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Pelagic dispersal of the brittle-star *Ophiothrix fragilis* larvae in a megatidal area (English Channel, France) examined using an advection/diffusion model

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Abstract

The brittle-star *Ophiothrix fragilis* (Abildgaard) is widely distributed in the English Channel and particularly on pebble areas which are characterised by strong tidal currents. The main populations are located between 20 and 80 m depth. Although larval dispersal and settlement are apparently under an unfavourable high hydrodynamical constraint (a megatidal regime which generates high tidal currents, and a northeastward tidal residual current from the English Channel to the North Sea which advects larvae away from the adult populations), the density of adult populations showed little year-to-year variability. In order to determine the origin of ophioplutei larvae and recruitment patterns, larval dispersal from eight populations in the English Channel was simulated using a 2D hydrodynamical Lagrangian model integrating both the tidal residual, the wind-driven circulation and the eddy-diffusion. Simulations showed different transport patterns of the passive *O. fragilis* larvae under advection and eddy-diffusion control in the English Channel and highlighted a significant role of wind forcing on larval dispersal. Larval losses by mortality could exceed losses by hydrodynamic processes. For almost all populations, larval retention appeared to be sufficient to ensure local recruitment regardless of meteorological conditions or larval life span, and to explain the inter-annual stability of adult stocks. The degree of connection among populations was highly variable. While some populations were mainly self-seeding, larval supply from neighbouring populations could exceed local retention for other populations depending on wind forcing.

Keywords: English Channel; larval dispersal; recruitment; modelling; metapopulation; echinoderms; *Ophiothrix fragilis*

1. Introduction

The brittle-star *Ophiothrix fragilis* (Abildgaard) is widely distributed in the English Channel (20–80 m depth) (Cabioch, 1968; Cabioch & Glaçon, 1977; Gentil, personal communication; Holme, 1966; Holme, 1984; Retière, personal communication), particularly on pebbles in the open sea in response to strong tidal currents (Larsonneur, Bouysset, & Auffret, 1982). Because of its suspension-feeding, its biomass (>60% of the total biomass of the community, which is 270 g m^{-2}, in the Dover Strait; Migné & Davoult, 1995), its density (up to 2000 ind. m^{-2} in the Dover Strait, Davoult, 1989; up to 7000 ind. m^{-2} in the Bay of Seine, Davoult & Migné, 2001), and its functioning based on allochthonous material and advection, the population appears to be an important source of carbon dioxide (Migné & Davoult, 1998). While ophioplutei larvae with a life span of about 26 days (MacBride, 1907), are exposed to high hydrodynamics (a megatidal regime which generates high tidal currents, and a northeastward tidal residual current from the English Channel to the North Sea), and could

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be transported over long distances, the few adult populations which have been studied for several years remain quite stable over time (Holme, 1984; Davoult, personal communication).

In order to explain this stability and determine the role of biological and physical processes involved in larval dispersal and recruitment, the occurrence of larvae in the water column and their vertical and horizontal distribution were investigated in the Dover Strait (eastern English Channel). *O. fragilis* larvae were found from June to September following a cyclical reproduction with a highest gonadal index in June and July (Lefebvre & Davoult, 2000; Lefebvre, Davoult, Gentil, & Janquin, 1999). Studies on larval vertical distribution have shown that larvae were evenly distributed over the water column whatever their development stage and exhibited no diel or tidal vertical migration (Lefebvre & Davoult, 1998). Consequently, they seem to behave as passive particles. Although the general residual drift reported in the Dover Strait could transport larvae away from their release area, a peculiar mesoscale circulation of water masses above the adult population could favour local retention and could partly explain the spatial and temporal stability of the adult population (Lefebvre & Davoult, 2001). The question of an allochthonous or autochthonous origin of larvae thus has to be resolved. On the one hand, Lagadeuc and Brylinski (1987) suggested that the recruitment of the polychaete *Polydora ciliata* in the Dover Strait results from an allochthonous larval supply. On the other hand, with regard to local circulation patterns in the area (Lefebvre & Davoult, 1998, 2001), part of newly settled individuals may come from self-sustained recruitment.

With regard to the biological characteristics of *O. fragilis*, the use of a numerical model can: (1) provide larval distribution patterns for a wide range of geographical, hydrodynamical and meteorological conditions; (2) quantify the relative importance of the main hydrodynamical processes involved in larval dispersal; and (3) determine the origin of settlers (Garvine, Epifanio, Epifanio, & Wong, 1997; Tremblay et al., 1994; Young, Bigg, Grant, Walker, & Brown, 1998). For the English Channel, a Lagrangian 2D numerical model of water circulation has been developed by Salomon and Breton (1991, 1993). This model, first used to study the hydrodynamics of the English Channel, has been used to simulate water mass exchange between the English Channel and the North Sea (Salomon, Breton, & Guegueniat, 1995) and the transport of dissolved substances (Breton & Salomon, 1995; Guéguéniat, Bailly du Bois, Salomon, Masson, & Cabioch, 1995). Recently, it has been applied to larval transport of the polychaete *Pectinaria koreni* in the Bay of Seine and showed a good agreement between field observations and simulated results in terms of larval dispersal schemes (Ellien, personal communication). The use of such depth-averaged models can be particularly justified in the investigation of *O. fragilis* larval dispersal as residual currents in the English are mainly barotropic and larvae act as inert particles.

In this context, the objectives of the present study are:

1. to characterise the spatial extent in larval dispersal of different populations of *O. fragilis* in the English Channel and to highlight the effect of potential retention or dispersion structures according to tidal residual circulation and wind-induced currents;
2. to quantify larval losses by advection and eddy-diffusion towards unfavourable settlement areas;
3. to assess larval exchanges between distant populations.

2. Materials and methods

2.1. Numerical model

The numerical model has been described at length in Salomon and Breton (1991, 1993), Salomon, Gareau, and Breton (1996) and Salomon, Guéguéniat, Orbi, and Baron (1988). The limits of the hydrodynamical model of the English Channel are 48°18′N and 51°02′N latitude, and 6°28′W and 3°00′E longitude. It is a submodel inserted inside a wider 2D model of the whole North European shelf limited by 47°N and 63°N latitude, and 12°W and 12°30′E longitude. Its mesh size is one nautical mile, thus forming a grid of 367 × 184 cells. The Navier and Stokes equation vertically integrated (i.e. Saint Venant equation) is solved using an alternate direction implicit (ADI) numerical method. The hydrodynamical model computes instantaneous and residual velocities and trajectories for different tide and wind conditions through the barycentric method (Salomon et al., 1996). Thus, each tide/wind combination results in a single residual velocity field which sums all components of the current: Euler residual, Stokes residual and Lagrangian drift.

The residual velocity field enables to solve the advection/diffusion-mortality equation using a numerical conservative method (Salomon et al., 1996)

$$\frac{\partial(HC)}{\partial t}+\frac{\partial(HuC)}{\partial x}+\frac{\partial(Hv)C}{\partial y}-\frac{\partial^2\left(KH\,\frac{\partial C}{\partial x}\right)}{\partial x}-\frac{\partial^2\left(KH\,\frac{\partial C}{\partial y}\right)}{\partial y}-mC=0,$$

where C is the larval concentration at any point in space and time (ind. m^{-3}), u and v the residual velocity components in the x and y directions, respectively, H the average water depth over a tidal cycle, K the coefficient of turbulent diffusion and m is the larval mortality rate.

