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ORIGINAL PAPER

Does larval supply explain the low proliferation of the invasive gastropod *Crepidula fornicata* in a tidal estuary?

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Abstract Human-mediated transport and aquaculture have promoted the establishment of non-indigenous species in many estuaries around the world over the last century. This phenomenon has been demonstrated as a major cause of biodiversity alterations, which has prompted scientists to provide explanations for the success or failure of biological invasions. *Crepidula fornicata* is a gastropod native from the East coast of North America which has successfully invaded many European bays and estuaries since the 19th century, with some noticeable exceptions. Its spread over Europe has been explained by a combination of human-mediated transport and natural dispersal through its long-lived planktonic larva. We here investigated whether larval supply may explain the failure in the proliferation of this species within a particular bay, the Bay of Morlaix (France). Patterns of larval distribution and larval size structure were analysed over ten sites sampled three times (20 July, 4 August and 21 August 2006), regarding characteristics of the adult population and environmental features. Our results evidenced a strong spatial structure in both larval abundance and size at the bay scale, even if larval abundances were low. In this scheme, the location of spawning adults played a critical role, with high numbers of early larvae above the main spawning location. The larval size structure further showed that settlement-stage larvae were rare, which suggested that released larvae might have been exported out of the bay. The use of an analytical model aimed to study the effect of tidal currents on the potential for larval exportation confirmed that larval retention within the bay might be low. The limitation in larval supply resulting from the interactions between spawning location and local hydrodynamics may thus impede the proliferation of this species which is well established for more than 50 years. This study provided an example of factors which may explain the failure of the transition between two major steps of biological invasions, i.e. sustainable establishment and proliferation.

Keywords *Crepidula fornicata* · Spatial distribution · Propagule supply · Larval dispersal · Bentho–pelagic cycle

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Introduction

In marine ecosystems, invasions by non-indigenous species (NIS) are a major component of biodiversity

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changes (e.g. Carlton and Geller 1993; Leppäkoski and Olenin 2000; Reise et al. 2006). Among marine ecosystems, bays and estuaries are particularly prone to invasions (Cohen and Carlton 1998; Nehring 2006) mostly due to human-mediated activities which largely contribute to the worldwide transportation and subsequent introduction of aquatic organisms (e.g. Carlton and Geller 1993; Naylor et al. 2001; Voisin et al. 2005). The success of biological introductions not only depends on the introduced species but also on the environmental conditions prevailing in the invaded bays and estuaries (Nehring 2006). Therefore, in the context of biological conservation and NIS management, it is crucial to analyse not only the factors which explain the success of introductions and invasions, but also the factors responsible for their potential failure.

In benthic marine invertebrates with a pelagic developmental stage, larvae are known to play a major role at all steps of the invasion process. Larvae may first be the primary introduction stage of a NIS, being transported within ballast waters for long periods (Carlton and Geller 1993). Due to their microscopic size, they may be transported in huge numbers and then may ensure propagule pressure (Simberloff 2009). Once a species has been introduced, its larvae may facilitate its long-term establishment by promoting the demographic reinforcement of its local benthic populations through recruitment (Dunstan and Bax 2007). Finally, larvae may in part allow the regional spread of the NIS through natural dispersal, and once several populations have been established larvae may ensure connectivity (Dupont et al. 2003, 2007; Kinlan et al. 2005). As such larval supply may thus play a major role in the failure or success of invasions.

Larval supply results from the balance between the arrival of larvae (either from the parental population, when retention occurs, or from distant populations) and the loss of locally produced larvae through dispersal and mortality. In this scheme, the adult populations obviously play a central role by supplying larvae, but also by determining the place where larvae will recruit (Roughgarden et al. 1988; Bhaud 2000), which is even more constraining in species with a gregarious behaviour. Therefore, local hydrodynamics will also control larval supply through either larval retention which will enhance larval settlement in the vicinity of adults or larval exportation. Understanding the processes responsible for the successful establishment of introduced species thus requires to jointly examine the larval pool distribution and the adult locations and characteristics.

In this context, this study aimed to investigate the spatial distribution of larvae of an emblematic marine invader of the North East Atlantic, the slipper limpet *Crepidula fornicata*, at a local scale (i.e. within a bay). This gastropod, native from the East coast of the USA, was first accidentally introduced into the UK at the end of the 19th century. This species was then introduced repeatedly along the European coasts during the 20th century mostly because of aquaculture and trade of the Japanese oyster *Crassostrea gigas* (Blanchard 1997). *C. fornicata* has successfully invaded many European bays and estuaries where it has major ecological and economical impacts (Reise et al. 2006). However, its success over Europe is not uniform, and in some places, this species failed to invade the introduced area. For instance, de Montaudouin et al. (2001) highlighted the role of several features, i.e. the presence of *Zostera* sp. beds and the absence of bottom trawl fishing, to explain why *C. fornicata* failed to invade the bay of Arcachon (France).

