

Modelling larval dispersal of *Pecten maximus* in the English Channel: a tool for the spatial management of the stocks

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Abstract :

The great scallop *Pecten maximus* supports one of the most important and valuable commercial fisheries around the British Isles and in the northwest of France, but the resource is mainly managed at the scale of each local fishing ground through a combination of European, national and local measures. To analyse the larval dispersal pathways and connectivity patterns among fishing grounds of the great scallop in the Celtic Sea and the English Channel, a particle tracking model was developed. The model combined a 3D physical circulation model that simulated currents and temperature fields and a scallop larval submodel that took into account a temperature-dependent planktonic larval duration and an active vertical swimming behaviour. Due to the lack of stock assessment at the regional scale, the location of the main fishing grounds was established by combining different sources (e.g. grey literature, unpublished scientific surveys, vessel monitoring data, fishermen) while the spawning biomass of each stock was estimated from landings data. Results indicated that each local stock could not be considered as a single independent management unit and that all stocks except that of the Bay of Brest were connected to neighbouring stocks, suggesting that the management should be defined in a metapopulation context. Three major groups of strongly interconnected stocks including two or three stocks exhibiting high retention and self-recruitment rates and some peripheral stocks with a low self-recruitment rate were defined: the North Brittany and Channel Islands, the eastern English Channel, and the SW of England. Our results were discussed in terms of the definition of management units in comparison with genetic and phenotypic data, and in terms of resource management in a transnational context.

Keywords : connectivity, English Channel, fishery management, great scallop, larval dispersal, particle-tracking model

Introduction

Inhabiting mainly sand and gravel bottoms, the great scallop *Pecten maximus* (L.) is widely distributed along the Northeast Atlantic coasts, from Norway to the north-western coast of Africa, and in the Mediterranean Sea (Brand, 2006). In European waters, commercial scallop fisheries have expanded rapidly since the 1970s in response to (i) an increase in fishing effort because of its high market value and the switching of target species by some boats (Beukers-Stewart and Beukers-Stewart, 2009), and (ii) more favorable environmental conditions (Shepard *et al.*, 2010). Around the British Isles and in the English Channel where the species is particularly abundant, *P. maximus* supports some of the most important commercial fisheries both in terms of landings and socio-economic values for French and UK coastal regions. For example, in 2007, the UK fishery for great scallops was ranked in the top five most valuable UK fisheries with a first sale value of £38.8 million and total landings of about 20,000 t (Beukers-Stewart and Beukers-Stewart, 2009). In 2011, the French scallop fishery in the English Channel included approximately 600 French ships and more than 2,000 fishermen amassing total landings of about 25,000 tonnes with a sale value of about 40 million euros. In more recent years (2002-2012), the official landings of scallops from both sides of the English Channel and its western approaches varied between 22,000 and 30,000 tonnes (ICES data).

Despite its high economic importance at the regional scale, there is currently no common stock assessment and management policy at the global (i.e. NE Atlantic) or at the regional (e.g. English Channel) scales. In the English Channel, each local scallop fishery is managed through a complex combination of regulations defined at the three distinct levels, i.e. European, national and local. These regulations of scallop fisheries consist of technical measures (e.g. minimum landing size, fishing gear specifications) and of measures controlling the access to the resources (e.g. special fishing permits, annual Total Allowable Catch, seasonal closures, limitation of the

fishing effort to certain times of the day, implementation of small marine protected areas) (Beukers-Stewart and Beukers-Stewart, 2009; Le Gallic and Fournier, comm. pers.). On the other hand, although the great scallop is largely distributed in the English Channel, scallops form natural aggregations targeted by fishermen only in some areas, i.e. scallop grounds, which remain partially identified. Furthermore, there is no evidence that these spawning grounds support discrete biological stocks assumed as distinct management units.

For species exhibiting a complex life cycle with a planktonic larval stage like the great scallop *P. maximus*, improved knowledge of larval dispersal pathways and demographic connectivity is a central issue for understanding the dynamics and the persistence of spatially distributed stocks (Hastings and Botsford, 2006), and also for implementing effective and sustainable fishery management strategies, i.e. delineation of spatial management units and design of marine protected areas (Fogarty and Botsford, 2007). While management units were traditionally identified on the basis of differences in morphological and demographic criteria, genetic markers, natural markers and tagging analysis (Cadrin *et al.*, 2014), the delineation of appropriate spatial scales of management requires assessing the larval exchanges among stocks in a metapopulation context (Kough *et al.*, 2013). In particular, in a network of local stocks, it is crucial (i) to identify local stocks that may consistently replenish themselves over time because of a sufficient local retention rate and (ii) to define local stocks that may contribute to the persistence of metapopulation at a regional scale through larval exchanges (James *et al.*, 2002; Burgess *et al.*, 2014; Lett *et al.*, 2015).

For benthic invertebrates, larval dispersal is a result of multiple interactions between hydrodynamics complexity and larval biological traits including spawning period, planktonic larval duration (PLD), larval mortality, and active larval behavior. Because of the complexity of the processes involved at different spatial and temporal scales, identifying dispersal pathways and connectivity remains a major challenge in marine ecology (Levin, 2006; Cowen and

Sponaugle, 2009; Lowe and Allendorf, 2010). During the last two decades, significant methodological development has been done to assess marine connectivity including population genetics and the development of next-generation sequencing (Benestan *et al.*, 2015; Gagnaire *et al.*, 2015), elemental fingerprinting of calcified structures using natural or artificial tags (Carson *et al.*, 2010; Cuif *et al.*, 2014), and individual-based biophysical modeling taking into account complex coastal hydrodynamics as well as larval biological traits (Robins *et al.*, 2013; Thomas *et al.*, 2014). Although most biophysical models do not integrate settlement and post-settlement processes involved in the recruitment and demographic connectivity of benthic invertebrates (Pineda *et al.*, 2009), they have the advantage to simulate larval pathways and quantify connectivity for multiple larval releases related to the complex spatial and temporal variability of local hydrodynamics. For example, looking at the giant scallop *Placopecten maximus* in the NW Atlantic, highly variable larval exchanges between scallop populations on the Georges Bank, as well as long-distance transport of larvae from the Georges Bank to the Middle Atlantic Bight were simulated using a 3-D Lagrangian-tracking model (Tian *et al.*, 2009; Gilbert *et al.*, 2010). Tian *et al.* (2009) suggested that the increase in spawning stocks on the Georges Bank following the implementation of closed areas may have contributed to the large recruitments observed in the Middle Atlantic Bight during some of the recent years. In the English Channel, Nicolle *et al.* (2013) developed a 3-D high resolution biophysical model including a temperature-dependent planktonic larval duration and an active swimming behavior to simulate larval dispersal of the great scallop *Pecten maximus* in the two coastal embayments, i.e. the Bay of Seine and the Bay of Saint-Brieuc, which harbor the main scallop fisheries along the French coasts. Within each bay, the analysis of connectivity suggested the presence of sources and sinks among areas in relation to the spatial heterogeneity of both local hydrodynamics and reproductive biomass.

In the present study, we performed the most complete and extensive review of data on the distribution of the great scallop *Pecten maximus* in the English Channel to identify the most important fishing grounds. Then, using the particle-tracking model developed by Nicolle *et al.* (2013), our aims were to simulate larval dispersal and connectivity between the local stocks located throughout the English Channel and their inter-annual variability. The results are discussed in terms of stocks' persistence in a metapopulation framework, and stock management.

Material and methods

Geographical setting

In the English Channel, hydrodynamics are mainly governed by strong instantaneous tidal currents because of the particular topography of the continental shelf that amplifies the tidal wave during its progression from west to east (Pingree, 1980). Residual currents which are the more relevant for the transport of material are due to the non-linearity in the tidal signal, and are generally one order of magnitude lower, i.e. below 5 cm s^{-1} , except locally around topographic irregularities of the northern coast of Cotentin where they exceed 20 cm s^{-1} (Salomon and Breton, 1993). The mean residual current flows from West to East. Permanent or transitory coastal eddies resulting from either of the tidal motion rotating around islands or from cape-effects are also observed. Permanent gyres are well developed in the Saint Malo gulf around the Channel Islands (Jersey, Guernsey, Alderney, Chausey) while transitory eddies are common in coastal waters (Salomon and Breton, 1993). Coastal eddies are commonly reported to trap particles and enhance larval retention. Ménesguen and Gohin (2006) distinguished two types of eddies in the English Channel: headland eddies that act as accumulation areas and eddies located around islands that form strong dispersal areas. Although tidal residual currents form the major part of the long-term water mass transport in the English Channel (Pingree and

Maddock, 1977), the wind regime which is characterized by two dominant directions, i.e. West/Southwest and East/Northeast can also play a significant role on circulation at scales of days or weeks (Salomon and Breton, 1993). At these scales, it can greatly influence larval dispersal by amplifying or counteracting tidal residual currents (Ayata *et al.*, 2009; Nicolle *et al.*, 2013). Density gradients due to temperature and salinity differences are another driving mechanism for water motions which produces three dimensional velocity structures. Because of the intense tidal vertical mixing and the low river run-off at spawning period, their effects are only significant in the western entrance of the Channel, where a seasonal thermocline and a thermal front, i.e. the Ushant tidal front, are observed (Le Boyer *et al.*, 2009), and in the ROFI system located along the French coasts of the English Channel, from the Bay of Seine to the Dover Strait (Sentchev and Korotenko, 2005). The Ushant front which occurs during the warmer season, from May to October, separates vertically mixed waters along the French inshore waters from warmer and stratified waters, offshore and along the UK coasts. The ROFI system breaks up two current regimes: an offshore regime with a low and nearly isotropic dispersion, and an inshore regime of higher dispersion in the eastern English Channel.

