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# A modelling study of the respective role of hydrodynamic processes and larval mortality on larval dispersal and recruitment of benthic invertebrates: example of *Pectinaria koreni* (Annelida: Polychaeta) in the Bay of Seine (English Channel)

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*The dispersal of Pectinaria koreni larvae released from the eastern Bay of Seine (English Channel) was studied using a two-dimensional hydrodynamic model which integrates tides, wind-driven currents and eddy diffusion, in order to examine the influence of environmental forcing and mortality on larval population dynamics. A broad agreement between predicted larval dispersal for two spawning events observed in 1987 and field data suggests that numerical modelling may be useful to analyse processes involved in the transport and the dynamics of larval populations. Larval mortality may be as important as hydrodynamic processes on larval losses for the adult population. Tides and eddy diffusion had some effects on larval dispersal, but wind forcing and the timing of spawning in relation to the meteorological environment are predicted to be the main source of variability in larval dispersal rates. Although wind-induced larval transport may produce interannual variations in larval retention and recruitment, predicted retention rates were always sufficient to ensure the maintenance of the adult population, regardless of hydrodynamic conditions. The long-range transport of larvae from the eastern Bay of Seine to distant populations was conditioned by constant strong winds, lasting 15 consecutive days, and should be considered an extremely rare event.*

## INTRODUCTION

Most coastal benthic invertebrates exhibit a complex life cycle, with one planktonic stage (i.e. larvae) and two benthic stages (i.e. juveniles and adults). For such species, recruitment [defined as the supply of early juvenile stages to an established population (Connell, 1985)] is one of the main processes governing the temporal fluctuations and the spatial structure of adult populations. This depends on a variety of physical and biological factors, which include (i) spawning and gamete fertilization, (ii) larval dispersal and survival, (iii) larval settlement and (iv) metamorphosis and post-settlement events (Eckman, 1996). According to the supply-side ecology theory, a dominant role is given to the larval phase that determines the initial conditions of recruitment (Roughgarden *et al.*, 1988). Either the number of settlers is not sufficient to saturate the habitat, thus limiting the population, or the supply of recruits is sufficient and adult abundance results from density-dependent post-settlement mechanisms (Caley *et al.*, 1996; Carroll, 1996). While numerous studies from rocky shores highlight the influence of larval supply on the adult population

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dynamics (Gaines and Roughgarden, 1986; Minchinton and Scheibling, 1991), the relative importance of pre- and post-settlement processes in soft sediments remains unclear (Olafsson *et al.*, 1994).

Because of the weak swimming abilities of planktonic larvae, larval dispersal depends mainly on local hydrodynamic features (Scheltema, 1986; Shanks, 1995). Hydrodynamic conditions, according to their intensity and direction, will either retain larvae in the vicinity of the adult population, enabling local recruitment, or export larvae away from the spawning population. In the latter case, export is favourable if the larval cohort can reach a distant but suitable substrate and colonize it effectively, but unfavourable if it leads to its loss (Scheltema, 1986; Ellien *et al.*, 2000). In addition to being influenced by water circulation patterns, the dispersal of planktonic larvae is also a function of biological parameters such as the location and timing of spawning, the duration of the planktonic phase and larval behaviour (Hill, 1991; Morgan *et al.*, 1996; Thiébaut *et al.*, 1998). According to the spatial and temporal variability of hydrodynamic conditions, variations in the location and timing of spawning may greatly modify larval dispersal patterns and settlement success (Tremblay *et al.*, 1994; Young *et al.*, 1998). Otherwise, the number of competent larvae reaching a suitable adult habitat will depend on larval mortality, which acts to decrease larval concentrations significantly during their transport (Cowen *et al.*, 2000).

In the English Channel, the tubicolous polychaete *Pectinaria koreni* is one of the dominant species of the muddy fine sand *Abra alba* community, confined to low tidal energy areas in bays and estuaries (Thiébaut *et al.*, 1997). Recently, different studies have identified the main processes involved in its larval dispersal in the eastern Bay of Seine: larval ontogenic vertical migration, the influence of the Seine river plume front, tidal residual currents and wind-induced currents (Lagadeuc, 1992a,b; Thiébaut, 1996; Thiébaut *et al.*, 1998). Regarding the two-layer estuarine circulation, the ontogenic migration of *P. koreni* larvae enables partial larval retention so that young larval stages preferentially located in the surface waters are transported to the open sea, whereas older stages distributed in the bottom waters are carried towards the coasts (Lagadeuc, 1992a). Horizontally, low tidal residual currents and the Seine river plume front also promote the retention of larval populations, whereas wind-induced currents produce a strong variability in larval distribution and generate an important offshore larval transport (Lagadeuc, 1992b; Thiébaut, 1996).

Field studies such as those cited above are an important step in identifying the main parameters involved in larval dispersal. However, recent developments in hydrodynamic modelling now provide quantitative methods of applying physical oceanographic information to the basic questions of larval dispersal [e.g. (Hill, 1994; Tremblay *et al.*, 1994; Garvine *et al.*, 1997; Manuel and O'Dor, 1997; Young *et al.*, 1998)]. These models can provide a synoptic view of larval distribution for a large range of geographic, hydrodynamic and climatic conditions at different spatial and temporal scales. They can also be used as a tool to determine the relative influence of various components of the water circulation and biological factors on larval dispersal. For the English Channel, a Lagrangian two-dimensional (2D) mathematical model of water circulation has been described by Salomon and Breton (Salomon and Breton, 1991, 1993). This model has been successfully used to simulate English Channel hydrodynamics, water mass exchange between the English Channel and the North Sea (Salomon *et al.*, 1995), and the transport of dissolved substances (Breton and Salomon, 1995; Guéguéniat *et al.*, 1995).

Using the 2D hydrodynamic model of the English Channel, the aims of the present study were: (i) to validate its use on larval dispersal studies by comparing simulated and observed distributions of *P. koreni* larvae in the eastern Bay of Seine; (ii) to assess the impact of tidal and wind-induced currents on larval dispersal; (iii) to show the effect of spawning timing on larval dispersal patterns; and (iv) to determine the importance of larval mortality on the success of recruitment relative to hydrodynamic conditions.

## STUDY AREA

Situated on the French coast of the English Channel, the Bay of Seine forms a rectangular embayment, ~65 by 140 km wide and 5–30 m deep, characterized by a macrotidal hydrodynamic regime (Figure 1). The major freshwater inputs into the bay are due to the Seine river, the discharge of which varies seasonally from a maximum of up to 2000 $m^3 s^{-1}$ in winter to a minimum of 100–200 $m^3 s^{-1}$ in summer. Residual circulation in the Bay of Seine depends on three factors: (i) tidal residual flow; (ii) horizontal density gradients due to the Seine freshwater inputs and mixing; and (iii) meteorological factors (e.g. wind stress) (Le Hir *et al.*, 1986). However, throughout the reproductive period of *P. koreni*, which occurs from May to July during low freshwater inputs, barotropic processes are the prevailing hydrodynamic features. Consequently, a 2D hydrodynamic model should provide satisfactory current fields over this period.

Benthic communities are distributed in relation to hydrodynamic and sedimentary gradients, from a muddy fine sand community in coastal shallow waters to a sandy gravel community further offshore (Gentil and Cabioch, 1997). In the eastern Bay of Seine, the *P. koreni* adult population covers a restricted area of ~400 $km^2$, and is patchily