The coefficient of turbulent diffusion was calculated according to Elder's law (Salomon & Breton, 1993).

2.2. Simulation parameters

The location and the extent of the main *O. fragilis* populations in the English Channel were assessed through the benthic studies of Cabioch (1968), Cabioch and Glaçon (1975, 1977), Gentil and Cabioch (1997), Davoult and Migné (2001), Holme (1966), Holme (1984), Retière (personal communication) and Sanvicente-Anorve (personal communication). According to the persistence of *O. fragilis* dense beds and the main parameters useful in understanding larval dispersal and exchanges (i.e. local hydrodynamics, adult density), eight larval release areas were used (Fig. 1 and Table 1). The suitable substrate for settlement corresponded to pebble areas, whereas release areas corresponded to well known dense populations of adults (Table 1).

Biological parameters used for simulations are given in Table 2. When not available, quantitative population density data were assessed using qualitative information: for example, relation between the surface of a given photograph and the number of individuals was used to assess density of population (Cabioch, 1968). Results from population dynamic studies of *O. fragilis* in the Dover Strait (Davoult, 1989; Davoult, Gounin, & Richard, 1990a,b) were generalised to all populations:

1. the sex-ratio was not significantly different from 1 : 1;
2. ripening ovaries contained approximately 190,000 oocytes;
3. according to Davoult et al. (1990a) and Smith (1940), individuals with disc diameter greater than 3 mm for males and 5 mm for females are mature; with regard to the population structure during spawning (i.e. 90% of individuals with disc diameter >5 mm in July), it was assumed that 90% of the females were able to spawn.

Although fertilisation success is dependent on, and highly sensitive to, population parameters and environmental conditions (Levitan, Sewell, & Chia, 1992), one oocyte was considered to allow the development of one larva. Thus, the number of releasing eggs per surface unit, Ω, was

$$\Omega = 0.5N \times 0.9F,$$

where N is the density of adults (ind. m^{-2}) and F is the mean fecundity of a female.

According to Lefebvre and Davoult (1997) and MacBride (1907), planktonic larval life span was estimated to be 26 days long. Moreover, Lefebvre and Davoult (1997) showed that larval development could be heterogeneous among a larval population and that a critical stage occurred between the 6-arm and 8-arm larval stages which could modify larval life span. Disparate studies suggest that over a great range of concentrations of natural food, the limited food supply extended the planktonic period by only a few days (Fenaux, Strathmann, & Starthmann, 1994). Consequently, simulations were made using a 21, 26 and 31 day long planktonic larval life.

Larval mortality was set to $0.06\,\mathrm{d}^{-1}$ according to Rumrill's (1990) study on meroplanktonic species. It is well known that larval mortality can vary among species by several orders of magnitude. In order to assess these variations, Figs. 2–6 show the modifications of calculated parameters with or without natural mortality.

All simulations were made in condition of average tide as Ellien (personal communication) showed that simulated larval dispersal in such conditions did not differ from those obtained taking into account the lunar tidal cycle. According to the study of different meteorological signal stations in the English Channel (Meteo France data) (Table 3) during the *O. fragilis* spawning period, two prevailing wind directions were tested, NE (i.e. direction 45°) and SW (i.e. direction 225°), and wind speed was set to $6\,\mathrm{m\,s}^{-1}$ (Table 3).

$$\text{loss due to mortality} = \left(1 - \frac{\text{number of larvae surviving at the end of larval dispersal}}{\text{number of released larvae}}\right)100, \tag{1}$$

$$\text{loss due to hydrodynamics} = \left(1 - \frac{\text{number of larvae settling on a suitable substrate}}{\text{number of larvae surviving at the end of larval dispersal}}\right)100, \tag{2}$$

$$\text{retention rate} = \left(\frac{\text{number of larvae settling on the suitable substrate of the parental population}}{\text{number of larvae surviving at the end of larval dispersal}}\right)100, \tag{3}$$

$$\text{colonisation rate} = \left(\frac{\text{number of larvae settling on the suitable substrate of distant populations}}{\text{number of larvae surviving at the end of larval dispersal}}\right)100. \tag{4}$$

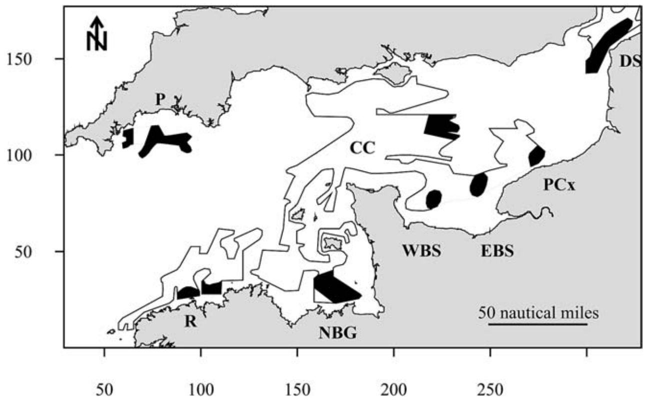

Fig. 1. Location of the spawning areas (▬) and the sedimentary favourable areas for settlement (▭) of *O. fragilis* larvae in the English Channel (P, Plymouth; R, Roscoff; NBG, Normanno-Breton Gulf; WBS, western Bay of Seine; EBS, eastern Bay of Seine; PCx, Pays de Caux; DS, Dover Strait; CC, Central Channel) (scale: arbitrary units).

For each population, different parameters were calculated at the end of larval dispersal

3. Results

Figs. 2–4 summarise changes in larval retention, in colonisation of distant populations, and in advection/diffusion loss with a mortality rate of $0.06\,\mathrm{d}^{-1}$ at 21, 26 and 31 days. Figs. 5 and 6 summarise changes in retention/colonisation and advection/diffusion loss without larval mortality.

3.1. Simulated larval dispersal for a planktonic life of 26 days, no wind

3.1.1. Plymouth spawning area

Most larvae released off Plymouth were transported northwards and then westwards by up to 60 nautical miles by weak tidal residual currents while some larvae moved to the east and the south against prevailing currents because of eddy-diffusion (Fig. 7a). Off Cornwall the increase of residual currents ensured the transport of a small fraction of larvae to the Irish Sea. At settlement, the highest larval densities (hereafter referred to $>10^3$ larvae m^{-3}) remained off Plymouth, so that 5.2% of the initial larval stock (retention + colonisation without mortality of 24.8%) settled on suitable substrates at Plymouth. None of the released larvae could reach other suitable areas in the English Channel.

3.1.2. Roscoff spawning area

The dispersal pattern of larvae released off Roscoff was relatively isotropic because of a moderate eddy-diffusion, despite a preferential transport by low tidal residual currents to the north-northeast (Fig. 7b). Larvae could be dispersed by up to 60 nautical miles from the release site. As the larval release site was located at the southern edge of the pebble substrate off Roscoff, the weak northwards and northeastwards dispersal favoured the maintenance of the highest larval densities above the favourable substrates of the adult population. The retention rate was equal to 11.9% of the initial larval stock (retention + colonisation without mortality of 56.9%). Few larvae were able to colonise the western and northern part of the Normanno-Breton Gulf or the central English Channel.