Scallop stocks

Scallop distribution was determined by combining several sources of information of diverse origin: (1) peer-review literature (Mason, 1983; Abbes, 1991, Tully *et al.*, 2006); (2) grey literature (Pitel *et al.*, 2001, Smith, 2005); (3) interviews of divers and fishermen conducted with the support of the regional fisheries committees; (4) stock evaluation surveys for the two main stocks in the English Channel (i.e. the Bay of Seine and the Bay of Saint-Brieuc monitored from 1990 and 1991 respectively) (Vigneau *et al.*, 2001); (5) unpublished results from scientific surveys (i.e. Channel Ground Fish Survey since 1988 and International Bottom Trawl Survey since 1997); (6) CPUE data (Tim Robbins, manager of the Devon & Severn Inshore Fisheries

and Conservation Authority, pers. comm.); (7) database queries (National Biodiversity Network, <http://data.nbn.org.uk>, consulted in June 2012); and (8) unpublished data from the Vessel Monitoring System (VMS). All collected data ranged from 1983 to 2012. As only few data were directly available in GIS layer format, the first step to collect data was to georeference the maps and to digitalize them. Pluri-annual data were generalized in order to bound a single outline. Then, all GIS digitalized layers were combined on a map identifying the main local stocks. As the different sources may overlap or indicate only the species occurrence, the final outlines were fitted based on expert judgement (Figure 1). A total of 22 discrete stocks were then identified.

As no data were available on the spawning stock biomass except for the Bay of Seine and the Bay of Saint-Brieuc, the relative size of each stock was estimated according to the average landings by the French and UK fleets which are the two major fleets operating in the study areas. Data on landings from 2008 to 2012 were provided by the SIH (Fisheries Information System, France) and the CEFAS (Centre for Environment, Fisheries and Aquaculture Science, UK) for the different ICES statistical rectangles (Figure 1). As the limits of scallop stocks do not match perfectly the limits of the ICES statistical rectangles, landings within a rectangle were assigned to one or several stocks according to their relative areas (Table 1). Although variations in scallop landings can be driven by several factors including stock size and fishing effort, significant relationships were reported between the adult biomass and the landings in the Bay of Saint Brieuc and the Bay of Seine (Supplementary Figure S1).

Numerical model description

Modelling was performed using MARS-3D (3D hydrodynamic Model for Applications at Regional Scale, Ifremer), a 3D primitive equation-free surface model applying the Boussinesq

approximation and hydrostaticity (see a detailed description in Lazure and Dumas 2008). Spatial discretisation was achieved using a staggered “C” grid and sigma vertical coordinates. The turbulent closure scheme used to compute the vertical turbulent diffusion coefficient was the k- ϵ model. In order to maintain horizontal mesoscale structures, horizontal viscosity was computed using a formulation proposed by Smagorinsky (1963), and dependent on local mesh dimensions and velocity gradients. The entire model domain covered the English Channel from 48°N to 51°N in latitude and from 7°W to 2°E in longitude with a horizontal resolution of 2 km and 30 sigma layers along the depth-axis (Figure 1). Larval trajectories were calculated for each time step from the velocity fields calculated by the 3D hydrodynamic model which simulated currents and temperature fields. The advection scheme was based on the second-order Runge Kutta method. The vertical displacement was induced by advection (i.e. vertical current and vertical larval behavior) and a non-naïve random walk based on the vertical profile of turbulent diffusion. Coastal boundaries were reflecting while the open sea boundaries were absorbing: a larva that was transported outside these boundaries was lost and could not return in the model domain. A detailed description of the biophysical model is available in Nicolle *et al.* (2013).

If the gametogenesis of the great scallop as well as the spawning are highly temperature-dependent, the spawning modalities varied among stocks (Lubet *et al.*, 1995). For example, in the Bay of Saint Brieuc, the first spawning event occurs when the sea temperature reached 16°C and the second three weeks later, generally in July. By contrast, in the Bay of Seine, multiple spawning events are scattered from May to October with the main ones in July and August. In the model, the link between temperature and the spawning date was based on the degree-days method as proposed by Lavaud *et al.* (2014) in a bioenergetics model of *Pecten maximus*. From a threshold of 12°C for the near-bottom waters, the spawning event occurred when 75 degree-days cumulated. Obviously, spawning events did not occur simultaneously for each stock and the delay could reach one month, for example between the Celtic Sea and the Bay of Saint-

Brieuc. For each stock, a second spawning event was simulated three weeks later. For each simulation, the total number of larvae, which were evenly released from the surface covered by each stock, varied according to the stock area, from ~ 250 to ~ 25,000 larvae for a mean value of 5,990 larvae. This number of particles was based on a trade-off between realistic dispersal schemes and time of simulation. For larger stocks, it allows us to take into account the heterogeneity in dispersal trajectories according to the larval release mesh.

The relationship between the planktonic larval duration (PLD in days) and the temperature (T in °C) was implemented in the model according to the following equation: $PLD = -4.277 T + 102.01$ ($n = 11$; $R^2 = 0.8467$; $p < 0.05$) established from a review of different laboratory experiments on *Pecten* larval development at different temperatures (Nicolle *et al.*, 2013). According to this relationship, estimation of *in situ* PLD was simulated as proposed by Dawirs (1985) to take into account the temporal variation of field temperature. First, the theoretical PLD was calculated from the temperature of the release time assuming that water temperature remained constant. During the first day, the daily development rate was $1/PLD$, which corresponds to the proportion of the total development. One day after spawning, water temperature encountered by larvae became either warmer or cooler so that the estimated PLD should be slightly shorter or longer. The real PLD of each larva on the basis of varying daily field temperature was then calculated by adding the reciprocal values of the PLD in different subsequent daily mean water temperatures. The total PLD equaled the number of days once this summation reached zero. Larval behavior was implemented in the model to simulate changes in the swimming and sinking velocities of scallop larvae during their ontogenic development as proposed by Nicolle *et al.* (2013). No planktonic larval mortality was considered. At the end of its planktonic life, each larva was allowed to settle whatever its vertical position if it was present above a suitable benthic habitat defined as the habitat of the adult stocks; otherwise, it

died. One can note that most larvae were confined in near-bottom waters at the end of their lifespan according to the larval vertical ontogenic migration simulated in the model.

This biophysical model was used to simulate larval dispersal for 22 different stocks over a ten-year period (2000-2009) and two spawning events per year. This series was assumed long enough to be representative of the year-to-year variability in environmental conditions (e.g. meteorological changes). To assess the robustness of our results, simulations were also performed for the year 2000 by increasing or decreasing the surface area of each stock, partly defined on expert judgement, by 10 %.

Data analysis

Different parameters commonly used to describe the dispersal kernels, the persistence of local stocks and the connectivity among stocks were calculated (Edwards *et al.*, 2007; Burgess *et al.*, 2014; Lett *et al.*, 2015): the mean dispersal distance (DD); the local retention rate (LR_{*i*}); the connectivity (C_{*i,j*}); the self-recruitment rate (SR_{*i*}); and the external recruitment rate (ER_{*j*}). The average, minimum and maximum values of dispersal distances were calculated between final position of all larvae and the initial position of the stock barycenter, i.e. the point representing the mean position of larvae in the water body in a 2D space. The local retention rate was the fraction of larvae produced by a local stock *i* that also settled into that stock. The connectivity was the proportion of larvae emitted by a stock *i* that settled in another stock *j*. The self-recruitment rate was the proportion of settlers in a stock *i* that were originally produced by this stock. The external recruitment rate measured the contribution of a stock *j* to the total recruitment of a stock *i*. It was defined as the number of settlers from a stock *j* in a stock *i* divided by the total number of settlers in the stock *i*. The self-recruitment rate and the external recruitment rates were weighted *a posteriori* according to the relative importance of each stock in the English Channel in terms of adult biomass estimated by landings. The mathematical

definitions of these different parameters are given in supplementary material (Supplementary Appendix 1).

The connectivity among local stocks was also analyzed and plotted using graph-theory which explores the patterns in spatial connections as well as the importance of each stock and dispersal pathways in the regional connectivity (Trembl *et al.*, 2008). In this approach, each local stock was represented by a node located at its centroid position while the connection between two stocks was represented by an edge which was proportional to the magnitude of the connection. The application of the graph theory to our results simulations generated many edges, even when just one larva from a stock i reached a stock j . To focus on connections which were the most meaningful in terms of demography and stock management, the network structure was described through the optimization of a modularity function according to Newman (2006). The connections among stocks were assessed using two different metrics: the connectivity and the external recruitment rate.

For each simulation, we computed: the graph size (i.e. total number of edges within the network) and the in- and out-degrees (the total number of edges coming into and leaving a node respectively) for each node. The cut-nodes, which are the nodes that connect two sub-graphs, were identified; if a cut-node was removed, the graph was then broken into two components, corresponding in our case to a management unit. Finally, the number of strongly connected components, defined as connected sub-graph, was determined.