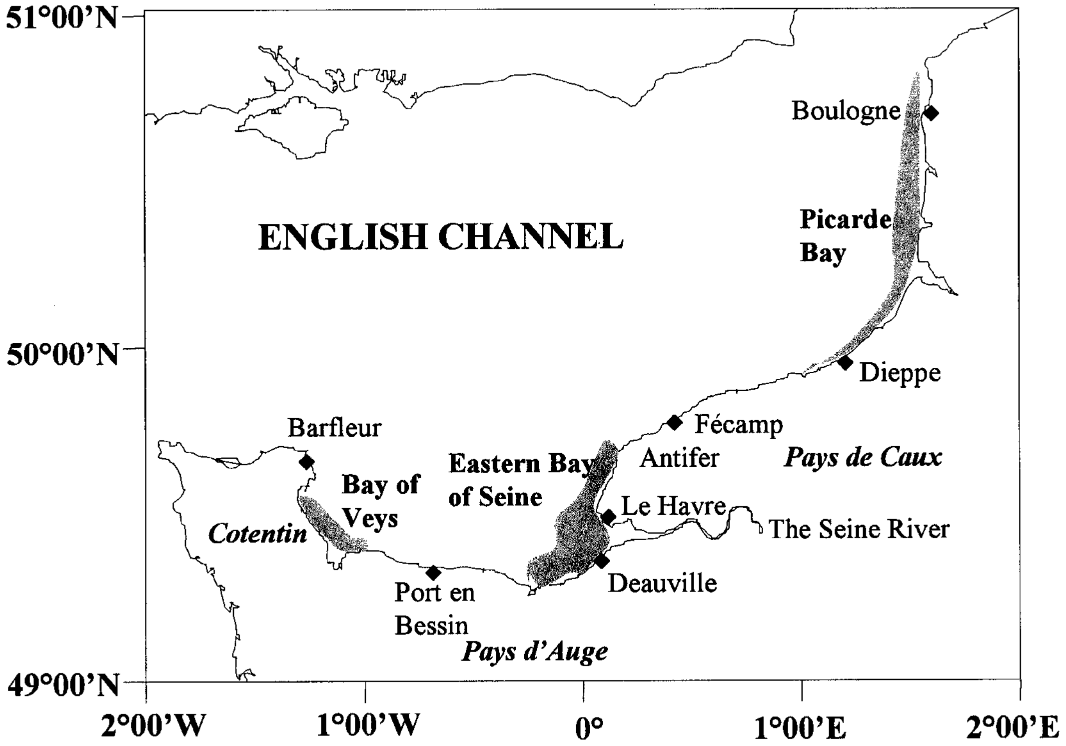

**Fig. 1.** Study area and location of *P. koreni* populations indicated by the grey area.

distributed, with maximum densities of >300 individuals (ind.) $m^{-2}$ located off the Seine estuary and off Deauville (Lambert, 1991; Thiébaut *et al.*, 1997). Two neighbouring populations of *P. koreni* have been recorded along the French coasts of the eastern English Channel at ~85 km to the west in the Bay of Veys, and at ~125 km to the NE along the coast between Dieppe and Boulogne (Figure 1).

## METHOD

### The hydrodynamic model

The English Channel hydrodynamic model is a numerical tidal current model solving the depth-integrated Navier–Stokes equations in their usual form:

$$\frac{\partial V}{\partial t} + V\nabla\zeta + 2\Omega\Lambda V = -g\nabla\zeta - \frac{gV|V|}{K_r^2 H^{4/3}} + \varepsilon\nabla^2 V \quad (1)$$

where $V$ is the average velocity on the vertical, $\zeta$ is the surface slope, $g$ is the acceleration due to gravity, $H$ is the water column depth, $K_r$ is Strickler's friction coefficient, $\varepsilon$ is the horizontal viscosity and $\Omega$ is the angular velocity of Earth's rotation.

Hydrodynamic equations are solved using an alternate direction implicit (ADI) finite difference method. The model takes into account shoaling banks. Boundary conditions are provided by a wider 2D model of the North European continental shelf, from 47°N to 63°N and from 12°W to 12°30′E (Salomon and Breton, 1991). This latter model is driven along opened boundaries by tidal conditions extracted from the atlas of Schwiderski (Schwiderski, 1983), and over its area by wind stress, which is assumed to be spatially uniform. The English Channel model is limited to 48°18′N and 51°20′N in latitude, and to 6°28′W and 3°00′E in longitude. Its mesh size is fixed to one nautical mile, thus forming a grid of 367 × 184 cells.

The model takes into account only the two major tidal components on the North-western European continental shelf, M2 and S2, whose combination gives a semi-diurnal tide. Wind stress on the water surface, which is another important driving force of water masses with no true periodicity, is evaluated as follows:

$$\tau = \rho_a C_w |W| \vec{W} \quad (2)$$

where $\tau$ is the wind stress, $\rho_a$ is the mass per unit volume of air, $C_w$ is the drag coefficient, equal to 0.0015, and $\vec{W}$ is the wind vector.

Initially, the hydrodynamic model was run for various combinations of tides and winds, to calculate a great number of long-term water particle trajectories over a given time.

Those trajectories are then transformed into Lagrangian velocities, which are related to the average geographical positions of the particles as they move back and forth during the tidal cycle, through the 'barycentric technique' described in detail by Salomon *et al.* (Salomon *et al.*, 1991), Breton and Salomon (Breton and Salomon, 1995) and Salomon *et al.* (Salomon *et al.*, 1996). This technique provides for each tide–wind combination a unique velocity field, which sums all the components of the current (i.e. Euler's residual, Stokes's residual and Lagrangian drift) (Breton and Salomon, 1995). In order to decrease computation time, the Lagrangian residual current calculation is run only on a finite number of tidal and wind conditions. Interpolations are made among the values to find solutions that correspond to any non-calculated tidal and meteorological situation (Salomon *et al.*, 1996).

## Larval transport model

Lagrangian residual velocities obtained from the hydrodynamic model enable a direct calculation, over long-term durations, of the transport and mixing of a dissolved or particulate substance, using the usual expression of the advection–diffusion equation. The advection–diffusion model solves the flux conservative form of the continuity equation describing the transport of a scalar quantity in two dimensions, given by:

$$\frac{\partial(HC)}{\partial t}+\frac{\partial(HUC)}{\partial x}+\frac{\partial(HVC)}{\partial y}-\frac{\partial^2\left(KH\frac{\partial C}{\partial x}\right)}{\partial x}-\frac{\partial^2\left(KH\frac{\partial C}{\partial y}\right)}{\partial y}-mC=0 \quad (3)$$

where $U$ and $V$ are the components of the residual velocities along $x$ and $y$, respectively, $m$ is the larval mortality rate, $C$ is the larval concentration (ind. $m^{-3}$), $H$ is the average water depth over a tidal cycle and $K$ is the coefficient of turbulent diffusion.

The diffusion coefficient ($K$) was calculated using Elder's law, linking this coefficient to average instantaneous current velocity ($U$) and average water depth ($H$), considering the proportionality coefficient ($\beta$) as a function of the time scale:

$$K=\beta\ U\ H \quad (4)$$

According to Salomon and Breton (Salomon and Breton, 1993), $\beta$ would be close to 0.3 for periods of about half a week.

In the larval transport model, two types of boundaries are considered. At open boundaries, larvae leaving the model domain are not allowed to return. Closed boundaries, which represent land, are considered as perfectly reflecting.

## Biological inputs

*Pectinaria koreni* is a univoltine species living 15–18 months, with its main breeding periods occurring between April and July (Elkaïm and Irlinger, 1987; Irlinger *et al.*, 1991). Larval development, which includes two trochophore stages and three metatrochophore stages, lasts for 11 days (Lagadeuc and Retière, 1993). After a pelagic stage, larvae produce a mucus tube and become aulophore larvae as a transitory stage to the benthic juvenile phase. Consequently, larval dispersal was simulated for a period of 15 days. Larvae are considered as inert particles and are constrained by a mortality rate of 0.06 $day^{-1}$, which is considered as constant during the whole life of the larvae. Owing to the lack of data on the mortality of polychaete larvae, this rate has been arbitrarily chosen as a low value among a range of mortality rates based on the monitoring of larval cohorts in the plankton for different meroplanktonic organisms (i.e. from 0.016 to 0.357 $day^{-1}$) (Rumrill, 1990). Consequently, the influence of mortality on larval supply is probably underestimated.

The location of larval release in the model corresponds to the observed distribution of *P. koreni* adult patches in the eastern Bay of Seine. The number of larvae released per surface unit was calculated from data on the distribution and abundance of *P. koreni* adults obtained in February 1987 (Lambert, 1991). These data are based on the sampling of 51 stations on a grid of 2.30′ in longitude and 1.50′ in latitude covering the whole muddy fine sand community of the eastern Bay of Seine. The abundance of *P. koreni* adults in each mesh of the model was calculated by linear interpolation. An exponential mortality law was assumed to determine adult abundance during the spawning events of May 1987:

$$N_t=N_0\ e^{-mt} \quad (5)$$

where $N_t$ is the adult abundance in May 1987, $N_0$ is the adult abundance in February 1987, $m$ is the adult mortality rate and $t$ is time.

Following Elkaïm and Irlinger, the adult mortality rate was fixed to 0.01 $day^{-1}$ (Elkaïm and Irlinger, 1987). The time between February and May 1987 was approximated as 90 days. The female spawning stock was estimated at half of the adult population, assuming a sex ratio of 1:1 (Elkaïm and Irlinger, 1987). Thus, the number of eggs released in each model mesh can be calculated as follows:

$$\Omega=N_t\times 0.5\times F \quad (6)$$

where $\Omega$ is the number of eggs released per model mesh and $F$ is the mean female fecundity.

Fecundity is linked to female size, which was estimated from the diameter of the cephalic disc (CD) through an allometric relationship (A.-S. Barnay, personal communication):

$$F = 333.6\ \mathrm{CD}^{3.525} \tag{7}$$

Before the breeding period, the mean size of a *P. koreni* CD in the eastern Bay of Seine was measured to be ~4.5 mm (Lambert, 1991). At spawning, only ~90% of the ovocytes are mature and can be fertilized (A.-S. Barnay, personal communication). It was assumed that each ovocyte produced a larva. From planktonic samples collected between 8 May and 5 June 1987, and meiobenthic samples collected between 14 May and 6 September 1987 (Lagadeuc, 1990; Lambert, 1991), three major spawning events were identified in May–June 1987. As the proportion of spawning females in each period remains unknown, we have arbitrarily assumed that only a third of them spawned at each time.