3.1.3. Normanno-Breton Gulf spawning area

Although residual current velocities are about $4\,\mathrm{cm\,s}^{-1}$ above the larval release site and can even reach more than $17\,\mathrm{cm\,s}^{-1}$ locally, larvae were slowly transported to the north up to 90 nautical miles and to the west up to 65 nautical miles (Fig. 8a). After 26 days, most of the larvae were still within the Gulf as a result of the occurrence of several clockwise and anticlockwise gyres, which could trap particles. At settlement, 6.8% of the released larvae (retention + colonisation without mortality of 35.7%) settled on suitable substrates of the gulf while 0.7% were advected to the north and colonised the substrates of the central English Channel.

Table 1
Main characteristics of the eight larval release areas selected for larval dispersal simulations

Areas	Size of suitable substrate (km^2)	Size of larval release area (km^2)	Depth (m)	MTCS (Knots)	u ($\mathrm{cm\,s}^{-1}$)	K ($\mathrm{m}^2\,\mathrm{s}^{-1}$)
Dover Strait	1410	461	30–40	3	3.5	20
Pays de Caux	1253	110	20–30	1–2	1.5	10–15
Eastern Bay of Seine	634	110	30–40	2	2	10
Western Bay of Seine	1256	113	30–40	2	3	50
Normanno-Breton Gulf	2784	709	30–40	3–4	4	15
Roscoff	2650	220	80	2	2	20
Plymouth	822	809	70	1–2	1	10–15
Central Channel	10,189	678	50	2	2	35–40

Maximum tidal current speed during mean spring tides (MTCS, in knots), mean tidal residual currents velocity (u) and coefficient eddy-diffusion (K) are given according to Salomon and Breton (1993).

Table 2
Biological parameters used for the simulation of *O. fragilis* larval dispersal in the English Channel

Areas	Density (ind. m^{-2})	Theoretical spawning females (ind. m^{-2})	Initial larval release (ind. m^{-2})
Dover Strait	1500	675	128.25×10^6
Pays de Caux	1000	450	85.5×10^6
Eastern Bay of Seine	4000	1800	342×10^6
Western Bay of Seine	1000	450	85.5×10^6
Normanno-Breton Gulf	500	225	42.75×10^6
Roscoff	500	225	42.75×10^6
Plymouth	500	225	42.75×10^6
Central Channel	500	225	42.75×10^6

3.1.4. Western Bay of Seine spawning area

Larvae released in the western Bay of Seine showed at first a significant westward transport and were then trapped within a clockwise gyre located off the Cotentin peninsula (Fig. 7a). Because of intense eddy-diffusion, the larval cohort was largely dispersed and reached the southern coasts of England, off the Isle of Wight. In the central English Channel, some larvae were advected to the northeast by the general drift of Channel waters. At settlement, although 5.6% of the initial larval stock (retention + colonisation without mortality of 79.1%) were retained on suitable substrates of the parental population, about 11% of released larvae colonised pebbles within the central English Channel.

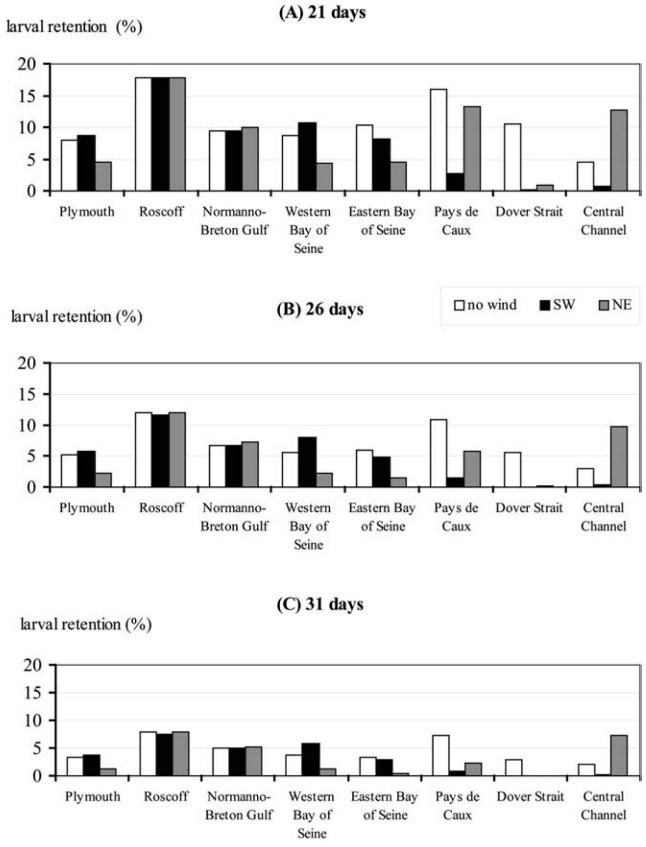

Fig. 2. Changes in larval retention according to larval life span of *O. fragilis* larvae on sedimentary favourable areas for settlement and according to wind conditions. A mortality rate of 0.06 d^{-1} generates a loss of 71.6, 79 and 84.4% of the initial stock over 21, 26 and 31 days, respectively.

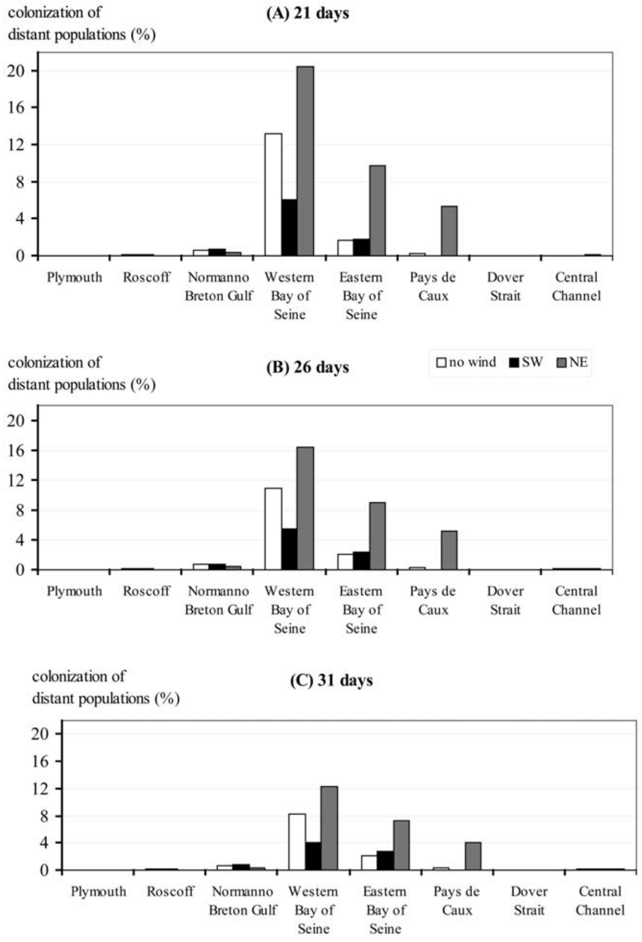

Fig. 3. Changes in colonisation of distant populations (%) according to larval life span of *O. fragilis* larvae on sedimentary favourable areas for settlement and according to wind conditions. A mortality rate of 0.06 d^{-1} generates a loss of 71.6, 79 and 84.4% of the initial stock over 21, 26 and 31 days, respectively.