Results

Mean Larval Trajectories

To summarize the larval dispersal patterns for all simulations, the averaged larval trajectories from the stock barycenter were drawn for each spawning event over 10 years (Figure 2). For most stocks, the mean larval transport followed mainly the coasts, from the south-west to the north-east for the stocks located in the eastern English Channel, and from west to east for the stocks reported along the coasts of the Great Western Bay (i.e. Brixham and Weymouth). For a release off Plymouth and Falmouth, released particles drifted westward and then northward along the coasts of Cornwall. For the stocks in the North Brittany, the main direction of larval transport was more variable among stocks according to more complex hydrodynamics. At the scale of the English Channel, the longitudinal transport was preponderant suggesting low exchanges across the Channel. The averaged value of the mean dispersal distance (DD) was highly variable among stocks (Table 2). Except for the Bay of Brest where it did not exceed 13 km, suggesting that this semi-enclosed embayment was largely isolated from the rest of the study area, the averaged value of DD ranged from 30 km in the Bay of Saint Brieuc to 90 km off Dieppe. It was generally higher along the coasts of the eastern English Channel where it commonly exceeds 50 km. Furthermore, in this area, this dispersal distance was probably underestimated as some larvae reached the limits of the model domain.

No major change in the mean axis of larval dispersal was reported among spawning events, within and between years, for all stocks except that of the North Celtic Sea (Figure 2). By contrast, there were large disparities of the mean dispersal distances between spawning events (Table 2). For example, for larvae released at Dieppe, the mean dispersal distance varied between 24 and 135 km depending on the date of larval release for an average value of 90 km. In extreme cases, a reverse in the mean direction of larval transport could be reported. For instance, larvae released off Brighton drifted more commonly eastward except on some dates for which a westward transport was predicted (Figure 2). Whatever this temporal variability in

the mean dispersal distance, it generally exceeded the boundaries of each scallop stock, and in some cases the distance between neighboring stocks.

Depending on the temperature encountered by larvae during their transport, the planktonic larval duration could vary by a factor of 2 from about 25 to 50 days (Figure 3). The PLD was slightly shorter for the second spawning event according to the summer warming of seawater temperature. The longest PLD were reported for stocks from the Celtic Sea and the south-west of England.

Local retention Rate (LR) vs Self-Recruitment rate (SR)

The mean local retention rate was highly variable among scallop stocks and fluctuated between 0.2% off Falmouth to 42.4 % in the Bay of Seine (Figure 4). The lowest values were observed (LR < 2.5 %) in Falmouth Bay, along the English coasts of the eastern Channel (i.e. Brighton, Eastbourne, Rye Bay), in the bays of Morlaix and Lannion, in the SE Jersey and at Vergoyer, for scallop stocks which either cover a small surface (Table 1) or are located in areas exposed to higher velocities of residual currents (see Figure 2). The highest values of retention rate (> 20 %) were reported off Brixham, in the Bay of Brest, in the Bay of Saint-Brieuc, in the Bay of Seine and in the Celtic Sea.

The mean self-recruitment rate was also highly variable from 0.6 % at Rye Bay from 100 % in the Bay of Brest. For 10 local stocks out of 22, the mean self-recruitment rate exceeded 50 % suggesting that the replenishment of the stocks depended largely on local processes. However, due to temporal variations of larval dispersal patterns, the variability of the self-recruitment rate among spawning events could be high, in particular for the stocks located in the eastern English Channel such as Dieppe, Greenwich and Brighton (see the standard deviation of the self-recruitment rate on the Figure 4) and for the stocks in the Celtic Sea. A significant and positive linear relationship was observed between LR and SR despite a strong

variability among spawning events for each stock ($n = 396$; $R^2 = 0.4083$; $p < 0.05$) (Figure 5). On average, the local stocks with a mean self-recruitment rate exceeding 50 % tended to have a mean local retention rate of more than 20 % (Figure 4). Only the local stock from the bays of Morlaix and Lannion differed strongly from this general pattern with a high self-recruitment rate and a low retention rate.

The temporal variability in the local retention rates and the self-recruitment rates did not covary between stocks in most cases (Table 3). However, values of both rates were significantly and positively correlated between some neighboring stocks such as Antifer and Vergoyer stocks or Greenwich and Rye Bay stocks in the English Channel, and Weymouth and Birxham. These correlations suggest that environmental conditions that promoted retention or self-recruitment in one stock also favored them in another one. Significant and positive correlations were also reported between distant stocks which were not connected. Finally some significant but negative correlations were calculated, in particular between the Plymouth stock and other neighboring or distant stocks.

These results on retention and self-recruitment were only marginally altered by the definition of the stock areas which were partly based for the details on expert judgement. Based on the simulations performed only for the year 2000, an increase of 10 % of all stock areas induced a mean increase in the retention rate of only 0.4% while a decrease of 10 % of stock areas generated a mean decrease of only 0.6% of the retention rate. These same changes induced a mean increase or decrease of the self-recruitment rate of 1.8 and 1.5 % respectively.

Connectivity

The analysis of the average network structure showing the mean local retention rate and the mean connections between the different stocks of *Pecten maximus* in the English Channel showed the occurrence of 4 major groups of inter-connected stocks (Figures 6 and 7). The first

group is only composed of the stock of the Bay of Brest. This isolated stock was characterized by a high retention rate with a low coefficient of variation. Although this stock persisted only through self-recruitment, it could slightly affect the recruitment in the bays of Morlaix and Lannion. The second group was composed of the four stocks of the Normano-breton Gulf (i.e. BSB, WJ, SEJ, SM/C), the stock from Cherbourg (i.e. C) and the stock from the bays of Morlaix and Lannion stock (i.e. M/L). The larval retention rate was higher for the stocks of the BSB, WJ and SM/C than for the peripheral stocks while larval exchanges were maximum between the BSB, SM/C and SEJ (Figure 6). Except for M/L and C, larval exchanges occurred between each pair of stocks in both directions. The retention rates as well as the connectivity exhibited low values of the coefficient of variation suggesting that the spatial dynamics of the stocks was relatively stable between spawning events. Only the stocks BSB and WJ in this group depended mainly on self-recruitment which ranged between 60 and 98.5 % (Figure 7). The SEJ stock and to a lesser extent the SM/C and C stocks with a self-recruitment of 9.1, 23.8 and 22.8 % respectively depended mainly on larvae from neighboring stocks. The two stocks from SEJ and SM/C were strongly connected; the SM/C stock contributed largely to the SEJ recruitment and vice versa. The stock received larvae from of different origins including WJ, SEJ, SM/C and the Bay of Seine.

The third group gathered all the stocks of the eastern Channel (i.e. BS, A, D, V, RB, G, E, B) (Figures 6 and 7). This group was connected to the former one through the stocks of Cherbourg (i.e. C) and the Bay of Seine. The local retention rates of the scallop stocks of this third group was highly variable among stocks: the stock of the Bay of Seine, had a high retention rate with low variations among spawning events while the retention rates of the stocks of Brighton, Eastbourne, Rye Bay and Vergoyer were below 2.5 % with large variations among spawning events (Figure 6). The stocks of Antifer, Dieppe and Greenwich had intermediate values of the local retention rate. In this group, the BS stock was only connected to the

neighboring stocks of Antifer and Dieppe while all the other stocks were highly connected. Larval exchanges among stocks were asymmetric and occurred mainly from west to east, but the high values of their coefficients of variation suggested a high variability in the magnitude of larval exchanges among spawning events. Only the stocks from the Bay of Seine and Greenwich exhibited a high self-recruitment rate and contributed significantly to the recruitment of other populations (Figure 7). In particular, the BS stock was the major contributor to the recruitment at Antifer while the stock from Greenwich contributed largely to the recruitment at Rye Bay, Eastbourne and Brighton.

The fourth group was composed of stocks located along the southwestern coast of England (i.e. F, ES, P, BX, W) and in the Celtic Sea (i.e. NCS, SCS). In this group, the stocks with the higher retention rate and self-recruitment rates were those from Brixham and the Celtic Sea (Figures 6 and 7). As predicted for the group 3, the exchanges between the stocks of this group were numerous but highly variable among spawning events underlining a probable instability of its network structure. This fourth group was totally isolated from the other stocks from South of England and North Brittany. The larval exchange was quite low (< 4 %) except between Brixham and Weymouth, and Brixham and Plymouth Sound (Figure 6). Nevertheless, these exchanges could contribute significantly to the recruitment of some stocks (Figure 7). For example, Plymouth Sound was a major contributor to the recruitment in Falmouth Bay, and to a lesser extent, in Eddystone and Brixham.

The Table 4 summarizes the main parameters of the network of scallop stocks and their variations among the 20 spawning events. The graph size ranged from 46 to 65 edges. The number of components varied from 2 to 4. If the stock of the Bay of Brest was always isolated from the others, the connections among or within groups 2, 3 and 4 occurred or not according to the spawning event and consequently the hydrodynamic conditions encountered by larvae. On average, the mean numbers of in-degrees and out-degrees were very similar and varied

between 0 and 6 with a mean value of 2.4. The number of cut-nodes which are critical to network-wide connectivity fluctuated between 5 and 8, suggesting that the disappearance of these stocks could lead to a fragmentation of the network into a higher number of components. These nodes, which were essential for the network consistency, concerned the stocks of Cherbourg, Morlaix/Lannion, North Celtic Sea, Brixham, Weymouth, West of Jersey, Bay of Seine, Greenwich and Vergoyer.