The spatial distribution of the habitat of *P. koreni* in the English Channel was represented as a spatial 0/1 grid (i.e. 0, unsuitable substrate for larval settlement; 1, suitable substrate for larval settlement) from the observed distribution of benthic communities (Cabioch and Gentil, 1975; Cabioch and Glaçon, 1975, 1977; Gentil and Cabioch, 1997). At the end of larval dispersal, the number of settling larvae on all favourable grid cells is calculated as the sum of the larvae settling on each cell multiplied by 0 or 1.

### Simulations

To calibrate the model, the simulated larval dispersal was compared visually to field observations. Although three spawning events occurred in 1987, larval dispersal was simulated in real conditions of tide and wind for only two events for which *in situ* larval distribution was available: 15 May and 26 May. The collection of field data has been described in detail by Lagadeuc (Lagadeuc, 1990, 1992b). Briefly, larvae were collected at two spatial scales. On a large scale, ~40 stations located between 15 and 30 nautical miles from the adult population were sampled during two cruises on 27–28 May and 2–3 June 1987 using vertical net hauls. On a small scale, to observe gradients in larval abundance near the adult population, sample collections were made continuously at 3 m depth with a volumetric pump during nine surveys. Every 5 min, a sample of 1.5 m$^3$ was filtered through an 80 μm mesh net. For each survey, 74–114 samples were collected. For the present study, only two surveys carried out after ~1 week of larval dispersal were exploited: 23 May and 2 June.

Two series of simulations were conducted to investigate the influence of the tide. Firstly, larval dispersal was studied in three conditions of constant tide (i.e. spring tide, average tide and neap tide) and with no wind during the duration of larval life. Secondly, simulations were run taking into account the lunar tidal cycle so that larvae were released in different tidal conditions (i.e. spring and neap tides).

To investigate the influence of wind stress, two types of wind forcing were applied to the model in conditions of an average tide. These were constant winds from the SW (i.e. direction 225°) and NE (i.e. direction 45°), speeds of which range from 0 to 15 m s$^{-1}$. These two compass directions correspond to the dominant winds in the bay during springtime (Météo-France data).

To study the influence of the spawning date on the larval dispersal of *P. koreni*, larvae were released every 2 days between 1 May and 16 July 1987. Larval dispersal was simulated in real conditions of wind and tide observed in the Bay of Seine at the same time. Wind data were provided by Météo-France, and tide data were taken from the Service Hydrographique et Océanographique de la Marine (Brest).

To investigate the relative importance of larval mortality and hydrodynamics for larval losses, simulations were carried out in three hydrodynamic conditions: (i) average tide without wind; (ii) average tide with a SW wind of 8 m s$^{-1}$; and (iii) average tide with a NE wind of 8 m s$^{-1}$. Larvae were subjected to mortality rates ranging from 0 to 0.4 day$^{-1}$, corresponding to the range of mortality rates reported for meroplanktonic species (Rumrill, 1990).

## RESULTS

### Simulated circulation in the Bay of Seine

Under average tidal conditions, water is mainly flushed westwards and northwestwards off the Seine estuary, and eastwards in the central Channel (Figure 2A). Within the eastern Bay of Seine, residual currents do not exceed 2–3 cm s$^{-1}$. Tide also generates clockwise gyres (i.e. off Barfleur, off Antifer and along the coasts of Pays d'Auge), which can locally increase the residence time of larvae.

Under SW and NE winds of 8 m s$^{-1}$, currents flush water approximately parallel to the coast and are oriented in the prevalent wind direction (Figure 2B and C). Under NE winds, current velocities increase mainly in shallow waters and reach ~5–6 cm s$^{-1}$ off the Seine estuary and off Antifer Cape, while all gyres are disrupted (Figure 2B). Under SW winds, the direction of

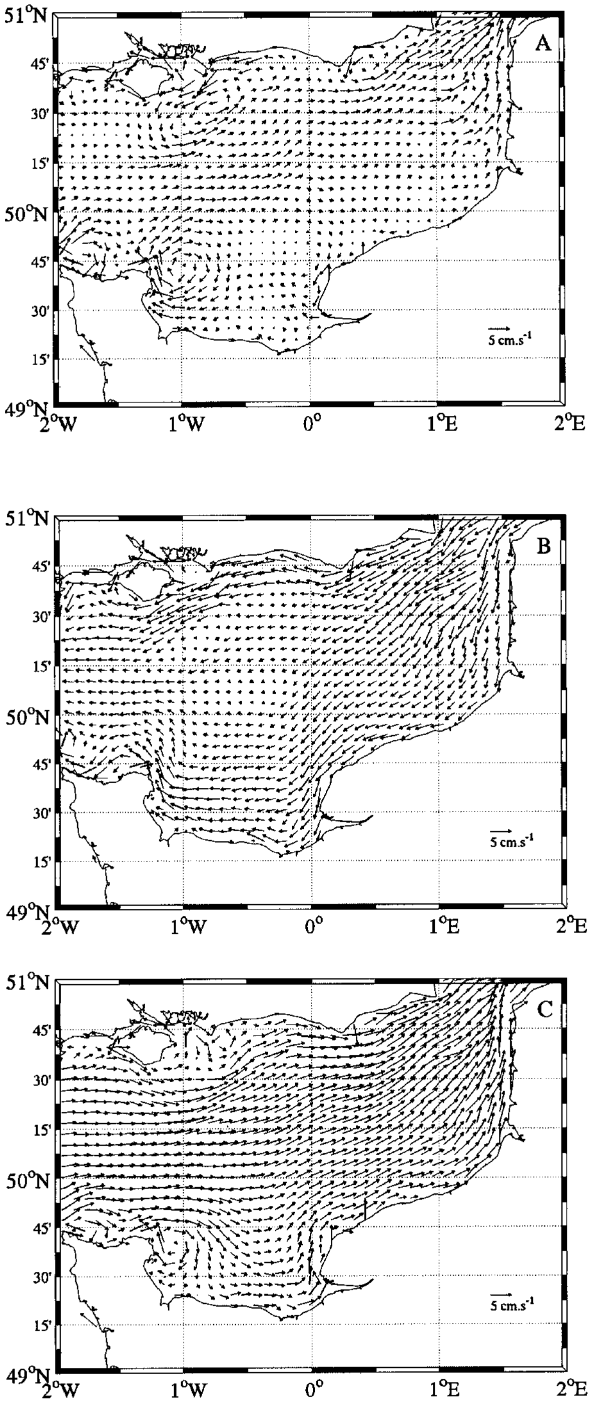

**Fig. 2.** Simulated residual Lagrangian velocity field in the Bay of Seine for (**A**) an average tide and no wind, (**B**) an average tide and an 8 m s$^{-1}$ NE wind and (**C**) an average tide and an 8 m s$^{-1}$ SW wind.

currents induced by winds is opposed to tidal residual currents, so that current velocities do not increase strongly and remain below 4 cm s$^{-1}$ (Figure 2C). The gyre located off Barfleur persists.

## Comparison between observed and simulated larval dispersal

For the first spawning event (i.e. 15 May 1987), the larval cohort is mainly dispersed westwards and northwestwards (Figure 3). Larvae were subjected to a weak W-NW wind (~3 m s$^{-1}$) during the first 3 days and then to a moderate N-NE-E wind (~7 m s$^{-1}$) during 8 days. These winds strengthen tidal residual currents advecting larvae to the west along the coasts of Pays d'Auge (Figure 3B). The last days of larval dispersal are mainly characterized by low W and NW winds (~3 m s$^{-1}$), thereby decreasing the extent of larval transport to the west (Figure 3C). At the end of the dispersal phase, 28.0% of larvae released during this spawning event are able to settle on a favourable substrate (i.e. average settler density = 60 595 ind. m$^{-2}$). The settlement occurs principally off the Seine estuary and along the coasts of Pays d'Auge where larval concentration exceeds 1000 ind. m$^{-3}$.

The observed small-scale distribution of *P. koreni* larvae on 23 May partly confirms the simulation results (Figure 3D). Thus, Lagadeuc stated that larvae are mainly advected to the south and the west in response to NE winds, so that maximal larval concentrations (>10 000 ind. m$^{-3}$) are reported off the Seine estuary and off Deauville (Lagadeuc, 1992b). The main difference between the two data sets is the very low densities of larvae off Le Havre reported from field observations. On a larger scale, Lagadeuc (Lagadeuc, 1990) observed no larvae west of Port-en-Bessin at the end of the larval dispersal on 27–28 May, while simulated data show that larvae can reach this area, but at very low densities (i.e. <1 ind. m$^{-3}$).