3.1.5. Dover Strait spawning area

Most larvae released in the Dover Strait were advected by moderate tidal residual currents toward the Southern Bight of the North Sea beyond the model limits (Fig. 7a). Some larvae were transported to the south along the Picarde Bay coast against prevailing currents by eddy-diffusion. At settlement, retention on local suitable substrate was 5.6% of released larvae (retention + colonisation without mortality of 26.7%). No colonisation of distant populations occurred.

3.1.6. Central English Channel spawning area

The larval population released in the central English Channel was spread over the whole width of the English Channel, from the Bay of Seine in the south to the Hampshire and Sussex coasts in the north by intense

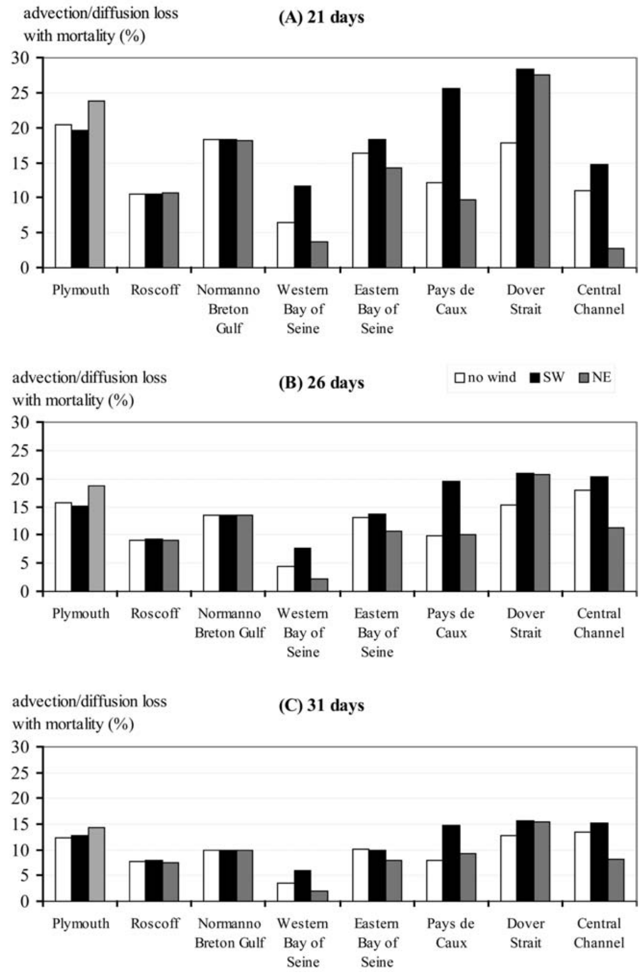

Fig. 4. Changes in advection/diffusion loss (%) for a mortality rate of $0.06\,d^{-1}$ according to larval life span of *O. fragilis* larvae on sedimentary favourable areas for settlement and according to wind conditions. A mortality rate of $0.06\,d^{-1}$ generates a loss of 71.6, 79 and 84.4% of the initial stock over 21, 26 and 31 days, respectively.

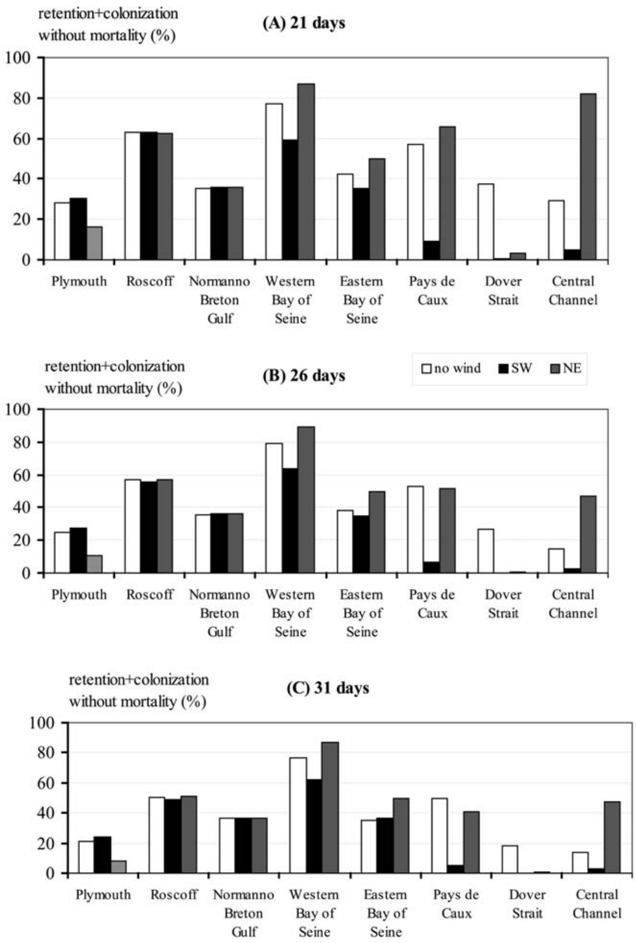

Fig. 5. Changes in retention + colonisation (%) without larval mortality according to larval life span of *O. fragilis* larvae on sedimentary favourable areas for settlement and according to wind conditions.

eddy-diffusion (Fig. 7b). Larvae were advected by weak residual currents to the north-northeast in offshore waters, while they were advected westwards along the English coasts toward the east of the Isle of Wight in inshore waters. Because of the large dispersal and the location of the larval releasing site (i.e. at the north-eastern edge of the favourable substrates area), highest larval densities were mainly reported outside the suitable substrates of the adult population. At settlement, local retention reached only 3% of the larval initial stock (retention + colonisation without mortality of 14.3%). About 0.1% of released larvae colonised suitable substrates in the Bay of Seine and along the Pays de Caux coasts.

3.1.7. Pays de Caux spawning area

Larvae released off the Pays de Caux coasts followed pathways induced by weak residual currents that lead either southwestward into the eastern Bay of Seine or northeastward along the coasts of the Picarde Bay (Fig. 8a). The larval cohort spread up to 50 nautical miles on both sides of the spawning area. Low eddy-diffusion enhanced dispersal in offshore waters up to 40 nautical miles. Because of the limited dispersal, partly south-westwards, and the location of the releasing site at the northeastern edge of the suitable substrates area, retention rate was equal to 10.8% of the larval initial stock (retention + colonisation without mortality of 52.9%) at settlement. Only 0.3% of released larvae colonised the neighbouring population located in the eastern Bay of Seine.