Discussion

Dispersal pathways and connectivity

The simulations revealed distinct dispersal pathways of scallop larvae which were strongly related to the general residual flow described in the English Channel, mainly oriented to the East in the eastern Channel and along the south coasts of England, and to the West along the south-western coasts of England (Salomon and Breton, 1993). Larval dispersal was more complex in the Saint Malo Gulf and around the Channel Islands where permanent gyres constrain the transport of larvae. Beyond this general pattern, larval trajectories, dispersal distances and connectivity between neighboring stocks could vary among spawning events according to the relative role of wind-induced currents on the general circulation at time scales of weeks (Barnay *et al.*, 2003; Nicolle *et al.*, 2013). Schematically, the variability of larval dispersal was lower in the Gulf of Saint Malo where tidal residual currents play at this time scale a more important role in the transport of water mass than in the rest of the English Channel. In a previous application of our particle-tracking model to simulate larval dispersal from the two main scallop grounds in the English Channel, i.e. the Bay of Saint-Brieuc and the Bay of Seine, a sensitivity analysis to the different biological parameters showed that they only marginally influence larval dispersal and retention rates (Nicolle *et al.*, 2013). While larval behavior is commonly reported as an important component of larval dispersal, its minor role

resulted both from the main effects of barotropic processes on the hydrodynamics in the English Channel and the rather simple behavior of scallop larvae implemented in the model that simulated only an ontogenic vertical migration based from laboratory observations. However, in the Celtic Sea and in the western approaches of the Channel where the water column is seasonally stratified, one cannot exclude a more complex pattern in the control of larval depth-distribution related to the thermocline as reported for the giant scallop *Placopecten magellanicus* on the Georges Bank with significant direct and indirect effect on horizontal dispersal (Tian *et al.*, 2009; Gilbert *et al.*, 2010). A better understanding on the field vertical distribution of scallop larvae and the processes that govern this distribution is needed to properly simulate dispersal in this region, especially as this may interact with the effect of temperature on the PLD. While the difference in the PLD between the two successive spawning events for a given stock was rather low and did not exceed a few days, the differences in the PLD among stocks could be higher according to the spatial variability in the 3D temperature distribution. In particular, the PLD was longer for the stocks of the Celtic Sea and the south-west of England where the water column is stratified and larvae spent part of their development below the thermocline.

Our results showed the geographic structure of the time-averaged connectivity of the great scallop stocks in the English Channel with four main groups of connected local stocks: (1) the bay of Brest which a semi-enclosed area in which larval retention could be favored; (2) the north Brittany and Channel Islands; (3) the south west of England and the Celtic Sea; and (4) the eastern English Channel. Mean dispersal distances were in a range of a few tens kms and rarely exceed 100 km so that connections occurred mainly between neighboring stocks. We found that larval retention and self-recruitment were significantly connected in agreement with recent empirical and theoretical results assuming no spatial variability in lifetime egg production (Lett *et al.*, 2015). These were highly variable among stocks and dates, resulting on

complex interactions between different biological and physical factors including the seascape (e.g. size of the adult stock, distance among isolated stocks), the characteristics of local hydrodynamics, the temperature-dependent planktonic larval duration and the reproductive output defined by the spawning biomass (Tremblay *et al.*, 2012). The model predicted that each group was composed of local stocks exhibiting either a low or a high retention rate suggesting that they played a different role in the temporal dynamics of metapopulations. Thus, within each group, only two or three local stocks with high retention and self-recruitment rates were expected to replenish themselves with larvae each year and acted as sources for peripheral stocks. These few local stocks were expected to play a crucial role in sustaining the scallop stocks at regional scales. Conversely, the peripheral stocks exhibited low retention and self-recruitment rates and their replenishment depended largely on external larval supply from the main source stocks or from other peripheral stocks. In this context, the metapopulation would persist through closed loops of connectivity between all or some local populations (Burgess *et al.*, 2014). In the northern Great Barrier Reef, James *et al.* (2002) showed that only few reefs with the strongest self-seeding reefs could ensure the metapopulation persistence of a damselfish.

On the other hand, connections between stocks varied between the different groups with possible consequences on the metapopulation dynamics. According to Watson *et al.* (2012), large fluctuations in the connectivity in the eastern English Channel and along the south coasts of England could have negative effect on the long-term growth of the metapopulation. Furthermore, this negative effect of temporal variability in connectivity should be strengthened if connectivity fluctuations covary (Snyder *et al.*, 2014) as reported for a few stocks in the eastern English Channel in response to wind-induced currents.

Delineation of management units

Different methods have been employed during the last two decades to analyze the spatial structuring of *Pecten maximus* stocks at different spatial scales. At large scales, from Norway to Iberian Peninsula, mitochondrial DNA and nuclear markers have shown that scallop stocks are clearly structured with two groups of stocks: a Norwegian group and an Atlantic group (Spain to northern North Sea) which probably reflect recent evolutionary history rather than actual pattern of connectivity (RFLP: Ridgway and Dahle, 2000; microsatellite data: Morvezen *et al.*, 2015). Such large scale differentiation among scallop stocks was also reported on phenotypic traits related to growth patterns between northern and southern populations, with individuals from the northern stocks showing a slower growth but a larger asymptotic size (Chauvaud *et al.*, 2012). The mechanisms involved in this differentiation remain largely unknown and can result from phenotypic plasticity or environmental adaptation associated with a genetic differentiation.

At regional scales, results on genetic structuring of scallop stocks or phenotypic traits provided contradictory results. Using 8 polymorphic enzyme loci, the investigation of the genetic structure of 13 scallop stocks from Ireland, Scotland and English Channel, including the Bay of Brest, the Bay of Saint Brieuc and the Bay of Seine, showed no genetic differentiation between any of the stocks, suggesting that there is only one panmictic population around the British Isles (Beaumont *et al.*, 1993). A lack of general genetic differentiation along all the Atlantic coasts, from Spain to Irish Sea, Scotland and the English Channel was also obtained using mtDNA or microsatellite markers (Wilding *et al.*, 1997; Heipel *et al.*, 1998; Morvezen *et al.*, 2015). Only structure at local scales was reported in some specific areas, for example in a semi-enclosed sea lough in Ireland (Wilding *et al.*, 1997). By contrast, the reproductive cycles and the timing of reproduction of *Pecten maximus* differ between stocks from Scotland, the Bay of Brest, the Bay of Seine and the Bay of Saint-Brieuc (Mackie and Ansell, 1993; Lubet *et al.*, 1995). In particular, scallops from the Bay of Saint Brieuc differ

from those of other stocks by a well synchronized peak of reproductive activity in early summer and an empty gonad until the following spring. Experimental transplants of scallops between Scotland, the Bay of Brest and the Bay of Saint Brieuc showed that transplants retain their characteristic reproductive cycle, suggesting a genetic basis of this trait and the specificity of the stock from the Bay of Saint Brieuc (Cochard and Devauchelle, 1993; Mackie and Ansell, 1993).

Our results on connectivity among the main local stocks of the great scallop in the English Channel suggested a rather different interpretation of the stocks' delineation and have highlighted the interest of combining different approaches to identify management units. Although the prolonged larval life span of *P. maximus* may promote direct or indirect exchanges among most stocks in the English Channel, our modelling results suggested that they do not form a unique panmictic unit as suggested by some genetic studies (Beaumont *et al.*, 1993; Morvezen *et al.*, 2015) and four major units of weakly connected stocks that can be assumed as distinct management units have been identified. Different hypotheses can be proposed to explain these discrepancies. First, the analysis of genetic structure or spatial distribution of phenotypic traits concerned only a few stocks in the English Channel in comparison to our study which include 22 stocks. For example, an analysis of the reproductive cycle for stocks strongly connected with the Bay of Saint Brieuc could be quite useful to confirm its specificity. Second, we focused our connectivity study only on the spatially discrete scallop grounds whereas the species is largely distributed in coarse sediments of the Channel, and on the major exchanges of larvae. One cannot exclude that small stocks which are not subject to identified commercial fisheries act as relays and strengthen gene flow in the whole English Channel, in particular between the western and eastern basin along the south coasts of England where the presence of scallop is regularly mentioned (National Biodiversity Network, <http://data.nbn.org.uk>). On the other hand, rare long-distance dispersal events can also promote gene flow. Such a low number

of migrants per generation is sufficient to lead to an apparent genetic homogeneity among distinct local populations and ensure genetic connectivity, but in no way contributes to the demographic connectivity. Third, for marine species which combined high fecundity and large population sizes like the great scallop, a lack of genetic differentiation may occur even if populations are rather demographically independent (Gagnaire *et al.*, 2015).