For the second spawning event (i.e. 26 May 1987), simulations show that larvae are mainly advected to the north off the Seine estuary and to the NE along the coasts of Pays de Caux in response to moderate westerly winds (Figure 4). At the end of the larval phase, only 17.43% of the larvae are able to settle on a favourable substrate, in areas principally located in front of the Seine estuary and along the coasts of Pays de Caux between Le Havre and Antifer Cape (i.e. average settler density = 37 659 ind. m$^{-2}$).

The dispersal features deduced from field observations (Lagadeuc, 1992b) are similar to those obtained by simulations. On 2 June, maximal larval densities (>10 000 ind. m$^{-3}$) were located in the same areas for both direct observations and simulations, off the Seine estuary and off La Hève Cape (Figure 4D). Low larval densities (<100 ind. m$^{-3}$) are reported in the western part of the sampling area. On a larger scale, after 1 week of larval dispersal on 2–3 June, Lagadeuc (Lagadeuc, 1990) observed the presence of larvae to the NE of Antifer Cape, and their apparent absence off Fécamp, which is in good agreement with our modelling results.

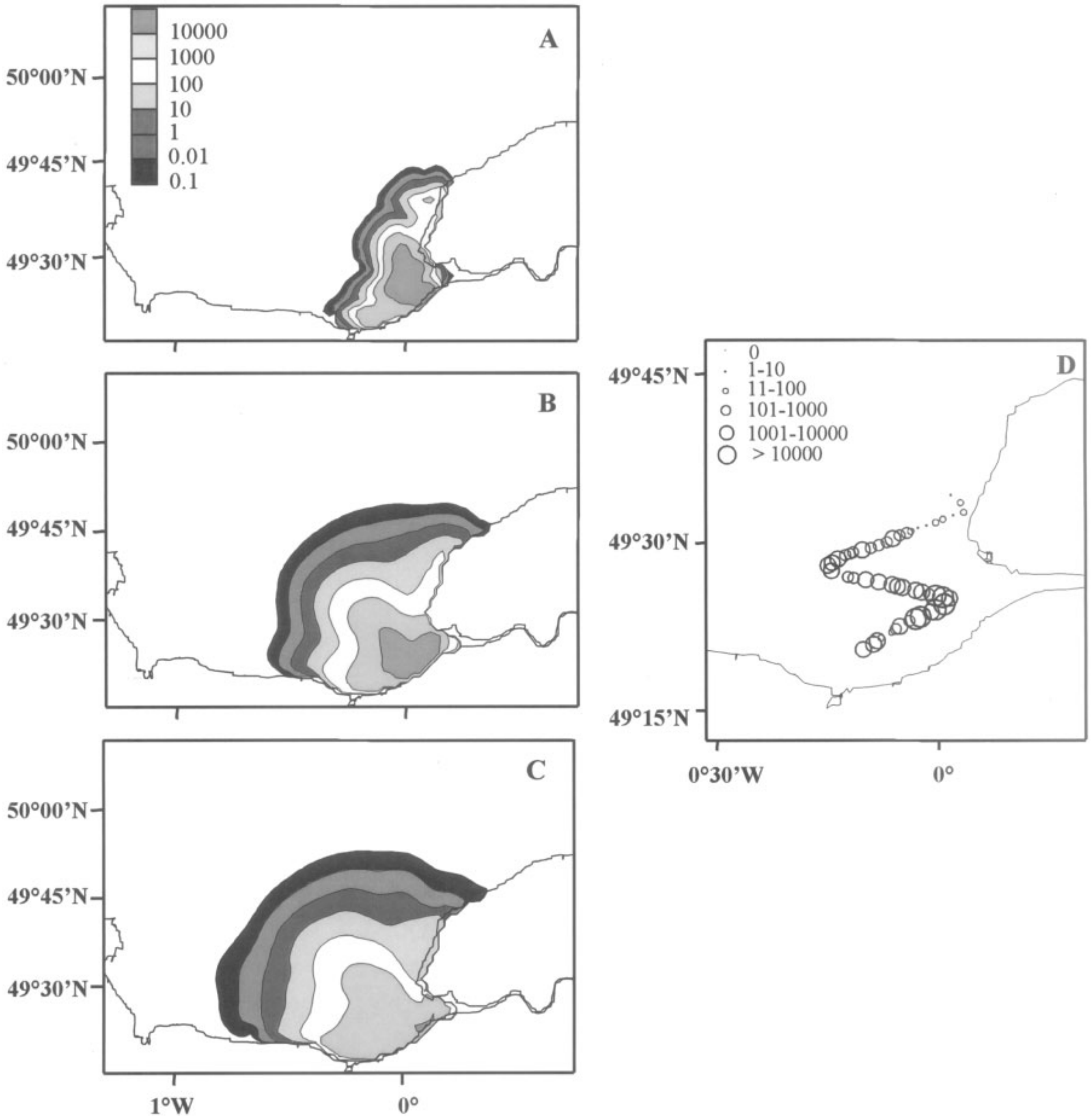

**Fig. 3.** Distribution of *P. koreni* larvae for a spawning date on 15 May 1987 in the eastern Bay of Seine. (**A**) Simulated larval distribution on 16 May, 1 day after the release. (**B**) Simulated larval distribution on 23 May, 8 days after the release. (**C**) Simulated larval distribution on 29 May, 14 days after the release. (**D**) Observed distribution at 3 m depth on 23 May [modified from Lagadeuc (Lagadeuc, 1990)]. Larval densities are expressed as ind. $m^{-3}$. For the simulations, larval mortality was set at 0.06 $day^{-1}$. Figure available in colour online as supplementary data at http://www.plankt.oupjournals.org

## Influence of tides on larval dispersal

In neap tide conditions, the plume spreads in an isotropic way mainly by eddy diffusion (Figure 5A). Maximal larval abundances (hereafter referred to as >1000 larvae $m^{-3}$) are observed off the Seine estuary: 32.3% of the larval cohort is retained on adult population areas after 15 days (i.e. average settler density = 69 627 ind. $m^{-2}$). In average tide conditions, the larval dispersal remains relatively isotropic, indicating that eddy diffusion is still the major process governing larval transport (Figure 5B). However, due to tidal advection, larvae are preferentially transported to the west and to the northwest. Consequently, the proportion of the larval plume retained on the adult area decreases to 25.7%, although maximum larval densities are principally reported above the favourable substrates of the eastern Bay of Seine (i.e. average settler density = 55 600 ind. $m^{-2}$). In spring tide conditions, the larval cohort spreads to the west, reaching the eastern coasts of Cotentin, and to the northwest (Figure 5C). Larval densities are maximal in the south