In the bay of Morlaix (France) *C. fornicata* was first recorded more than 50 years ago (Blanchard 1995). Although this population is well established, it is less invasive as compared to other bays along the French coast of the English Channel (e.g. Bay of Mont Saint-Michel; Blanchard 2009) where *C. fornicata* is proliferating. Habitat availability can not explain this observation. *C. fornicata* usually occurs over a wide range of substrata, both in its native and introduced areas, from muddy sediments to gravels and pebbles (e.g. Barnes et al. 1973; Loomis and Van Nieuwenhuyze 1985; Ehrhold et al. 1998; Sauriau et al. 1998; de Montaudouin and Sauriau 1999), and can be found both subtidally (up to 50 m depth) and intertidally (Deslous-Paoli 1985). All these potential substrata are found in the bay of Morlaix (Cabioch 1968). In addition, there is no evidence of particular environmental biotic and abiotic factors (temperature, salinity, species composition) that may limit its proliferation. Consequently, factors involved in such a low proliferation of *C. fornicata* in this bay are still unknown.

In this paper, we addressed the question of the potential role played by the larvae of *C. fornicata* in the maintenance of the population in the bay of

Morlaix. We investigated the hypothesis of a limitation in larval inputs rather than a limitation directly mediated by the adult stage. To address this hypothesis, we focussed on the spatial distribution of the larvae (both in terms of abundance and size structure) at ten sites of the bay sampled three times during the main breeding season, and analysed these data regarding both adult distribution (abundance and reproductive status) and environmental characteristics. We addressed more specifically the following questions: (1) do the abundance and mean larval size differ among sites within the bay? (2) how much the larval pool distribution is controlled by the adults distribution or the variation in environmental variables (i.e. temperature, depth, salinity, chlorophyll *a*)? By addressing these questions, we aimed to examine the importance of the larval-adult coupling in the dynamics of marine invader populations and how local hydrodynamic processes affect the larval supply.

Materials and methods

Sampling

The sampling was conducted in the bay of Morlaix (48°38′–48°44′N; 3°49′–3°59′W) which is located in northern Brittany along the English Channel (Fig. 1).

Crepidula fornicata larvae were sampled at three dates over a period of 1 month, during the main breeding period, in summer 2006. Sampling was conducted at ten sites (numbered 0–9, Table 1), chosen to cover the inner and outer parts of the bay within a $\sim 6 \times 6$ km grid. For each date, samples were collected over 4–5 h around the neap high tide using a WP2 plankton net with a 200 µm mesh size (UNESCO 1968). For the first (20th July 2006) and second (04th August 2006) dates, vertical tows from the bottom to the surface were used in order to get measures of larval concentrations. For the third one (21st August 2006), oblique 5-min tows, corresponding to ca. 70 m^3 of water filtered, were carried out to increase the amount of larvae collected in order to analyse the size structure of the larval pool. Each plankton sample was placed in a 2-l bottle and preserved in the laboratory in 96% ethanol within 5 h after collection. Larvae of *C. fornicata* were sorted, counted and their shell length measured using a dissecting microscope (×500 magnification) with an ocular micrometer. For the first and second sampling dates, concentration of larvae m^{-3} was calculated using the abundance and the filtered volume, measured by means of a flowmeter (TSK model) mounted on the net aperture.

Environmental parameters were measured with a CTD probe (SBE 19+) at each sampling site. We calculated the mean water temperature and salinity, because (1) the water column of the bay of Morlaix is

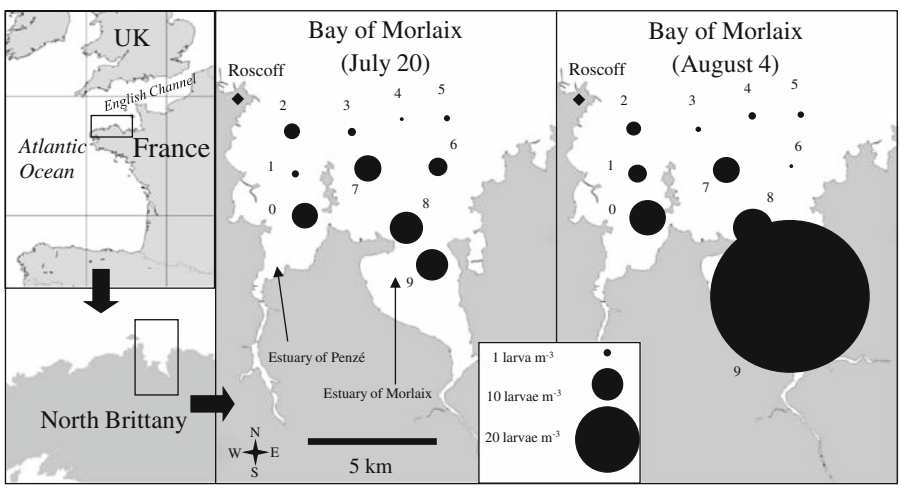

Fig. 1 Location of the ten sampling sites in the Bay of Morlaix and spatial distribution of the abundance (larvae m^{-3}) of *Crepidula fornicata* larvae for the 20 July (1st) and 4 August (2nd) sampling dates. *N* North direction