Implications for stocks management

Connectivity among stocks could have profound management and assessment implications. Interestingly, the pattern of structuring predicted by the model does not fit the current management units as they are defined by the local, regional, national and European authorities according to administrative boundaries. For a species which is not of Community interest like the great scallop *Pecten maximus*, the unique transnational regulation concerns the landing size. Most other regulations are defined locally and differ between territorial waters (< 12 nautical miles), where States implement direct management, and the rest of the EEZ. Furthermore, even in territorial waters, regulations are generally implemented locally by Sea Fishery Committees in UK and by Regional Committees for Maritime Fisheries and Marine Fish Farming in France. For instance, no less than 10 management units and 18 fishing areas are defined for the French scallop fisheries in the Channel. Conversely, our results suggested that (1) at least 3 national or transnational management units composed of connected stocks should be considered (i.e. the eastern English Channel which concerns France and UK; the Saint Malo Gulf and Channel Islands which concern France and two non EU states, Jersey and Guernsey; the South-west of England); (2) within each management unit, the management of scallop stocks should favor a more conservative management of the areas that greater contribute to stock growth rates and reproductive outputs due to their disproportionate importance for managing the overall productivity of the regional metapopulation. Such transnational management of a marine

resource will require large effort to homogenize the regulation rules which are defined to ensure the sustainability of fisheries resource but also that of the companies exploiting them. For instance, in the eastern English Channel, local stocks located in the territorial waters of UK and mainly exploited by artisanal fisheries are predicted to depend on larval supply from offshore stocks mainly exploited by different fleets from France, UK, Belgium and the Netherlands.

In parallel to the exploitation of wild stocks, aquaculture and sea-ranching of *Pecten maximus* have developed since the 80s to support local fisheries. Knowledge of larval dispersal and connectivity can then help in defining transfer strategy from one area to another and assessing the potential consequences of scallop transfer on wild stocks. In particular, in France, production of juvenile great scallops concerns mainly one hatchery located in the Bay of Brest which appears isolated from the other stocks in our study although a recent analysis showed an apparent genetic homogeneity of stocks in the English Channel and did not detect a significant long-term effect of the hatchery production on the genetic diversity in the Bay of Brest (Morvezen *et al.*, 2015).

The criteria that can be used to assess the self-persistence of a single local stock or a network of connected stocks have been the subject of recent studies (Hastings and Botsford, 2006; Burgess *et al.*, 2014; Lett *et al.*, 2015). In a network of stocks or metapopulations as reported for the great scallop in the English Channel, persistence of local stocks will occur if each local stock can persist independently and/or through closed loops of connectivity among local stocks within a metapopulation. In both cases, the assessment of retention rate and probability of exchanges among stocks provided by the particle tracking model are not sufficient to properly describe the long-term persistence of stocks in a context of resource exploitation, and estimates of fecundity, fertilization rate, larval mortality and survival from recruitment to a given age for all stocks are also required. However, it remains a first essential step as other empirical methods to determine the origins and destinations of larvae are missing

or currently failed to identify local stocks (e.g. natural microchemistry, genetic methods). In this general context, the implementation of coordinated stock assessment surveys at the scale of the English Channel is a central issue to improve stock management for several reasons. First, they would contribute to improve larval release in the model by taking into account the observed distribution of scallop densities or biomass rather than landings even if we are relatively confident on our estimation of demographic connectivity considering the large differences in the size of the different stocks. Second, they would contribute to assess the relationships between stocks in terms of recruitment magnitude in parallel to the model predictions. Third, they would provide demographic parameters such as mortality, including mortality due to the resource exploitation, that could assist in the future development of metapopulation models.

Supplementary material

Supplementary material is available at ICESJMS online version of the manuscript.

Acknowledgements

This research was supported by the ANR project COMANCHE (ANR-2010-STRA-010-02). We are grateful to Spyros Fifas who provided us the stock estimate of scallops in the Bay of Saint Brieuc. We would like to thank the two anonymous referees who greatly contribute to improve the manuscript by their comments during the review process. Thanks to Joseph Kenworthy for English proof reading.

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Figure 2: Average larval trajectories for each stock of the great scallop *Pecten maximus* in the English Channel. Each trajectory represents the time evolution of the average position of the larval population originated from each stock. The trajectories corresponding to the first spawning event for a given year are represented in red whereas the trajectories associated to the second spawning event are in blue. The stock barycenter is represented by a green dot while the barycenter of the final positions of larvae is represented by a cross. A total of 20 spawning events was considered.

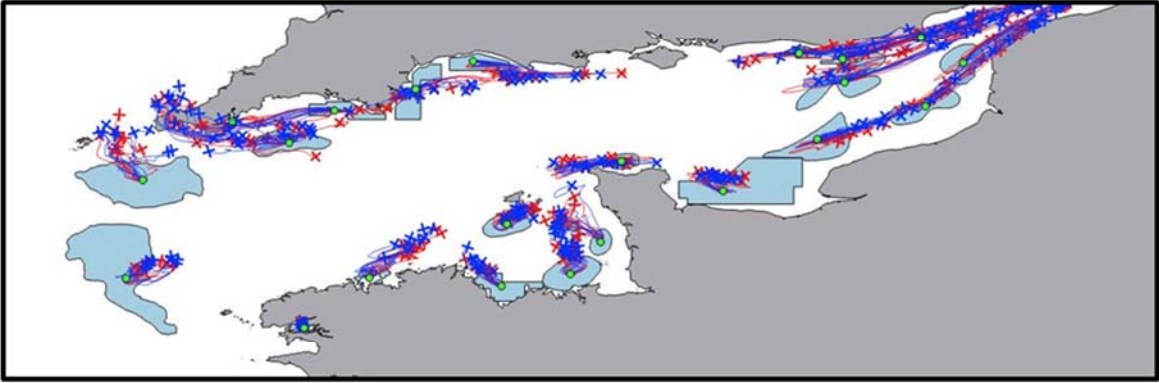


Figure 3: Mean planktonic larval duration of *Pecten maximus* larvae (\pm standard deviation) according to the release stock and the spawning event.

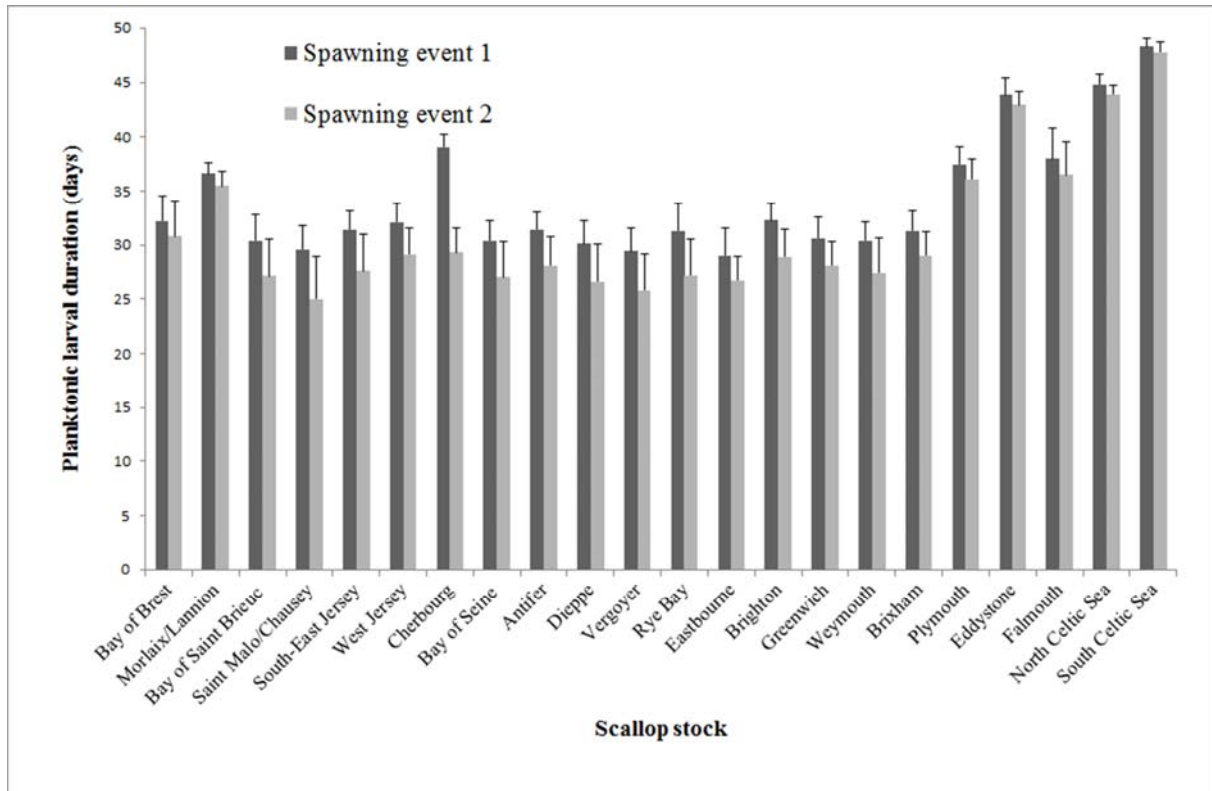


Figure 4: Averaged self-recruitment rate and retention rate (\pm standard deviation) for each stock of the great scallop *Pecten maximus* in the English Channel. Averaged values are based on 20 distinct spawning events over 10 years.