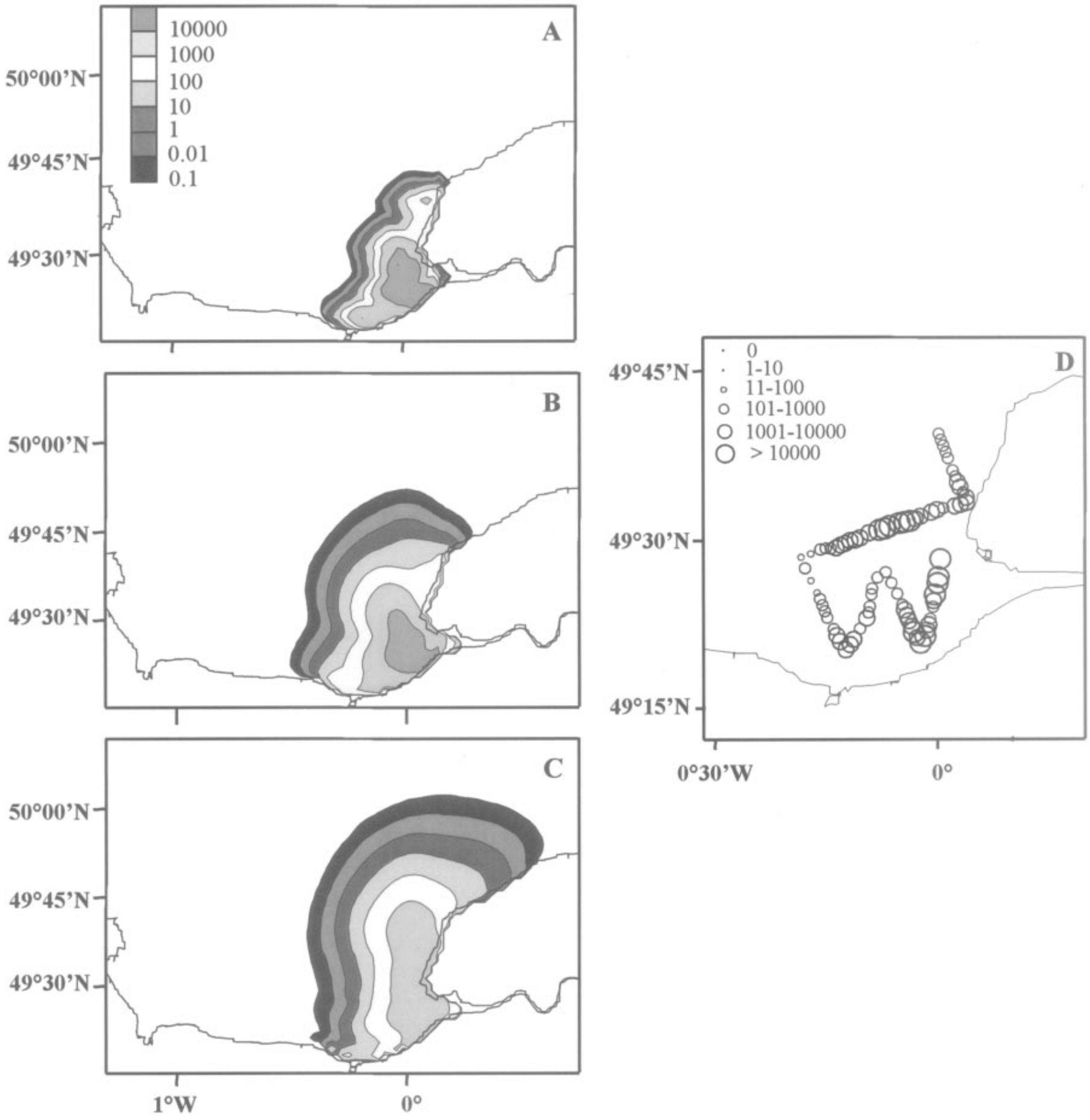

**Fig. 4.** Distribution of *P. koreni* larvae for a spawning date on 26 May 1987 in the eastern Bay of Seine. (**A**) Simulated larval distribution on 27 May, 1 day after the release. (**B**) Simulated larval distribution on 2 June, 7 days after the release. (**C**) Simulated larval distribution on 9 June, 14 days after the release. (**D**) Observed distribution at 3 m depth on 2 June [modified from Lagadeuc (Lagadeuc, 1990)]. Larval densities are expressed as ind. $m^{-3}$. For the simulations, larval mortality was set at 0.06 $day^{-1}$. Figure available in colour online as supplementary data at http://www.plankt.oupjournals.org

of the eastern Bay of Seine. Only 13.8% of the larval population is retained on the favourable substrates of the adult population (i.e. average settler density = 26 453 ind. $m^{-2}$). Larvae released from the eastern Bay of Seine are able to colonize the favourable substrates of the Bay of Veys at a very low rate of $1.9 \times 10^{-4}$%; average settler density reaches only 27 ind. $m^{-2}$.

Thus, larval dispersal patterns and levels of retention depend on tidal intensity. The retention is favoured in neap tide conditions, while spring tide conditions enhance dispersal and colonization. A 3-fold decrease in larval retention rate and settler density occurred between neap and spring tides.

When the lunar tidal cycles are taken into account, the patterns of larval dispersal are very close to those obtained in conditions of constant average tide (Figure 5D and E). The proportion of larvae retained on the favourable substrates of the Bay of Seine is equal to 21.1% for a neap tide release and 24.3% for a spring tide release (i.e. average settler density = 45 564 and

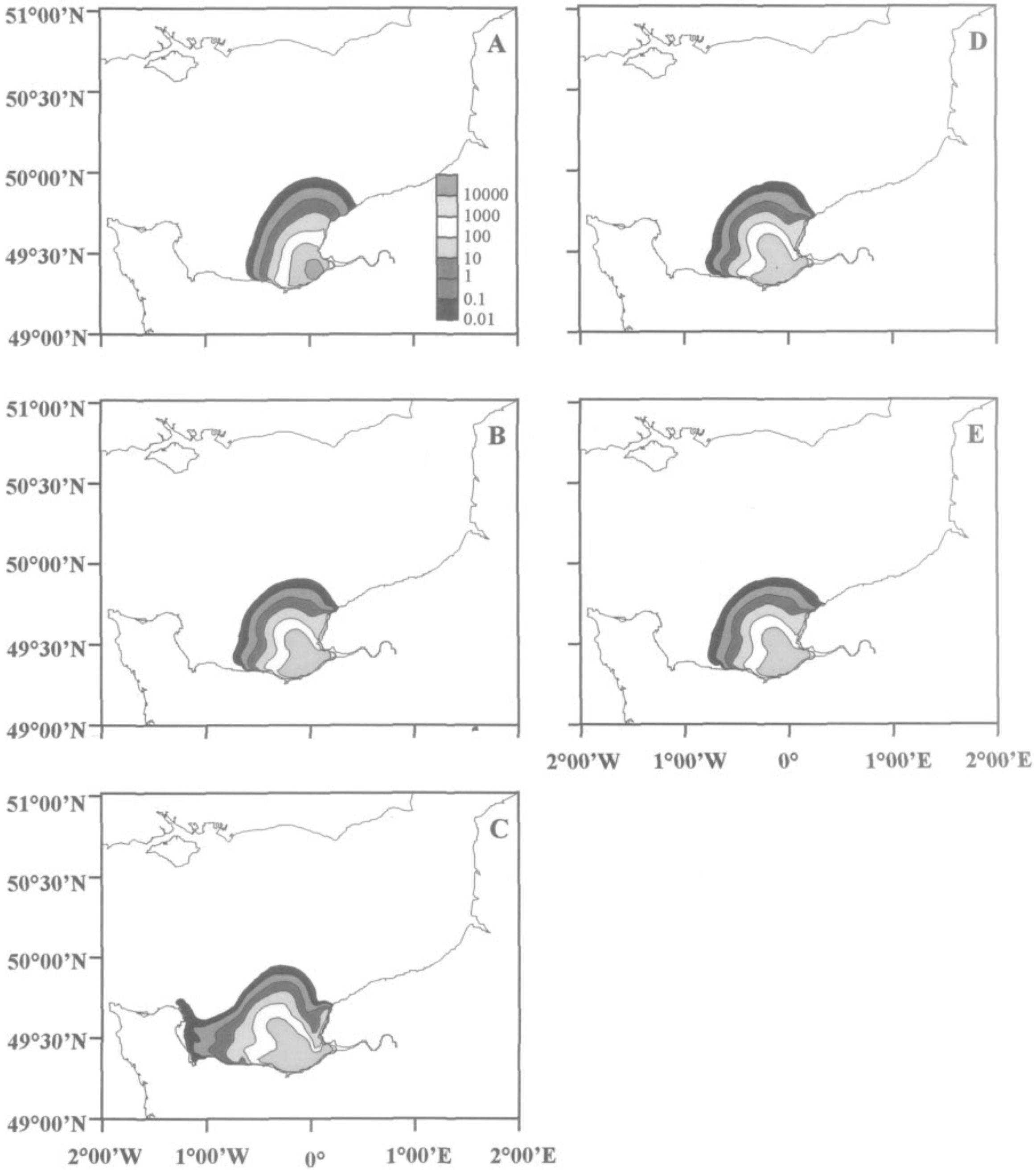

**Fig. 5.** Simulated distribution of *P. koreni* larvae 15 days after a release in the eastern Bay of Seine according to tidal conditions. (**A**) Constant neap tide. (**B**) Constant average tide. (**C**) Constant spring tide. (**D**) Neap–spring–neap cycle. (**E**) Spring–neap–spring cycle. Larval mortality was set at 0.06 day$^{-1}$. Larval densities are expressed as ind. m$^{-3}$. Figure available in colour online as supplementary data at http://www.plankt.oupjournals.org

52 474 ind. m$^{-2}$, respectively). These two retention rates are quite similar to that resulting from larval dispersal under constant average tide conditions (i.e. 25.7%). This little difference may be explained by the fact that, whatever the time of larval release, the evolution of tidal range in relation to the lunar cycle during 2 weeks may be considered to be equivalent to a constant average tide.

## Influence of winds on larval dispersal

The study of wind forcing shows that variations in larval retention and colonization rates, and dispersal patterns, depend on wind direction and intensity. For SW wind speeds ranging from 0 to 8 m s$^{-1}$, the proportion of larvae retained on suitable substrates of the Bay of Seine decreases slightly from 25.7% to 19.3% (i.e. average settler density from 55 498 to 41 677 ind. m$^{-2}$) (Figure 6A). Despite the low variations in the retention rate, the pattern of larval dispersal is greatly modified. While larvae are transported to the W and to the NW for low wind (e.g. 2 m s$^{-1}$) (Figure 6B), the larval plume spreads northeastwards for a moderate wind (e.g. 8 m s$^{-1}$) with maximal larval densities restricted to a continuous area from the Seine estuary to the Antifer Cape (Figure 6C). For SW wind speeds $\geq$9 m s$^{-1}$, retention rates decrease sharply from 15.6% for a speed of 9 m s$^{-1}$ to 1.3% for a speed of 15 m s$^{-1}$ (i.e. average settler density from 33 687 to 2807 ind. m$^{-2}$) (Figure 6A). Although retention rates remain non-negligible, the larval plume is advected along the coasts of Pays de Caux (Figure 6D). Thus, the colonization rates on the suitable substrates located off Dieppe increase from 1.7 × 10$^{-3}$% for a SW wind of 12 m s$^{-1}$ to 1.0% for a SW wind of 15 m s$^{-1}$ (i.e. average settler density from 12 to 6584 ind. m$^{-2}$).