3.1.8. Eastern Bay of Seine spawning area

Larvae released from the eastern Bay of Seine were advected to the west up to 70 nautical miles and to the northeast up to 50 nautical miles by weak residual currents (Fig. 8b). At settlement, 5.9% of released larvae (retention + colonisation without mortality of 38.1%) remained on the suitable substrates of the parental population (Table 4), while 2.1% colonised distant populations, mainly of the western Bay of Seine.

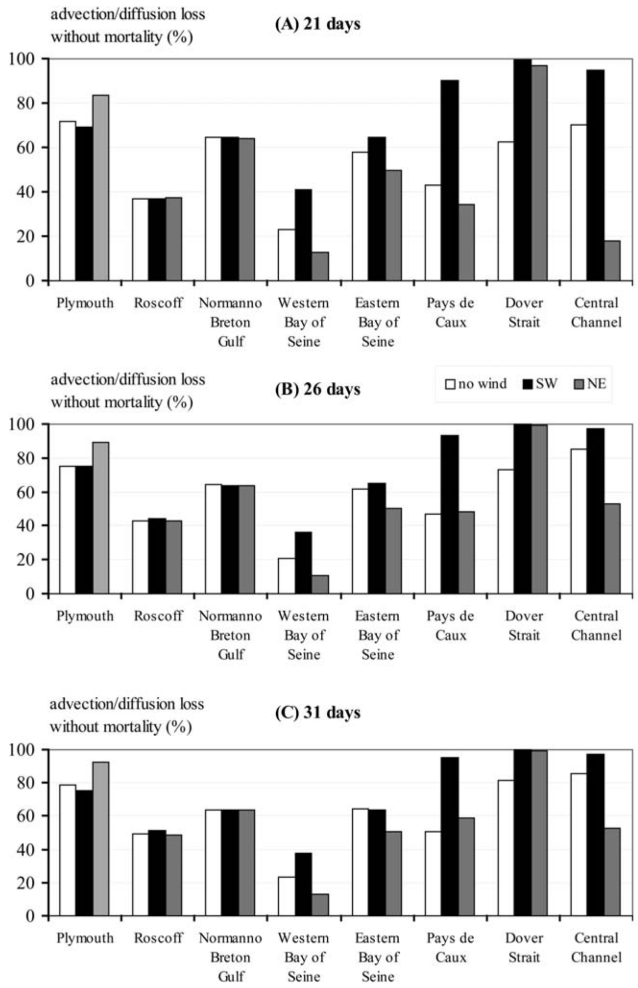

Fig. 6. Changes in advection/diffusion loss (%) without larval mortality according to larval life span of *O. fragilis* larvae on sedimentary favourable areas for settlement and according to wind conditions.

3.2. Simulated larval dispersal for a planktonic life of 26 days, SW or NE wind

Larval dispersal patterns as well as larval retention rates were significantly modified by wind forcing which either strengthens tidal advection or counteracts its effects for all the studied sites (Figs. 2–6 and 9) except off Roscoff (Fig. 9) and in the Normanno-Breton Gulf. In these two latter areas, moderate winds had a low influence on the tidal residual circulation.

In some sites (i.e. off Plymouth, the western Bay of Seine, the central English Channel), a wind of only one direction influenced the retention abilities of ophioplutei on suitable substrates for settlement. As an example, off Plymouth, a SW wind reduced the westwards and northwards tidal residual currents so that the retention rate increased slightly from 5.2% without wind to 5.8% with a SW wind. On the contrary, a NE wind amplified the effects of tidal residual currents, velocity of which increased from $<1\,\mathrm{cm\,s^{-1}}$ for an average tide to around $6\,\mathrm{cm\,s^{-1}}$: the advection of larvae to the west was enhanced and the retention rate decreased from 5.2% without wind to 2.3% for a NE wind (Figs. 2–6). In the central English Channel, where tidal residual currents are oriented northeastwards offshore, and westwards in English coastal waters, a NE wind induced a shift of residual currents to the west in offshore waters and an amplification of westwards advection in the coastal zone. Thus, the retention rate was multiplied by a factor 3 from 3% without wind to 9.7% with a NE wind (Figs. 2–6). Conversely, a SW wind amplified offshore tidal residual currents to the northeast while westwards coastal residual currents were lowered. In these conditions, larval dispersal was enhanced and the retention rate decreased by about one order of magnitude from 3% without wind to 0.5% for a SW wind (Figs. 2–6).

For all the other sites (i.e. eastern Bay of Seine, Pays de Caux, Dover Strait), wind forcing induced a decrease of retention rates; although the level of decrease was dependent on wind direction. Larval dispersal in the Dover Strait and off the Pays de Caux was particularly representative of such a wind effect. In the Dover Strait, a SW wind of $6\,\mathrm{m\,s^{-1}}$ increased residual velocities from about 4 to $>17\,\mathrm{cm\,s^{-1}}$, so that the larval cohort was largely exported to the North Sea (Figs. 3–7); the retention rate strongly decreased by two orders of magnitude from 5.6 to less than 0.1%. On the contrary, a NE wind of $6\,\mathrm{m\,s^{-1}}$ counteracted tidal residual currents and induced a southwestwards flow characterised by a east–west decreasing velocity gradient, from $17\,\mathrm{cm\,s^{-1}}$ in the Dover Strait to $3\,\mathrm{cm\,s^{-1}}$ in the central English Channel. The larval cohort was thus advected southwestwards so that the retention rate decreased to 0.2% (Figs. 2–6). Off the Pays de Caux, a NE wind of $6\,\mathrm{m\,s^{-1}}$ induced a massive larval transport to the west so that larval retention decreased to 1.4% compared to 10.8% without wind. For a SW wind of $6\,\mathrm{m\,s^{-1}}$, the retention rate was less pronounced and was 5.8% (Figs. 2–6 and 9).

Despite the diverse effects of wind forcing on larval dispersal, larval losses by advection/diffusion were in general either unchanged (e.g. off Plymouth) or enhanced (e.g. Dover Strait) (Figs. 2–6). They were reduced only in a few cases (e.g. western Bay of Seine with a SW wind, central English Channel with a NE wind). In most cases, wind forcing tended to enhance larval exchanges among distant populations.

3.3. Simulated larval dispersal for different larval life span

Larval dispersion patterns observed with a 26-day larval life were not greatly affected by changes in larval life span (26 days ± 20%) (Figs. 2–6). Reduction of the larval life span increased larval retention by 24–78% (mean: 39.9%) depending on the release site and the

Table 3
Mean frequency (%) and velocity ($m\,s^{-1}$) of prevailing winds in the Dover Strait (i.e. Dunkerque signal station, Dun.), in the central English Channel (i.e. La Hague signal station, Hag.) and in the North Brittany (i.e. Batz Island signal station, Batz) during *O. fragilis* spawning period from 1951 to 1980 (MeteoFrance data)

	NE wind						SW wind					
	Frequency			Velocity			Frequency			Velocity		
	Dun.	Hag.	Batz	Dun.	Hag.	Batz	Dun.	Hag.	Batz	Dun.	Hag.	Batz
June	32.2	26.2	29.8	6.0	5.4	5.8	37.6	42.3	26.3	6.5	6.4	5.8
July	25.6	21.9	25.9	5.6	5.1	5.0	41.6	46.1	28.4	6.7	6.7	5.4
August	25.6	22.1	23.1	5.5	5.4	5.1	40.2	41.1	31.8	6.6	7.4	5.8
September	22.4	24.7	24.8	5.6	7.1	6.3	40.3	37.1	32.5	6.6	8.4	5.6

NE wind: direction from 0° to 90° SW wind: direction from 180° to 270°.

meteorological conditions, and consequently self-sustained recruitment possibilities. Such a reduction resulted on both a decrease of losses by advection and diffusion processes, and a decrease of losses by natural mortality (Figs. 2–6). On the contrary, an increase of larval life span limited larval retention by 25–71% (mean: 38.5%) but enhanced, on the one hand, larval losses by natural mortality, predation or advection/diffusion processes and, on the other hand, colonisation possibilities of distant populations (Figs. 2–6). Regardless of larval life span and wind forcing, larval losses by natural mortality for a mortality rate of $0.06\,d^{-1}$ generally exceeded larval losses by hydrodynamical processes.