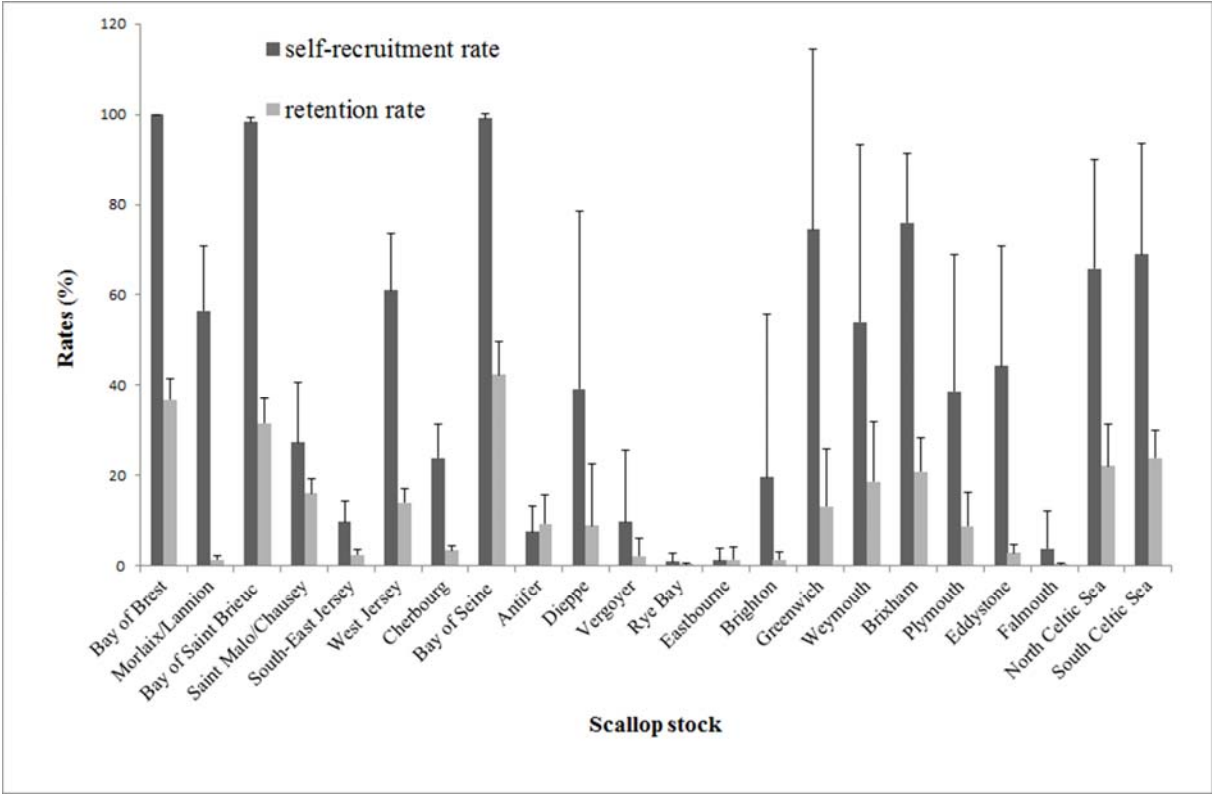


Figure 5: Relationship between the local retention rate and the self-recruitment rate for the 22 local stocks of *Pecten maximus* in the English Channel. For each stock, the rates are mean values calculated on 20 different spawning events over 10 years.

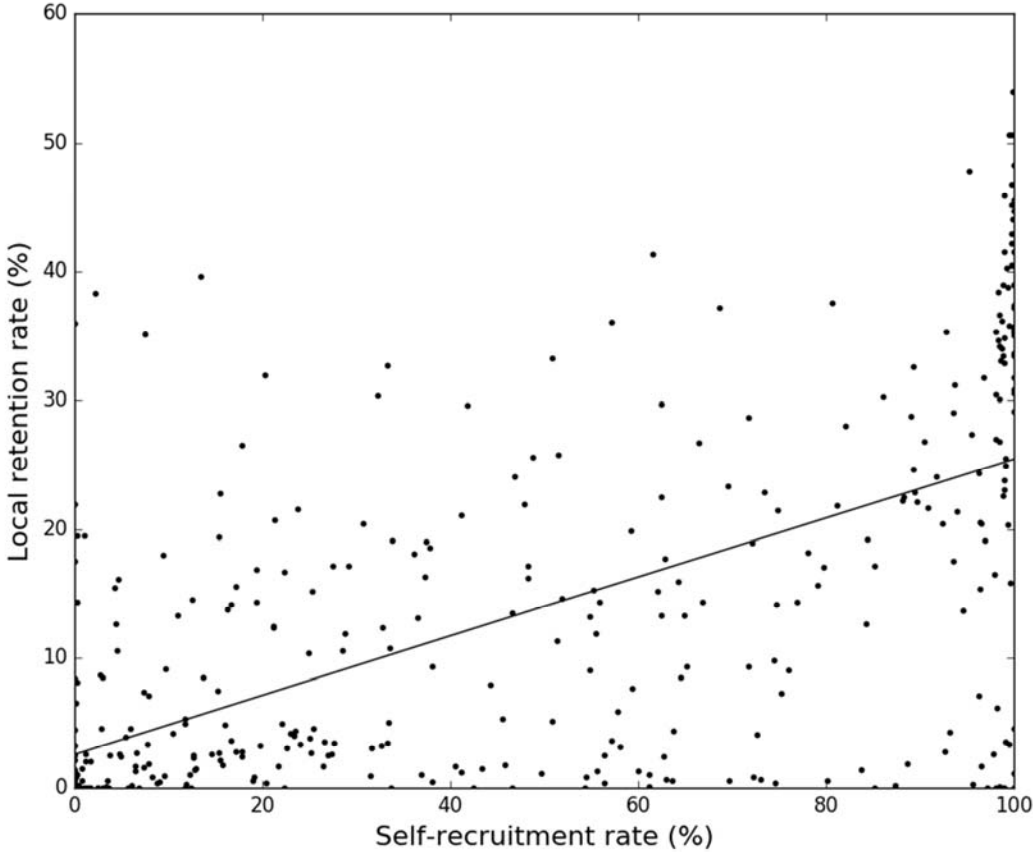


Figure 6: Map representing the local retention rate and the main dispersal connections among the local populations of the great scallop *Pecten maximus* in the English Channel. The retention rate of each local population is symbolized by the relative size of the scallop and the connectivity by lines. Cut-nodes are indicated by circles.

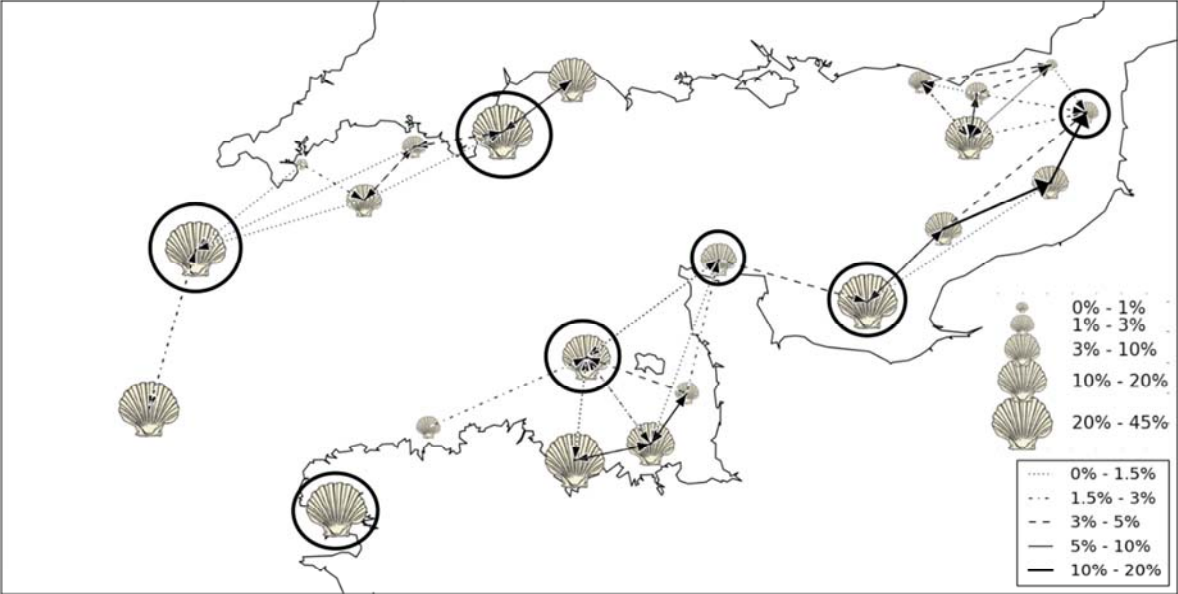


Figure 7: Map representing the average self-recruitment and the external recruitments among the local populations of the great scallop *Pecten maximus* in the English Channel over 10 years. The self-recruitment is symbolized by the size of the scallop and the external recruitment by lines. Cut-nodes are indicated by circles.