For NE wind, wind-induced currents work in conjunction with tidal residual currents and amplify larval transport to the west. For velocities ranging between 0 and 4 m s$^{-1}$, the proportion of larvae retained within the eastern Bay of Seine increases slightly from 25.7% to 27.6% (i.e. average settler density from 55 498 to 59 601 ind. m$^{-2}$) (Figure 7A). Within this range, the wind-induced circulation concentrates larvae off the Seine estuary and along the coasts of Pays d'Auge (Figure 7B). For NE wind speeds $\geq$5 m s$^{-1}$, larval retention decreases from 26.6% for a NE wind of 5 m s$^{-1}$ to 2.1% for a NE wind of 15 m s$^{-1}$ (i.e. average settler density from 57 441 to 4535 ind. m$^{-2}$) (Figure 7A) as the larval plume is advected westwards to the coasts of Cotentin (Figure 7C and D). The colonization rate on the favourable substrates of the Bay of Veys increases by several orders of magnitude, from 4.0 × 10$^{-4}$% for a NE wind of 9 m s$^{-1}$ to 3.4% for a NE wind of 15 m s$^{-1}$ (i.e. average settler density from 3 to 24 197 ind. m$^{-2}$). Thus, in response to larval dispersal to the west, the colonization rate of the favourable substrates of the Bay of Veys may exceed the retention rate observed in the eastern Bay of Seine.

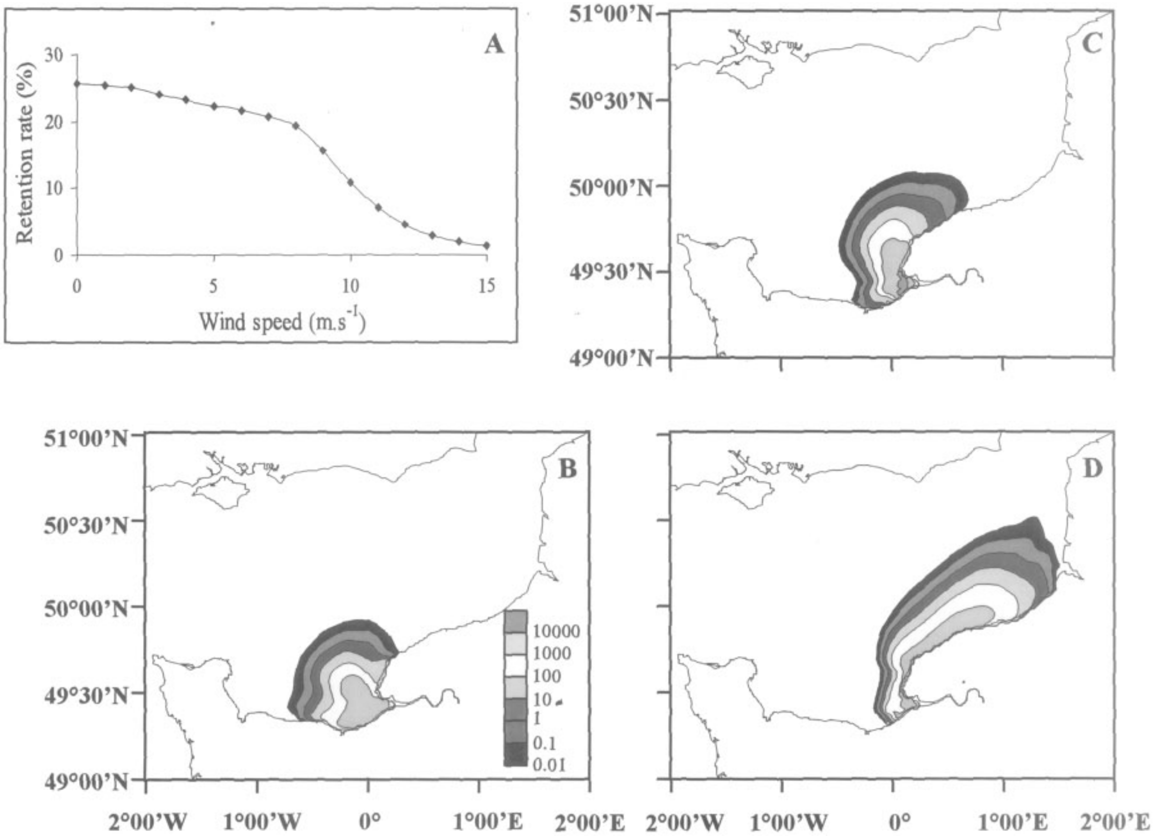

**Fig. 6.** Influence of a constant SW wind forcing on larval dispersal in the eastern Bay of Seine. (**A**) Evolution of the larval retention rate in the eastern Bay of Seine in relation to wind speed. (**B**) Simulated distribution of *P. koreni* larvae 15 days after a release in the eastern Bay of Seine for a SW wind of 2 m s$^{-1}$. (**C**) Simulated distribution of *P. koreni* larvae 15 days after a release in the eastern Bay of Seine for a SW wind of 8 m s$^{-1}$. (**D**) Simulated distribution of *P. koreni* larvae 15 days after a release in the eastern Bay of Seine for a SW wind of 14 m s$^{-1}$. Larval mortality was set at 0.06 day$^{-1}$. Larval densities are expressed as ind. m$^{-3}$. Figure available in colour online as supplementary data at http://www.plankt.oupjournals.org

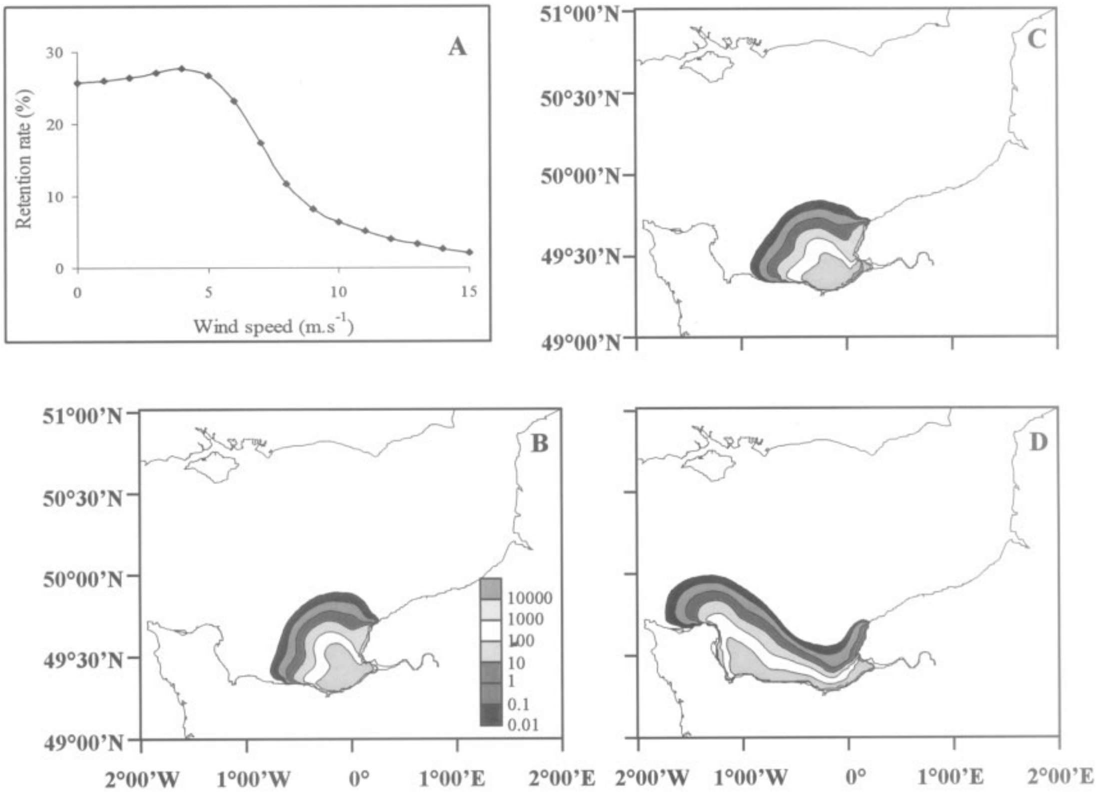

**Fig. 7.** Influence of a constant NE wind forcing on larval dispersal in the eastern Bay of Seine. (**A**) Evolution of the larval retention rate in the eastern Bay of Seine in relation to wind speed. (**B**) Simulated distribution of *P. koreni* larvae 15 days after a release in the eastern Bay of Seine for a NE wind of 2 m s$^{-1}$. (**C**) Simulated distribution of *P. koreni* larvae 15 days after a release in the eastern Bay of Seine for a NE wind of 5 m s$^{-1}$. (**D**) Simulated distribution of *P. koreni* larvae 15 days after a release in the eastern Bay of Seine for a NE wind of 14 m s$^{-1}$. Larval mortality was set at 0.06 day$^{-1}$. Larval densities are expressed as ind. m$^{-3}$. Figure available in colour online as supplementary data at http://www.plankt.oupjournals.org