4. Discussion

The acquisition of knowledge on larval life of *O. fragilis* by in situ studies in the Dover Strait has made a significant contribution to explain the processes in-

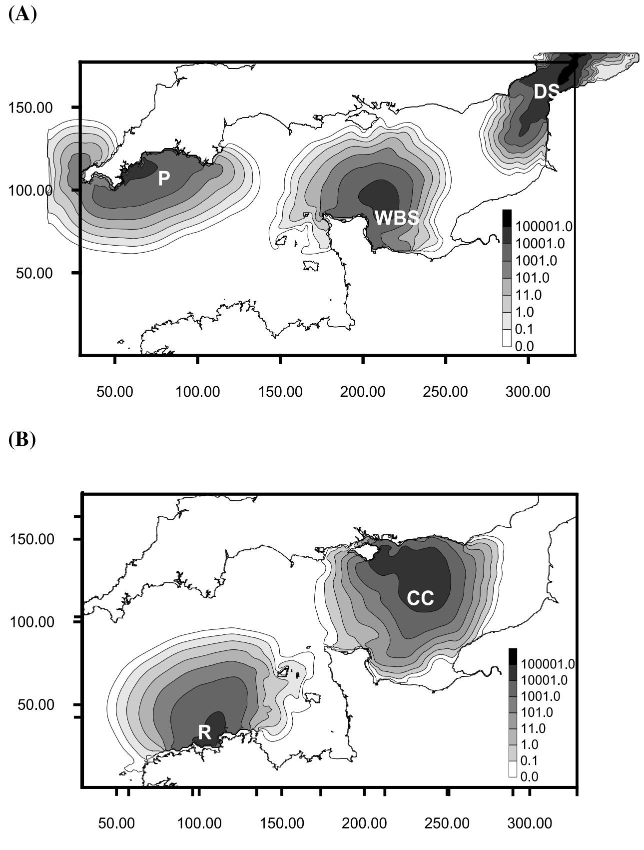

Fig. 7. Simulated dispersion of an *O. fragilis* ophioplutei cohort with a 26-day pelagic life and without wind, released from (A) the Plymouth (p), western Bay of Seine (WBS) and Dover Strait (DS) areas, (B) the Roscoff (R) and central Channel (CC) areas. Larval mortality was set to $0.06\,j^{-1}$ (X/Y scales: arbitrary units—contours: log ind. m^{-3}).

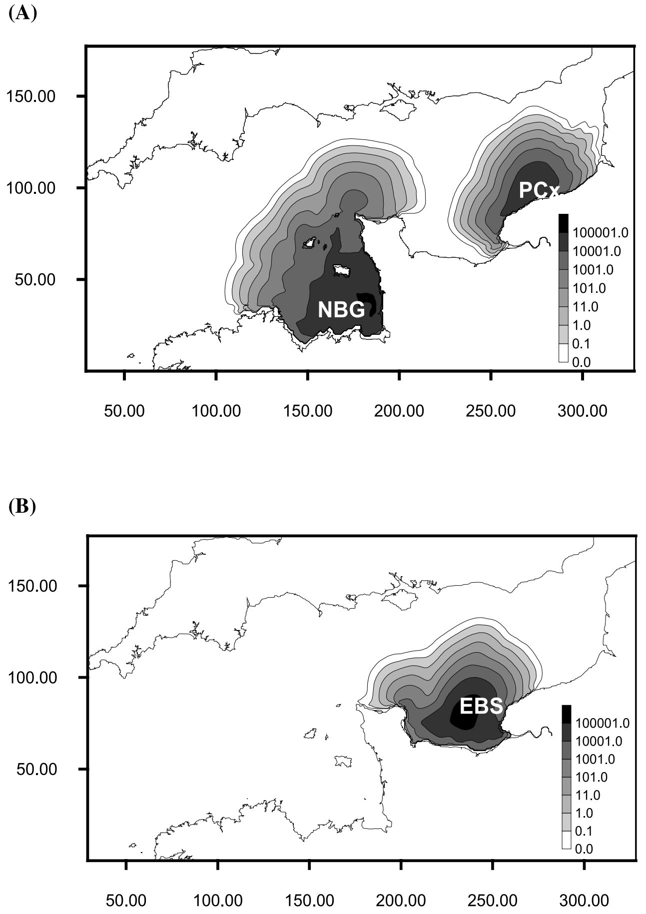

Fig. 8. Simulated dispersion of an *O. fragilis* ophioplutei cohort with a 26-day planktonic life and without wind, released from (A) the Normanno-Breton Gulf (NBG) and Pays de Caux (PC) areas, (B) the eastern Bay of Seine (EBS) area. Larval mortality was set to $0.06\,j^{-1}$ (X/Y scales: arbitrary units—contours: log ind. m^{-3}).

Table 4
Relative importance of allochthonous larval supply (%) according to the spawning areas and meteorological conditions for a larval life span of 26 days

Spawning areas	Tide	NE wind of 6 m s^{-1}	SW wind of 6 m s^{-1}
Plymouth	0	0	0
Roscoff	0.064	0.20	0.058
Normanno-Breton Gulf	0.28	0.087	0.36
Western Bay of Seine	58.99	93.78	4.62
Eastern Bay of Seine	1.23	46.96	0.15
Pays de Caux	0.86	0.013	87.13
Dover Strait	0	0	0.61
Central English Channel	59.38	39.07	85.23

volved in the recruitment and settlement patterns in a system strongly influenced by local and regional hydrodynamism (Lefebvre & Davoult, 1998, 2000, 2001). The temporal variability and origin of larval supply however remained unclear at the temporal scale of the larval life span and at the spatial scale of the English Channel because of the difficulties of larval tracking. Simulations of larval transport using a 2D hydrodynamical Lagrangian model, could then be a particularly suitable tool for larvae evenly distributed within the water column as ophioplutei, and in a zone, such as the English Channel, where currents are mainly barotropic (Ellien et al., 2000; Salomon, 1990).