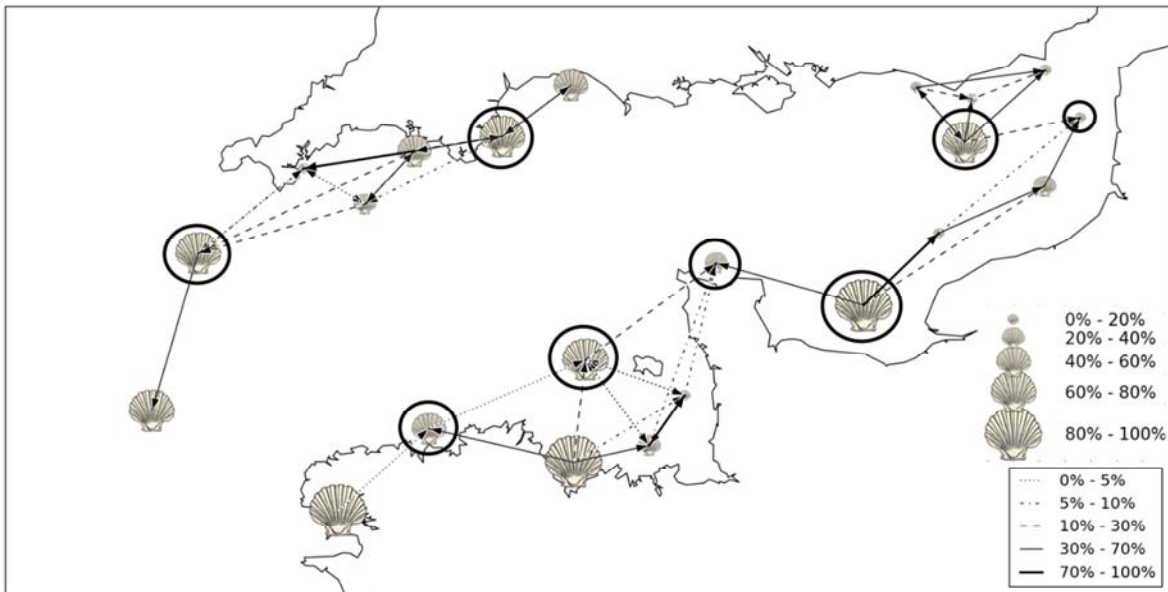


Table 1. Main characteristics (surface area, location, landings) of the main stocks of the great scallop *Pecten maximus* in the English Channel

Scallop Stock (acronym)	Surface area (km²)	ICES Division	ICES Statistical Rectangle	Mean landings (t)	Relative contribution to the regional stock (%)
Bay of Brest (BB)	68.5	VIIe	25E5	234	0.6
Bays of Morlaix and Lannion (M/L)	140.5	VIIe	26E6	726	2.0
Bay of Saint-Brieuc (BSB)	630	VIIe	26E7	6695	18.1
Saint Malo – Chausey (SM/C)	870	VIIe	26E8	888.5	2.4
SE Jersey (SEJ)	260	VIIe	27E8	269	0.7
W Jersey (WJ)	507	VIIe	27E7	1030	2.8
N Cherbourg (C)	248	VIIId	28E8	534.5	1.4
Bay of Seine (BS)	2550	VIIId	27E9 + 28E9 + 27F0	12554	34.0
Antifer (A)	1130	VIIId	28F0	579	1.6
Dieppe (D)	678	VIIId	29F0	4459	12.1
Vergoyer (V)	654	VIIId	29F1 + 30F1 + 30F0	1750	4.7
Rye Bay (RB)	132	VIIId	30F0	79	0.2
Eastbourne (E)	148	VIIId	30F0	89	0.2
Brighton (B)	187	VIIId	30 E9	261	0.7
Greenwich (G)	1160	VIIId	29E9	2032	5.5
Weymouth (W)	480	VIIe	30E7	429	1.2
Brixham (BX)	632	VIIe	29E6+30E6	1819	4.9
Plymouth Sound (P)	470	VIIe	29E5	1856	5.0
Eddystone (ES)	760	VIIe	28E5	447	1.2
Falmouth (F)	30	VIIIf	29E4	77	0.2
North Celtic Sea (NCS)	2560	VIIIh/VIIe	27E3+27E4+28E3+28E4	114	0.3
South Celtic Sea (SCS)	3430	VIIIh	25E3+25E4+26E3+26E4	13	0.04

Table 2. Mean characteristics of the larval trajectories for the 20 larval releases carried out for each stock of the great scallop *Pecten maximus* in the English Channel and Celtic Sea over 10 years.

Scallop Stock (acronym)	Average value of the mean Dispersal Distance (Km)	Minimum value of the mean Dispersal Distance (Km)	Maximum value of the mean Dispersal Distance (Km)	Mean Azimuth (°)
Bay of Brest (BB)	13.1	9.4	18.5	344.6
Bays of Morlaix and Lannion (M/L)	58.9	30.8	93.1	40.7
Bay of Saint-Brieuc (BSB)	29.8	24.1	48.0	327.6
Saint Malo – Chausey (SM/C)	39.7	30	54.1	5.5
SE Jersey (SEJ)	50.7	37.6	70.1	313.9
W Jersey (WJ)	40.9	33.5	52.9	41.2
N Cherbourg (C)	50.1	42.2	57.8	265.1
Bay of Seine (BS)	30.7	22.7	53.3	51.3
Antifer (A)	57.3	23.1	113.8	63.8
Dieppe (D)	90.2	24	134.7	39.6
Vergoyer (V)	77.4	37.2	84.3	45.1
Rye Bay (RB)	69.2	54.9	79.9	64.3
Eastbourne (E)	83.0	22.3	125.2	63.8
Brighton (B)	81.3	26.7	141.2	70.2
Greenwich (G)	72.9	16.7	141.0	51.5
Weymouth (W)	42.3	20.1	81.2	107.8
Brixham (BX)	39.9	20.4	71.9	174.6
Plymouth Sound (P)	77.8	39.1	114.9	264
Eddystone (ES)	56.6	22.3	100.5	302
Falmouth (F)	62.3	38.2	77.2	326.1
North Celtic Sea (NCS)	58.0	36.7	84.1	341.8
South Celtic Sea (SCS)	53.7	41.6	69.0	127.7

Table 3. Pearson product-moment correlation coefficient between each pair of scallop stocks in the English Channel for the local retention rate (above the diagonal) and the self-recruitment rate (below the diagonal). Significant values ($p < 0.05$) are indicated in bold.

	M/L	BSB	SM/C	SEJ	WJ	C	BS	A	D	V	RB	E	B	G	W	BX	P	ES	F	NCS	SCS
Bay of Brest (BB)	-0.6073	-0.0485	0.0536	-0.1882	0.1011	0.1210	0.0291	-0.1608	-0.0989	-0.0950	-0.0491	-0.0849	-0.3165	-0.3538	-0.3034	-0.4442	0.1529	-0.1461	0.3368	0.4400	-0.0481
Bay of Morlaix/Lannion (M/L)	-	0.0238	-0.1884	0.2097	-0.1094	-0.0198	-0.0959	-0.1517	-0.3560	-0.2108	-0.3238	-0.0965	0.3059	-0.0597	-0.0217	0.3059	0.0208	-0.0415	-0.4072	-0.5595	-0.2431
Bay of Saint-Brieuc (BSB)	0.1342	-	0.2610	0.1335	-0.0183	0.0991	0.4050	0.3896	0.2304	0.5001	0.2994	0.4046	0.3078	0.2460	0.3268	0.0076	-0.4157	0.4893	-0.4234	0.3936	0.3790
Saint Malo-Chausey (SM/C)	-0.3670	-0.4249	-	0.1686	0.3314	0.2251	0.3968	0.1281	0.4613	0.1927	0.6598	-0.0591	0.2417	0.0902	0.4141	0.2429	-0.2987	0.0478	0.3139	0.0475	0.6410
SE Jersey (SEJ)	-0.0172	-0.4141	0.1818	-	-0.1798	-0.0960	0.0524	-0.2298	0.1791	-0.2152	0.2706	-0.2071	0.5275	0.2284	0.4027	0.5300	-0.2448	0.0895	0.1747	-0.0147	0.3469
W Jersey (WJ)	-0.0087	0.2739	-0.0321	-0.2954	-	0.3082	0.3234	0.4557	0.5004	0.1957	0.3646	-0.3449	-0.1448	0.0278	0.1800	-0.0485	-0.1278	0.1726	0.4017	0.1471	0.0780
N Cherbourg (C)	0.4205	0.3990	-0.2358	-0.0591	0.2806	-	0.2125	-0.1151	0.2944	-0.1370	0.3175	-0.1444	-0.2994	-0.1328	-0.3557	-0.2520	-0.0514	-0.4250	0.1450	-0.1313	-0.0622
Bay of Seine (BS)	0.3376	0.1253	0.1486	-0.2461	0.1387	0.2347	-	0.4640	0.3272	0.0963	0.3863	0.2535	0.0253	0.4486	0.4598	0.4838	-0.3092	0.2101	-0.2227	0.1426	0.1491
Antifer (A)	-0.1472	-0.2480	0.1085	-0.0287	-0.0406	-0.2833	0.3058	-	0.4604	0.6091	0.3321	0.0578	-0.1430	0.3817	0.4947	0.1826	-0.3097	0.6842	-0.1660	0.4022	0.0406
Dieppe (D)	-0.4666	-0.0659	0.5346	-0.1439	0.1161	-0.1523	0.2217	0.6936	-	0.5465	0.7141	0.0748	0.0054	0.4368	0.4287	0.1792	-0.5105	0.2313	0.2557	0.3106	0.3219
Vergover (V)	-0.4235	-0.0767	0.4549	-0.0351	0.1823	-0.0945	0.1707	0.5257	0.8151	-	0.3481	0.4117	0.0610	0.3099	0.2934	0.0500	-0.3863	0.5163	-0.1204	0.2802	0.1350
Rye Bay (RB)	-0.4710	0.1837	0.6840	0.0560	0.0543	0.0231	0.1934	0.0327	0.5396	0.4566	-	0.0161	0.0702	0.5490	0.3451	0.3745	-0.4820	0.3950	0.2882	0.3828	0.3759
Eastbourne (E)	0.2349	0.3578	-0.1048	-0.2994	-0.1541	0.1507	0.1725	0.2764	0.3496	0.0453	0.0071	-	-0.0403	0.5601	0.0580	0.2684	-0.3658	0.0230	-0.2659	0.0685	-0.1801
Brighton (B)	0.1187	0.1078	-0.0596	-0.0819	-0.1457	-0.0770	0.0095	-0.1403	-0.2594	-0.2784	-0.1773	-0.1703	-	0.0881	0.5902	0.4001	-0.3474	0.2854	-0.1806	-0.1099	0.5551
Greenwich (G)	0.1297	-0.1612	0.2485	0.2542	-0.2524	0.1538	0.5216	0.4445	0.4042	0.2869	0.2076	0.1966	-0.0953	-	0.4671	0.7200	-0.6570	0.4181	-0.1433	0.3263	-0.0501
Weymouth (W)	-0.2194	-0.3203	0.4328	-0.0615	-0.3163	-0.2545	0.3519	0.7615	0.6860	0.4310	0.2902	0.4268	-0.1530	0.6462	-	0.6557	-0.5808	0.5640	-0.0294	0.2371	0.5221
Brixham (BX)	0.0777	0.0765	0.2662	-0.1918	-0.1292	0.0194	0.7309	0.4889	0.4335	0.2520	0.3400	0.3891	0.1502	0.6178	0.7090	-	-0.5667	0.3398	-0.1002	-0.0195	0.0952
Plymouth Sound (P)	0.0658	-0.0105	-0.3050	0.0104	0.1823	0.0042	-0.4800	-0.6466	-0.6023	-0.4361	-0.4207	-0.4715	0.1226	-0.6953	-0.8630	-0.8701	-	-0.3824	0.0893	-0.4497	-0.1713
Eddystone (ES)	0.1784	-0.1533	0.2223	-0.0405	-0.4910	-0.1881	0.2388	0.3306	0.0943	0.0597	0.0649	0.2079	0.0213	0.4348	0.6239	0.5011	-0.5756	-	-0.1337	0.5322	0.1499
Falmouth (F)	-0.2842	-0.2770	0.1423	0.5020	-0.0146	-0.0453	-0.8304	-0.3516	-0.1440	-0.1067	0.0139	-0.1862	-0.2385	-0.2838	-0.2733	-0.6704	0.3888	-0.2126	-	0.0641	0.1258
North Celtic Sea (NCS)	-0.0111	0.2418	-0.5286	0.0779	0.1616	0.1044	-0.3264	-0.4599	-0.5646	-0.5320	-0.1961	-0.3071	-0.2350	-0.3989	-0.6128	-0.6249	0.5747	-0.5092	0.2373	-	0.2450
South Celtic Sea (SCS)	0.5210	0.0566	0.3295	0.4192	-0.0531	0.2371	0.3601	-0.0075	0.0556	-0.0208	0.2750	0.2601	0.0922	0.4402	0.1299	0.4270	-0.3978	0.1897	-0.0995	-0.3336	-

