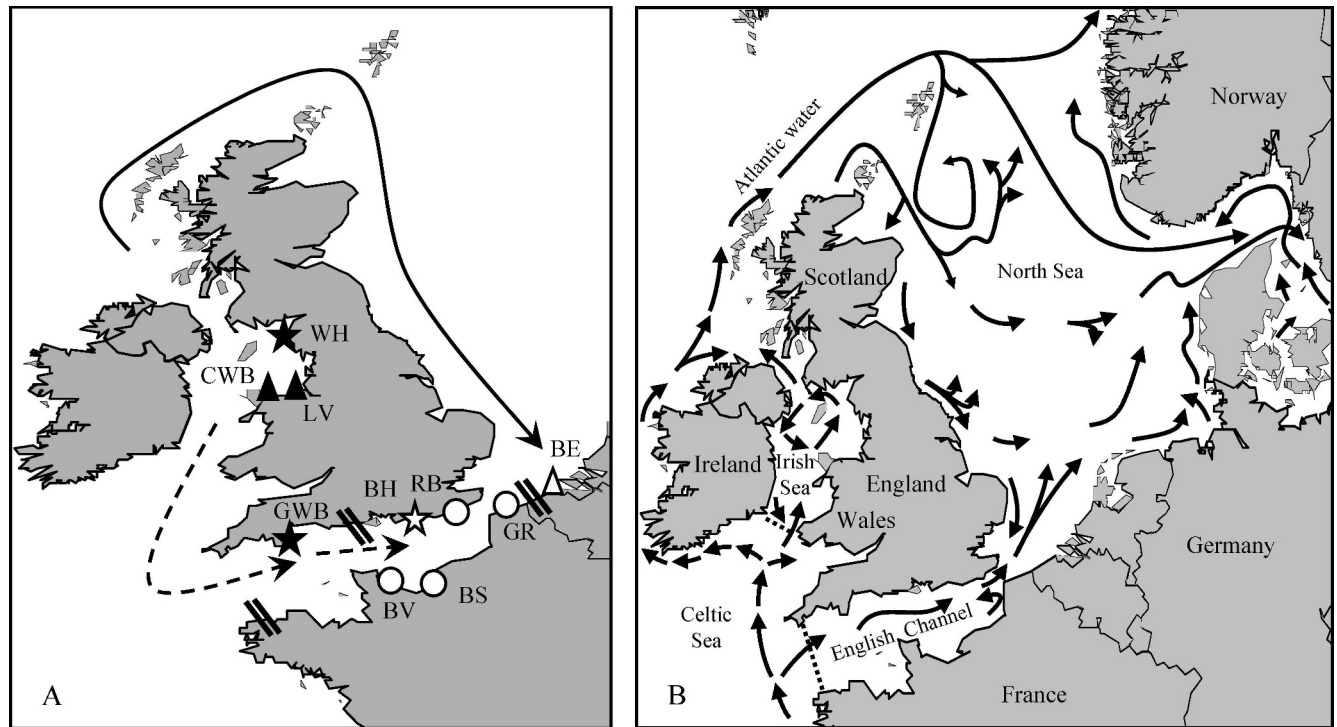


Fig. 7. *Pectinaria koreni* (clade 1). Maps showing (A) the predominant patterns of gene flow inferred using the mtCOI gene (broken arrows; Jolly et al. 2006) and four microsatellite loci (full arrow). Triangles, bullets, and stars represent respectively clusters 1, 2, and 3 of the PCA on the basis of microsatellite data; black and white filled symbols represent respectively clusters 1 and 2 of the PCA on the basis of non-singleton mtCOI haplotypes. Areas of secondary contact are illustrated by double bars; the double bars on the north coast of Brittany represent a secondary contact zone between two highly divergent evolutionary lineages, or cryptic species. (B) Simplified circulation of long-term marine currents around the British Isles (redrawn from Turrell 1992; Bailly du Bois et al. 2002; Brown et al. 2003); small dotted black lines depict major oceanic fronts.

migration of propagules along the coasts through small transient and putative “relay” populations (BSO, Baie de Canche, DP) was not part of the most likely gene flow pattern. Although this may raise the hypothesis of rapid range expansions over recent times, it is undeniable that long-term gene flow does occur along the French coastline for a variety of marine species with broad dispersal capabilities. Given our genetic data, the most likely migration scenario does indeed include putative “past” cross-channel fluxes, but that are weaker relative to the gene flow observed along the French coast. This scenario is also the one that fits best the larval dispersal modeling work.

From our modeling study, only the BS population may be described as a major source of migrants contributing to replenish, directly or indirectly, other populations. These results were also reflected in all migration scenarios simulated using MCMC. In relation to wind-induced currents and the stochastic nature of larval dispersal, both retention and self-recruitment rates highlighted among putative sink or relay populations clearly play a role in the patterns of genetic differentiation observed among all populations of the English Channel. Could decoupling of local population dynamics and reproductive asynchrony be produced from such stochasticity? It seems clear that such contemporary processes, including the potential for stepping-stone dispersal, cannot be fully revealed by micro-

satellite markers without reducing the spatial scale of study to a few populations, and adopting a temporal sampling scheme.

Hydrodynamic modeling, however, highlighted the relative importance of external larval supply on the population dynamics of RB, BH, GR, and BSo, compared to the retention of locally released larvae at these sites. Nevertheless, these populations should probably not be regarded purely as sinks, but considered as transient relays positioned at the confluence limits of larval dispersal from at least two stable source populations. Indeed, relative to the connections highlighted between these populations, all populations have a significant number of private mitochondrial haplotypes (Jolly et al. 2005). For example, roughly 8% of all haplotypes found in RB occur only within that population. To some extent, this means that the population dynamics of putative sinks might not be governed only by external larval input, but that an effective retention of larvae must also occur at these sites.