Simulations showed the mode of *O. fragilis* larval dispersal under advection by tide and wind-induced current, and eddy-diffusion processes in the whole English Channel, and highlighted the significant role of wind forcing on the distribution pattern of larvae. Without wind and for a 26-day larval life span, the release sites off Roscoff and the Pays de Caux were characterised by the highest retention of larvae on the suitable substrates for settlement (11.9 and 10.8%, respectively). In decreasing order, the Dover Strait, eastern Bay of Seine, Normanno-Breton Gulf, western Bay of Seine and Plymouth sites had an intermediate larval retention rate (i.e. >5%), whereas the central English Channel site exhibited a retention rate below 5%. Wind forcing induced a more or less favourable retention of ophioplutei larvae near their releasing sites, or a more or less efficient transport towards distant suitable areas. It appeared that wind was of little influence on the retention pattern in the Normanno-Breton Gulf and off Roscoff according to the characteristics of local hydrodynamics. The Normanno-Breton Gulf was characterised by the occurrence of permanent gyres whatever the meteorological conditions were, whereas the northward residual drift off Roscoff was slightly modified by moderate wind (Salomon & Breton, 1993). For other sites, wind forcing significantly altered larval retention in relation to its direction. Northeast

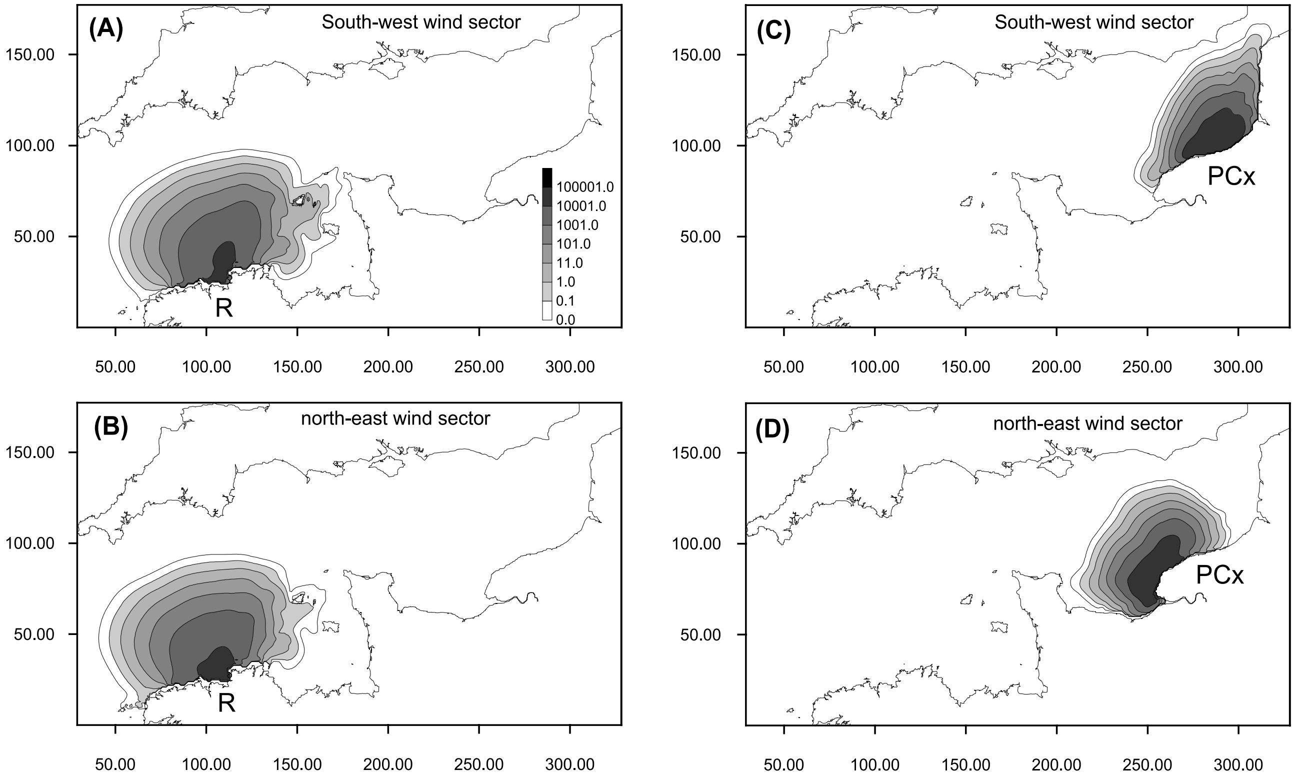

Fig. 9. Simulated dispersion of an *O. fragilis* ophioplutei cohort with a 26-day planktonic life released from the Roscoff (A,B) and the Pays de Caux (C,D) areas with a southwest (A,C) or northeast wind sector (B,D) (location of letters indicates releasing gametes point source). Larval mortality was set to 0.06 j^{-1} (X/Y scales: arbitrary units—contours: log ind. m^{-3}).

wind was particularly influent on local retention off Plymouth and in the Bay of Seine, while southwest wind decreased retention rates off the Pays de Caux and in the central English Channel. The Dover Strait was particularly sensitive to both wind directions considered in the present study.

Parallel to the influence of hydrodynamics, retention rates were affected by biological parameters including the relative location of *O. fragilis* beds within pebble area and the larval life span. For example, in the central English Channel where the larval release site was located on the edge of suitable substrates, southwest wind-induced currents advected larvae away from settlement favourable zone so that retention rate fell to 0.5%. Modifications of larval life span of a few days induced significant changes in larval retention, the magnitude of which varied among sites and meteorological conditions. The potential effects of wind-induced currents on larval dispersal could also be related to the duration of larval life because of its frequent changes in direction. For species with a short larval life span (<2 weeks), such as the polychaete *P. koreni*, Lagadeuc (1992) and Thiébaut, Lagadeuc, Olivier, and Retière (1998) argued that episodic wind events can disrupt larval retention and export larvae away from the parental population over a few days. By contrast, for species with a longer larval life duration such as *O. fragilis*, frequent changes in wind direction and intensity tend to diminish wind events effects (Salomon, 1990; Thiébaut, Dauvin, & Lagadeuc, 1994) so that larval dispersal could be a function of mean meteorological conditions. Although larval mortality can greatly vary among species, geographical areas and years for a same species (for review see Rumrill, 1990), this demographic parameter could be a major cause of losses during larval dispersal and a key parameter to determine the magnitude of the recruitment (Cowen, Lwiza, Sponaugle, Paris, & Olson, 2000). Loss by natural mortality could be higher than advection/diffusion loss with a mortality rate of greater than $0.06\,\mathrm{d}^{-1}$. With a very low mortality rate, advection/diffusion loss will be of prime importance. For a population of the annelid *P. koreni* in the Bay of Seine, Ellien et al. (personal communication) showed that loss by natural mortality became superior to advection/diffusion loss with a mortality rate of 0.03–$0.04\,\mathrm{d}^{-1}$ (simulations during 15 days, without wind).