### Influence of the spawning time on larval dispersal

From May to July 1987, the proportion of larvae retained on the suitable substrates of the eastern Bay of Seine varied with spawning time between 16.5 and 30.4% (i.e. average settler density from 35 630 to 65 647 ind. m$^{-2}$). For two consecutive release events, the largest difference in the retention rates may exceed 4.5%, while a 10 day gap in the date of spawning may induce a 2-fold difference in retention rate from 29.4% to 16.5%. The strongest retention rates (i.e. ~30%) are observed during periods characterized by an alternation of easterly and westerly winds during a few days. Conversely, the weakest retention rates (i.e. 16–17%) are detected for spawning events occurring during a period of constant wind. While frequent changes in wind direction promote larval retention, periods of uniform wind favour larval export. There was no detectable effect of variations in tidal range.

### Influence of larval mortality

According to hydrodynamic conditions (i.e. average tide, average tide and a SW or NE wind of 8 m s$^{-1}$), 59.6–28.8% of the released larvae remain above the favourable substrates of the eastern Bay of Seine when the mortality rate is set to 0 (Figure 8). The effect of larval mortality on the proportion of settlers exceeds the effects of hydrodynamic processes above a mortality rate of 0.03–0.04 day$^{-1}$ for an average tide, 0.05 day$^{-1}$ for an average tide with a SW wind of 8 m s$^{-1}$ and 0.08–0.09 day$^{-1}$ for an average tide with a NE wind of 8 m s$^{-1}$. The influence of larval mortality on larval losses decreases as the residual current velocities increase. As a result of both hydrodynamics and larval mortality, the proportion of settlers on the suitable substrates of the eastern Bay of Seine decreases exponentially with an increase in mortality rate and tends to 0 when the mortality rate exceeds 0.2 day$^{-1}$.

## DISCUSSION

### Comparisons between observations and simulations

For each of the two spawning events occurring in 1987 and simulated in the present work, our results show a

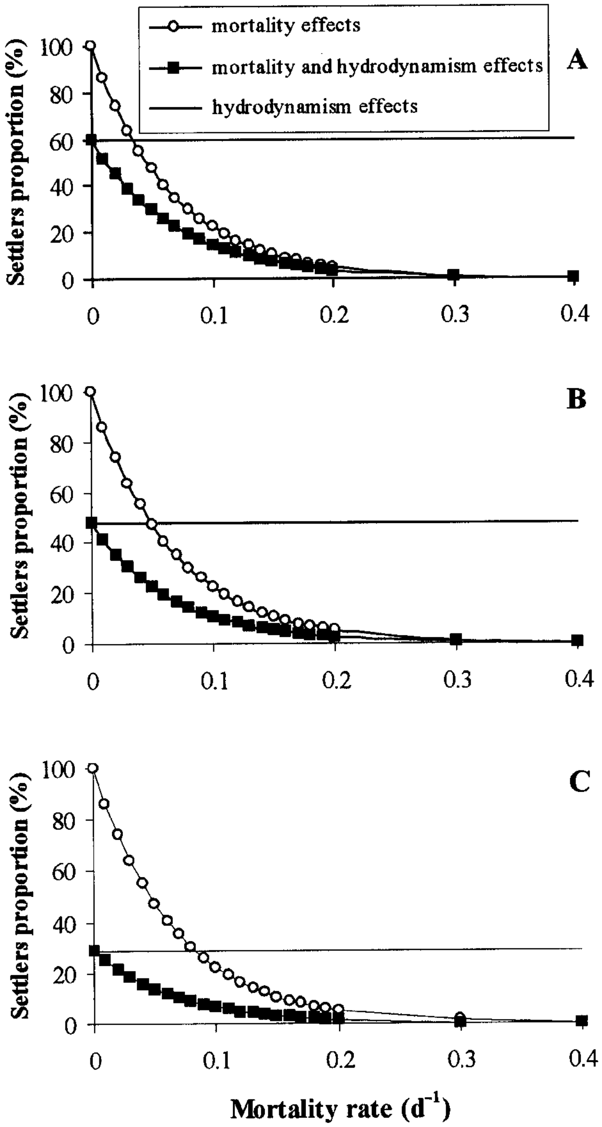

**Fig. 8.** Relative influence of larval mortality and hydrodynamics on the proportion of released larvae settling on the suitable substrates of the eastern Bay of Seine 15 days after larval release. Larval dispersal was simulated for (**A**) a constant average tide, (**B**) a constant average tide and a SW wind of 8 m s$^{-1}$ and (**C**) a constant average tide and a NE wind of 8 m s$^{-1}$.

broad agreement between simulations and field observations. In particular, simulations describe well the main larval dispersal axis observed *in situ* for each spawning event. However, some discrepancies are reported between observed and simulated data: (i) field observations show a higher degree of patchiness than simulated results; (ii) the model sometimes overestimates the extent of the larval cohort; and (iii) for the first spawning event, the transport of larvae from the coasts of Pays de Caux to the southern part of the Bay of Seine is not observed in the simulations. These differences could be attributed either to the accuracy of field observations and/or to the limits of the model.

The difficulties in tracing realistic patterns of larval dispersal by traditional sampling techniques via nets or pumps have been detailed by Gaines and Bertness (Gaines and Bertness, 1993). Overall, point samples provide a poorer estimate of the average larval abundance at any given site than the model. Firstly, sampling accuracy at low larval densities is diminished dramatically. Secondly, field samples used for the small-scale study were collected at a constant 3 m depth, whereas the model provides depth-integrated larval densities. Although we focused on field data corresponding to a 1-week-old larval cohort, larval densities could have been partly underestimated in the field as older larvae tend to remain deeper in the water column as a result of ontogenic migration (Lagadeuc, 1992a).

The lack of any significant correspondence between observed and simulated data may also be linked to the inherent limitations of a 2D hydrodynamic model. Those differences may have arisen from the inability of the model to represent baroclinic processes (i.e. the two-layer estuarine circulation and the frontal structure of the estuary plume). Lagadeuc argued that the ontogenic vertical migration of *P. koreni* larvae modified its larval dispersal pattern and favoured retention off the Seine estuary when calm weather prevailed (Lagadeuc, 1992a). Younger larvae, mainly located in the diluted surface layer, are carried downstream, whereas older larvae, found in the deeper saline layer, are advected shorewards towards the adult population. Similarly, Thiébaut showed that the frontal structure of the plume estuary may act as a physical boundary, thereby limiting the offshore export of larvae (Thiébaut, 1996). However, both of these limits have to be balanced. During the spawning period of *P. koreni* (i.e. May–June), the Seine freshwater discharge is characterized by low flow rates (i.e. often <200 m$^3$ s$^{-1}$) so that baroclinic processes in this period are minimal. Moreover, for moderate winds (i.e. $\geq$7 m s$^{-1}$), the baroclinic effects on larval dispersal are sharply reduced. During wind events, larvae are evenly distributed vertically over the water column and can be considered as passive particles (Lagadeuc, 1992a). The frontal structure of the plume is disrupted, favouring the dilution of the plume waters and larvae (Thiébaut, 1996). Therefore, low freshwater discharge and wind events could both limit the influence of baroclinic processes on larval lifespan during dispersal over the reproductive period of *P. koreni*. In addition, in the model, the wind is averaged over 4 days, so that the instantaneous effects of wind events are smoothed. This contrasts with Lagadeuc, who has shown that transitory wind events have a strong influence on larval dispersal and could transport larvae over ~20–35 km in a few days (Lagadeuc, 1992b).