If BS is indeed the only source of migrants for populations along the French coast of the eastern English Channel, then some kind of IBD should be observed. The fact that it has not means that either (1) the level of migration, the mutation rate of loci, and the effective population size are sufficient to guarantee genetic homogeneity over that region; (2) past gene flow blurs this pattern completely; or (3) more than one source exists

within the metapopulation, whether in the English Channel or outside its boundaries. Note that model selection always preferred a one-source model (BS) rather than a two-source scenario with RB and BS (results not presented). Concerning this latter hypothesis, however, there is a strong indication that populations in the southern North Sea (possibly in the Thames estuary) might be leaking some alleles to the eastern English Channel by contributing migrants to local populations residing in the vicinity of the Dover Strait. Indeed, a strong interannual variability of the water circulation at the northern entrance of the English Channel makes it possible for North Sea water to enter the English Channel (Otto et al. 1990). This may also be indicated by the limited genetic differentiation observed between GR and RB ($p = 0.036$), despite the presence of a frontal zone between both French and English coasts (Brylinski et al. 1988). If such a two-source structure exists, sink populations located at the confluence of the regional sphere of influence of the two sources, in terms of larval dispersal, would demonstrate genetic differentiation purely on the basis of larval dispersal potential. As a result, at least some sink populations may be structured in a mosaic composed of a mixture of individuals from both sources, but where only localized interbreeding may take place, if any, since pure sink populations do not generally export. Such a structure, maintained by reproductive asynchrony between source populations, may help explain the genetic differentiation observed in the southern North Sea between GR and BE, in which these populations may receive larvae from both sources.

Although populations in the eastern English Channel appear relatively closed with respect to both genotype and haplotype information, it remains unclear whether a dispersal corridor still exists between the Irish Sea and the western English Channel. Despite considerable sampling effort, only one individual was obtained from the south coast of Wales and none from the north coast of Cornwall. In addition, only 14 individuals were sampled on the southwest English coast. Either those populations were missed, or both the Celtic Sea and western English Channel are so poorly supplied in larvae that no large and stable population actually exists. Nevertheless, mitochondrial sequences indicate IBD between the Irish Sea and the English Channel (Jolly et al. 2006) but microsatellite loci do not. This is an indication that gene flow existed in the recent past and that it might be masked either by greater effective population sizes at nuclear markers, or by a reversal in the direction of gene flow. Brown et al. (2003) described a northeastward flow along the Cornish coast, which would make it easier for larvae to disperse in such direction than otherwise. Combining genetic markers with a 2-D model of coastal circulation along the coasts of Cornwall, Gilg and Hilbish (2003) suggested that larval transport of *Mytilus* larvae was mainly directed from the south coast of Devon (western Channel) toward the north coast of Cornwall, at the entrance of the Bristol Channel. In this case average traveling distances were in the order of 30–60 km and rarely 100 km. Despite this, the fact that both GWB and WH were two of the most closely related populations at both mitochondrial and microsatellite allele frequencies may suggest population connectivity over many generations.

Molecular markers gave complementary information on the present genetic structure of *P. koreni* populations. Microsatellite data and hydrodynamic modeling in particular gave similar results with respect to the different directions of colonization around the British Isles, and the strong connectivity existing between populations of the Baie de Seine. This combination of methods recognized past gene flow inferred from mtDNA and allozymes from present patterns corresponding to larval dispersal largely restricted to the coastline. Nevertheless, contemporary mesoscale patterns of connectivity cannot fully explain the present genetic structure among populations of the eastern English Channel. Of course, discrepancies may have also been induced by a combination of a low number of individuals sampled in key populations (GWB, BH, and BSo), a limited number of microsatellite loci screened, and inherent modeling problems. More particularly, modeling problems may have consisted in the following: (1) small intermediate and transient populations along both coastlines (e.g., along the Cotentin Peninsula and the southern English coasts) may be present but presently not observed, and could act to decrease the traveling distance of larvae between neighboring populations; (2) the model does not include larval behavior and baroclinic circulation, which may affect dispersal distances; and (3) in the less-rich waters of the open sea, larvae may delay metamorphosis, thus maybe increasing larval life span more than only 2 weeks. Concerning this last possibility, although Lambert et al. (1996) estimated larval life to last about 15 d from in situ observations, Cazaux (1981) previously gave an estimate of 58 d on the basis of the rearing of larvae in aquaria. Such a wide difference would suggest that under certain conditions (maybe reduced growth), metamorphosis could be delayed and long-distance dispersal enhanced. If such an exchange is effective, this would provide an alternative explanation for the genetic homogeneity observed between BS and GR, and maybe also for the limited genetic differentiation observed between BS and RB.

Studies aiming to understand population connectivity, especially among recently established populations, should include the use of hydrodynamic models alongside genetic data sets. However, the proof that past gene flow may still contribute significantly to the observed genetic population structure for various benthic populations in the English Channel means that contemporary patterns of effective dispersal would be better understood by simulating genetic data sets over a number of generations using a hydrodynamic model of larval transport. Making the genetic system evolve, controlling the influence of local extinction events, reproductive asynchrony, and larval dispersal on the dynamics of both local populations and the metapopulation itself would greatly enhance our understanding of the functioning of marine communities in relation to global climatic changes and anthropogenic pressures.

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