Simulations performed with a larval life duration of 26 ± 5 days showed that all studied populations of *O. fragilis* exhibited significant larval retention rates on suitable substrates, which could optimise the recruitment and partly explain the spatio-temporal stability of adult populations. Campion (personal communication) assessed from a study in the Dover Strait, that, on an average, one juvenile was associated (i.e. living on the disc or in the genital bursa) with at least one adult during the main recruitment process, so that the established population stability seemed to require a renewal rate of one juvenile for one adult living in the population. Considering the density of larvae able to settle on adult favourable areas, all populations could present a sufficient number of larvae to be self-sustained, whatever the meteorological conditions were, despite large variations of the density of settlers. Thus, for a 26 day larval life span, the number of larvae which settled on suitable substrates ranged from 1.2×10^4 to $3.5 \times 10^6\,\mathrm{ind.\,m}^{-2}$ for the different wind forcing and populations. In the Dover Strait, where adult population density reached about $1000\,\mathrm{ind.\,m}^{-2}$ during the main recruitment period in September (Davoult, 1989), 1000 settlers per square metre surviving to the juvenile stage would be sufficient to ensure the population persistence. According to simulations, the number of larvae settling on this area characterised by the lowest retention rate ranged between 3059 and $4.7 \times 10^6\,\mathrm{ind.\,m}^{-2}$ whatever the wind forcing or the larval life span could be. According to the above hypothesis, the stability of the Dover Strait population could be nearly exclusively explained by self-sustainment and allochthonous larval supply could be of second interest, in opposition to the hypotheses of Davoult et al. (1990a) and Gounin (personal communciation). The importance of local recruitment to the stability of the adult population has already been reported for other echinoderms such as the Asteroid *Pisaster ochraceus* (Sewell & Watson, 1993) and the Echinoid *Evechinus chloroticus* (Lamare, 1998). Moreover, as no recruitment was observed outside the areas occupied by *O. fragilis* adults (Davoult et al., 1990b), Lefebvre (personal communication) suggested that adult–larval interactions (e.g. morphological adaptation of larvae, attraction processes) could be involved at settlement and could limit larval losses as suggested by Hendler (1991, Chap. 6), Thorson (1966) and Warner (1971) for other echinoderms. On the contrary, larval choice at settlement at this small scale could reduce retention and colonisation rates and enhance advection/diffusion loss (advection towards a potential suitable substrate on a sedimentary and hydrodynamical point of view but without the triggering settlement factor).

Simulations also revealed possibilities of larval exchanges between distant populations which could generate a multiple origin of settlers for several areas and increase the density of settlers (Fig. 10). Considering the eight larval release areas, only the Plymouth population was isolated from the rest of the English Channel and received no settlers from distant populations, whatever the larval life duration and the wind conditions were. Although larval exchanges between populations were generally low (i.e. $<1\,\mathrm{ind.\,m}^{-2}$), they were more important among four neighbouring populations: in the central English Channel, the western and eastern Bay of Seine, and off the Pays de Caux. For

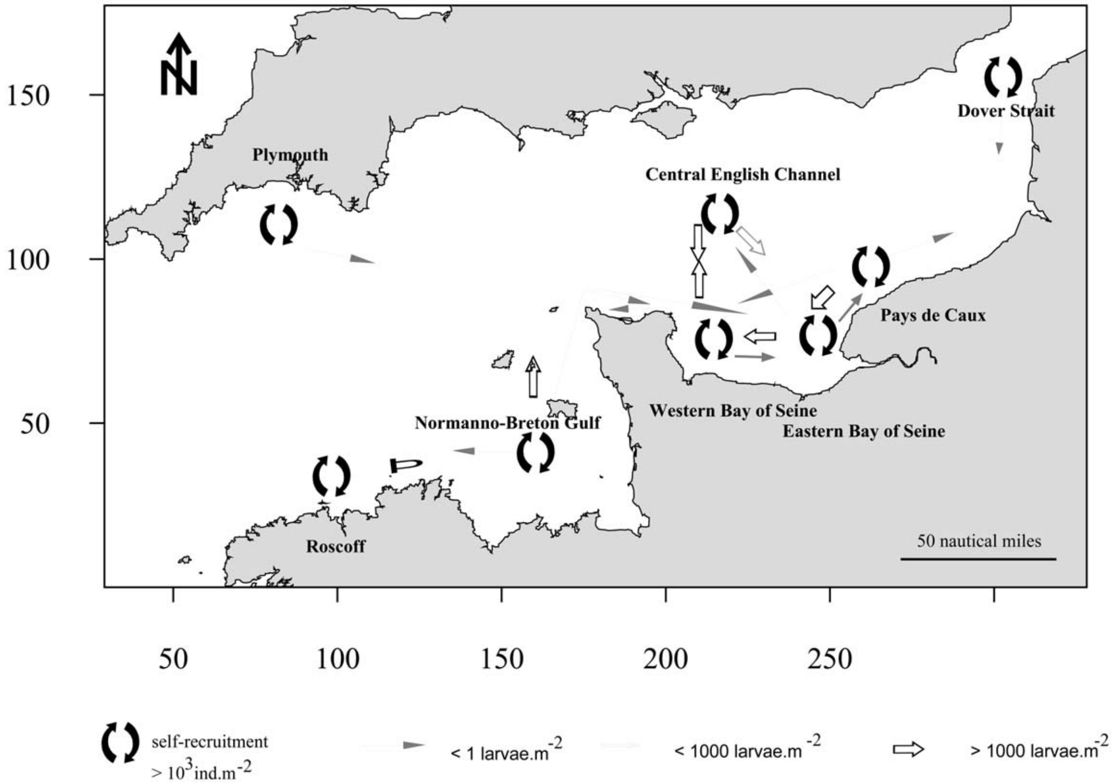

Fig. 10. Main recruitment patterns and connections among *O. fragilis* populations at the English Channel scale (larvae with 26-day-long pelagic life—simulations without wind) (scale: arbitrary units).

these four populations, larval supply from distant populations could be as important as or more important than larval supply from local population depending on meteorological conditions. While local retention ensured a significant recruitment each year regardless of wind forcing, the variability of larval supply from distant populations in relation to meteorological conditions could be an important source of year-to-year variation in recruitment level. These populations could be defined as open populations so that the recruitment is uncoupled from local offspring production (Caley et al., 1996). By contrast, the other populations (i.e. Roscoff, Normanno-Breton Gulf and Dover Strait) were mainly self-sustained. Nevertheless, in the long-term, larval exchanges could favour genetic flow and induce a genetic homogenisation between populations as has been commonly reported for Echinoderms (Benzie, 1992; Hunt, 1993; Williams & Benzie, 1996). However, one must take care to consider the potential role of small populations previously unnoticed that may be present between the eight major populations used in this work. These small populations would enhance larval exchange between main populations at the English Channel scale. However, since such small populations were not wide spread and because of their low density, no significant modification would occur on retention and colonisation rates.

To conclude, populations of *O. fragilis* in the English Channel seemed to act partly as a metapopulation with a flux of migrants varying among populations and in relation to wind forcing (Botsford et al., 1994; Hanski & Simberloff, 1997; Levins, 1970). Two types of populations were identified: (1) populations which were mainly self-seeding although larval retention rate exhibited large variations according to wind forcing; and (2) populations for which larval supply from distant populations could greatly exceed larval retention for some wind forcing. In this context, genetic studies will be needed to validate the hypotheses about the importance of hydrodynamics on larval dispersal and the degree of connection between populations.

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