The 2D residual model tends either to over- or underestimate larval dispersal. However, the broad agreement between the simulated predictions and the observed data supports the idea that the depth-averaged model is efficient in approximating the respective roles of different hydrodynamic and biological processes involved in larval dispersal within the eastern Bay of Seine. Conversely, simulations of *P. koreni* settlement do not match the observed levels. Thus, for the two spawning events of 15 and 26 May, the predicted numbers of retained and settled larvae on 29 May and 9 June were 60 595 and 37 659 ind. $m^{-2}$, respectively, while Lambert reported average settler density of 3955 ind. $m^{-2}$ on 1 June and 18 730 ind. $m^{-2}$ on 11 June off the Seine estuary (Lambert, 1991). Different explanations may be proposed to account for the inaccuracy of the model in reproducing the magnitude and the temporal variability of the observed settlement rates: (i) an overestimation of fertilization success; (ii) an inaccurate estimation of the proportion of spawning females at each date; (iii) an inexact estimation of larval mortality rate (see later); (iv) a high post-settlement mortality during the first days or weeks of juvenile life which was reported for most benthic marine invertebrates (Gosselin and Qian, 1997).

## The relative importance of hydrodynamic processes

The dispersal patterns of a larval cloud depend on the relative importance of advection and eddy diffusion (Hill, 1990). In an area where residual currents are weak, the larval cohort may be transported in a preferential direction, but diffusion makes it possible for larvae to come back against the advective flux, thereby favouring local retention. Inversely, if residual currents are strong, the larval plume can be rapidly driven downstream of the adult population and retention is then only possible if the current's trajectory is closed (e.g. gyres).

In the eastern Bay of Seine, high retention rates can be explained by diffusive processes that are dominant in conditions of neap and average tide. In conditions of spring tide, or for moderate and strong winds, the advective processes increase and can become stronger than the diffusive ones. Thus, larval dispersal is mainly isotropic in conditions of neap or average tide and larval retention decreases only by a factor of 1.26 between both these conditions. Conversely, advective currents mainly transport larvae to the west during spring tide so that larval retention decreases by a factor of 1.86 between an average and a spring tide.

In the English Channel, wind-induced currents may be greater than tidal residual currents (Salomon and Breton, 1991). Although tidal residual currents are responsible for half of the long-term water mass transport, Prandle indicated that wind-induced currents can play an important role in the variability of the residual circulation at a time scale of <1 month (Prandle, 1978). For a time scale of 2 weeks, the duration of *P. koreni* larval life, the different simulations carried out in the present study are in good agreement with Prandle's assumption, and confirm the conclusions of Lagadeuc (Lagadeuc, 1992b) about the prevailing role of wind-induced circulation in the variability of larval dispersal. Although the wind can increase larval export offshore, it may however favour the colonization of other suitable substrates far from the release site.

For SW winds, the retention rate remains roughly unchanged for low and moderate winds, and decreases sharply when the wind speed exceeds 9 m $s^{-1}$. Colonization of the Picarde estuaries sites occurs when the SW wind speed reaches 12 m $s^{-1}$ during 15 days. For NE winds, retention rates increase slightly for wind speeds ranging between 0 and 5 m $s^{-1}$ because of the concentration of larvae on suitable substrates in the southern part of the bay. Beyond this threshold value, the retention rate decreases sharply, while the colonization of suitable substrates of the Bay of Veys is reported when the wind speed is $\geq$9 m $s^{-1}$. Regardless of wind direction and speed, local retention rates in the eastern Bay of Seine generally outweigh larval export and the effective colonization of distant habitats.

An analysis of long-term wind data (from 1962 to 1996) during the reproductive period of *P. koreni* provides an interesting view of the potential impact of wind-induced currents on the colonization of distant habitats. While wind speed may occasionally exceed 15 m $s^{-1}$, averaged speeds are equal to 6.0 and 4.9 m $s^{-1}$ for SW and N-NE winds, respectively, and the duration of winds gusting over 10 m $s^{-1}$ rarely exceeds two consecutive days. Moreover, frequent changes in wind speed and direction over time tend to smooth out its effect on larval dispersal. Consequently, the colonization of distant favourable substrates, which requires constant strong winds during 15 consecutive days, should be considered as an extremely rare event. Allochthonous larval import of *P. koreni* therefore probably play a minor role in the dynamics of local populations because of their short larval lifespan (Ellien *et al.*, 2000).

The investigation of the influence of spawning time in relation to hydrodynamic conditions confirms that wind is the main source of larval dispersal variability, by locally altering dispersal patterns and the larval retention/larval export ratio. Periods of frequent changes in wind direction would result in good larval retention, whereas periods of uniform wind would promote larval export. Thus, the unpredictable hydrodynamic environment generated by wind on a short temporal scale implies that a gap of a few days in spawning events may alter the level of larval retention. Finally, variations in larval dispersal patterns in relation to the wind may affect the distribution of settlers. These different points are well illustrated by the simulations of the two spawning events occurring on 15 and 26 May 1987. The first spawning leads to a retention rate of 28.0%, with maximal larval abundances located off the Seine estuary and along the coasts of Pays d'Auge at the end of the larval dispersal, while the second spawning event leads to a retention rate of 17.4% with maximal larval abundances located in front of the Seine estuary and along the coasts of Pays de Caux. In another tidal area, the Wash (East England), Young *et al.* used a depth-integrated hydrodynamic model and also showed that wind forcing was the most important cause of variability in the transport of bivalve larvae and in the number of settling larvae, thereby potentially contributing significantly to interannual recruitment variation (Young *et al.*, 1998).

## The relative importance of hydrodynamics and mortality rates

Larval mortality is mainly caused by predation, unfavourable environmental conditions and diseases, all of which are usually pooled under the term 'natural mortality' (Young and Chia, 1985; Rumrill, 1990). The unfavourable environmental conditions rarely induce a direct mortality, but rather an indirect one, by prolonging the planktonic phase, so that larvae are exposed longer to the planktonic dispersion, predation or starvation. In his review on larval mortality rate, Rumrill showed that the estimations of this demographic parameter from the monitoring of larval cohorts vary widely between species, from 0.016 to 0.357 day$^{-1}$ with an average value of 0.223 day$^{-1}$ (Rumrill, 1990).

Our study highlights the significant role of mortality relative to the effects of hydrodynamics on larval losses and subsequent settlement. A low mortality rate ranging between 0.03 and 0.09 day$^{-1}$ was equivalent to losses by hydrodynamic processes induced by an average tide with or without a moderate wind. For the two larval cohorts simulated in real conditions of tide and wind, larval losses by a mortality rate of 0.06 day$^{-1}$ exceeded by at least 2-fold larval losses induced by advection–diffusion. Such a result confirms previous observations on the dominant impact of the mortality of marine larvae in structuring planktonic assemblages (Landry, 1976). However, using a theoretical 2D advection–diffusion–mortality model, Hill emphasized the minor role of larval mortality, compared to hydrodynamic processes, on larval losses over the northwestern European continental shelf (Hill, 1991). His simulations were based on a larval life of 50 days, a mortality rate between 0 and 0.1 day$^{-1}$, and a horizontal advection in the range of 0–0.1 m s$^{-1}$. This author showed that minor changes in advection intensity may have an effect on larval survival equivalent to substantial changes in larval mortality and concluded that dispersal was the most important process controlling the number of larvae surviving to the recruitment site. The importance of *P. koreni* larval mortality in the eastern Bay of Seine can be partly related to the short duration of its larval life stage and to the low intensity of residual currents. The respective role of hydrodynamics and mortality in larval losses during the planktonic phase therefore appears to be site and/or species dependent.

The present results raise the problems of the accuracy of estimations of larval mortality because of its large variability among species and its formulation in the model. Mortality may vary in time and space, and may greatly influence the simulated distributions of larvae (Steele and Henderson, 1992; Dekshenieks *et al.*, 1997). Therefore, the risk of a misrepresentation of larval mortality remains, and can introduce a bias in our understanding of the dynamics of marine invertebrate larval populations (i.e. fate of larval supply, fluxes of larvae between distant populations) (Cowen *et al.*, 2000).

# CONCLUSION

The larval phase has been described as a very important step in the life cycle of bentho-pelagic species, and has been for several years the subject of numerous studies, either in the field or using a modelling approach. In the eastern Bay of Seine, we used a numerical model to establish the larval dispersal patterns of *P. koreni* under different hydrodynamic conditions, and to quantify the losses due to the larval phase. Larval losses due to mortality may be as important as larval losses caused by hydrodynamic processes. Depending on spawning time, larvae are subjected to a variable hydrodynamic environment, which may significantly modify larval dispersal patterns. Wind-induced currents are the major source of variability in the amount of larvae settling in the eastern Bay of Seine, and in the location of the settlers. Although a 2-fold difference in the larval retention rate was reported depending on meteorological conditions, this modelling study confirmed that the population of *P. koreni* in the eastern Bay of Seine is mainly self-sustained. Regardless of hydrodynamic conditions, the predicted retention rates would always be sufficient to ensure maintenance of the adult population. This result is in good agreement with field observations, which showed that the adult stock in the eastern Bay of Seine is characterized by a low interannual variability (Thiébaut *et al.*, 1997). Larval transfer to other distant populations may occur, but requires specific wind conditions (i.e. strong and uniform wind during all the dispersal phase).

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