Table 4. Main parameters of the network of the great scallop stocks in the English Channel.

	Mean	Minimum	Maximum
Graph size	53	46	65
Number of components	2.7	2	4
Mean number of in-degrees	2.4	0	6
Mean number of out-degrees	2.4	0	6
Number of cutnodes	7	5	8

Supplementary appendix

Definition of connectivity and recruitment parameters

Suppose n stocks that release larvae and receive settlers. For $i, j \in \{1, 2, \dots, n\}$, we define:

- L_i , the number of larvae released by the stock i ;
- $S_{i,j}$, the number of larvae released from stock i that settled on stock j ;
- LR_i , the local larval retention rate which is the fraction of larvae produced by a local stock i that settled into that population;
- $C_{i,j}$, the connectivity between the stocks i and j defined as the proportion of larvae emitted by a stock i that settled in another stock j ;
- SR_i , the self-recruitment rate of the stock i which is the proportion of larvae that settled in a stock i and were originally produced by this stock;
- ER_j , the external recruitment rate which measures the contribution of a stock j to the total recruitment of a population i .

$$LR_i = \frac{L_i}{S_{i,i}} = C_{i,i}$$

$$C_{i,j} = \frac{L_i}{S_{i,j}}$$

$$SR_i = \frac{S_{i,i}}{\sum_{j=1}^{j=n} S_{j,i}} = \frac{C_{i,i} \cdot L_i}{\sum_{j=1}^{j=n} C_{i,j} \cdot L_j}$$

$$ER_j = \frac{S_{j,i}}{\sum_{j=1}^{j=n} S_{j,i}} = \frac{C_{j,i} \cdot L_j}{\sum_{j=1}^{j=n} C_{i,j} \cdot L_j}$$

For the calculation of the local recruitment rate and the connectivity, the number of larvae released by a stock i , i.e. L_i , depended on its area. Conversely, for the calculation of the self-recruitment rate and the external recruitment rate, the number of released larvae were weighted *a posteriori* according to the relative importance of each stock in terms of adult biomass estimated by landings as follows:

$$SR_i = \frac{C_{i,i} \cdot B_i}{\sum_{j=1}^{j=n} C_{i,j} \cdot B_j}$$

$$ER_j = \frac{C_{j,i} \cdot B_j}{\sum_{j=1}^{j=n} C_{i,j} \cdot B_j}$$

with B_i , the relative contribution of each stock to the total landings in the English Channel (see Table 1).

Supplementary Figure

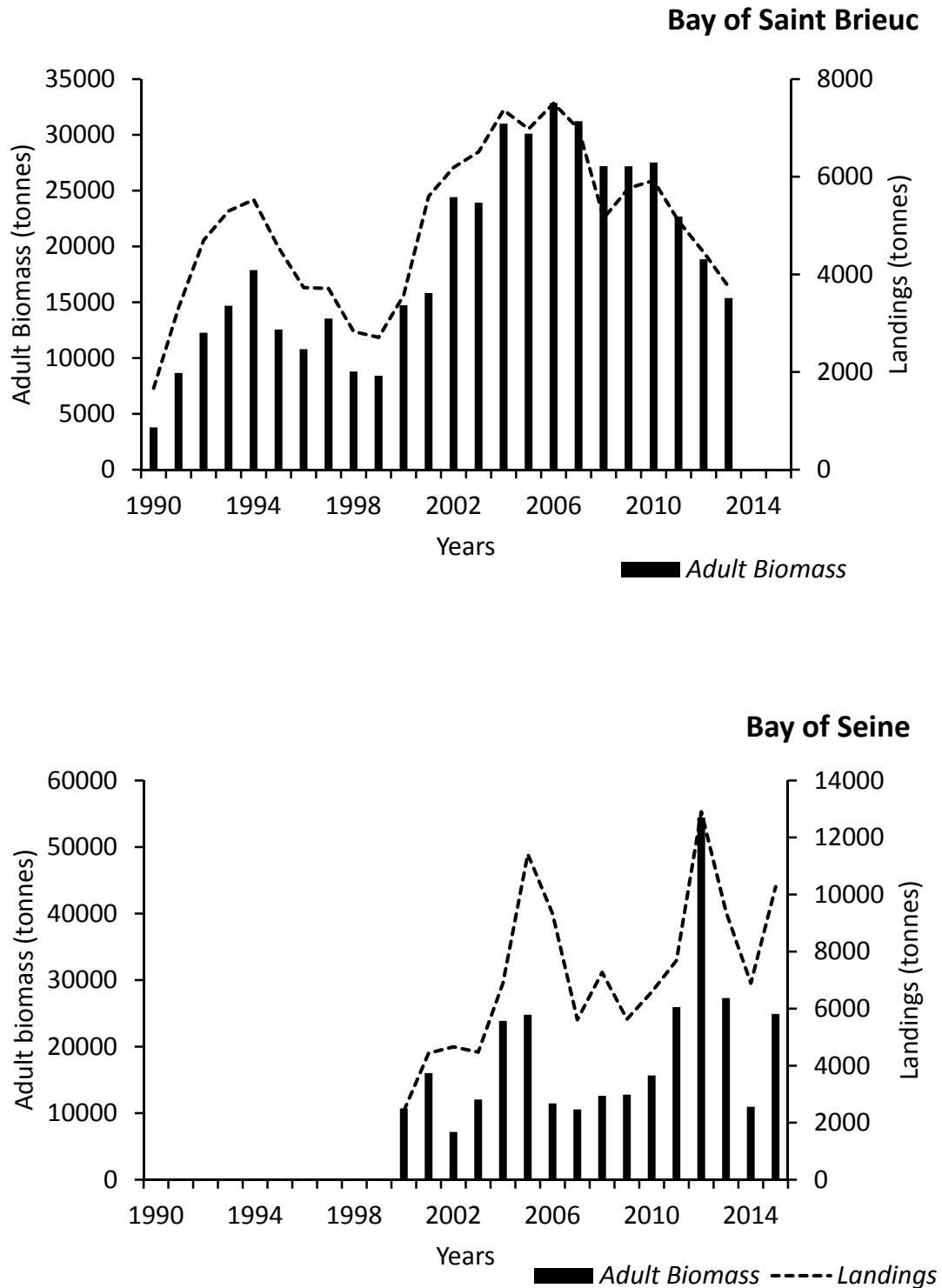


Figure S1: Long-term changes in adult biomass and landings for two major stocks of the great scallop, *Pecten maximus*, in the English Channel, i.e. the Bay of Saint Brieuc and the Bay of Seine, from 1990 to 2015.