Table 1 Location (coordinates and depth) of the ten sampling sites

Sites	Coordinates (°, min)		Depth (m)	Benthic adult characteristics	
	Latitude (°N)	Longitude (°W)		Number of mature individuals	Number of brooding females (% of sampled ind.)
0	48° 40,579	3° 56,192	15	29	8 (27.6)
1	48° 41,510	3° 56,473	27	9	4 (44.4)
2	48° 42,454	3° 56,580	28	0	0
3	48° 42,440	3° 54,773	20	34	9 (26.5)
4	48° 42,723	3° 53,255	28	0	0
5	48° 42,742	3° 51,895	26	0	0
6	48° 41,664	3° 52,161	25	0	0
7	48° 41,583	3° 53,980	18	7	3 (42.9)
8	48° 40,185	3° 53,162	12	304	88 (28.9)
9	48° 39,488	3° 52,343	19	115	29 (25.5)

For each one, the number of mature individuals and number of brooding females are indicated

well mixed, with some occasional thermal stratification (Conq et al. 1998; Rigal 2009), and (2) the vertical distribution of *C. fornicata* larvae is unknown. Depth was also recorded at each site. The chlorophyll *a* concentration was measured only for the first and second dates from surface water and measured with a Turner Design fluorometer, following the method of Lorenzen (1966).

At each of the ten sites, stacks (i.e. perennial groupings of individuals, a typical feature of this species; Coe 1936) of benthic adult *C. fornicata* were sampled 1 week before the first larval sampling by scuba diving following a semi-quantitative approach: all the stacks or isolated individuals found by two divers during a 13-min dive were collected. *C. fornicata* is a sequential protandrous hermaphrodite (i.e. it changes sex from male to female) and females breed their embryos during several weeks (Chipperfield 1951). The sex and the presence of brooded embryos or larvae were thus recorded to examine the reproductive status of individuals from each site.

Data analyses

Two main larval features were studied: abundance and size structure. To investigate the spatial structure of larval abundances, data from the first and second sampling dates were used. First, multiple regression analyses with abundance (larvae m^{-3}) and geographical coordinates as explanatory variables were performed to test for the homogeneity of the larval abundances across the bay. Then, to investigate the relationships between larval abundance, benthic population characteristics (adult abundance and reproductive status) and environmental variables, a normalized principal component analysis (PCA) was carried out using the software StatBox v. 6.40 pro.

To analyze the larval size structure, the mean size at each site was compared by using a multiple comparison Kruskal–Wallis test for each of the three sampling dates. When significant differences were detected, an a posteriori test was used to determine which sites contributed to the observed differences. To further analyze the size structure, data from the third sampling date (i.e. for which large samples were obtained) were used to generate larval size-frequency histograms using 40 µm size-class intervals, first for each site then by pooling data over the ten sites. The size-class interval fits three criteria: (1) size classes have at least 5 individuals; (2) the number of adjacent empty classes is minimized and (3) the interval is larger than the error on measurements (Jollivet et al. 2000). Size-frequency histograms were smoothed using a weighted moving average at the 3rd order to rule out spurious peaks (Frontier and Pichod-Viale 1991). The number of size groups was estimated using the Normsep software (Gros and Cochard 1978) which assumes that the sizes within each age-group follow a Gaussian distribution. Based on maximum likelihood criteria, it then allows the overall size-frequency histogram to be split into several age-groups.

Finally, to determine if the size structure displayed a spatial structure, a canonical redundancy analysis (RDA, Legendre and Legendre 1998) was performed

using the table of size classes across sites as response variables and geographical coordinates as explanatory variables. The RDA is a direct extension of the multiple regression analysis for the modelling of multivariate response data (here the size-class distributions). For this analysis, we did not use the environmental variables available (i.e. number of mature individuals, number of brooding females, salinity, mean temperature and depth) as explanatory variables because most of them were found to be highly collinear, as revealed by the calculation of the Variance Inflation Factor (VIF), an index used to assess multicollinearity between non-orthogonal variables (Kutner et al. 2004; Blanchet et al. 2008). Before the RDA computation, the numbers of larvae per size class were transformed using the Hellinger transformation (Legendre and Gallagher 2001) in order to lower the weight of the small size classes (which are very abundant). The contribution of the two geographical variables and the significance of the RDA axes were tested by analyses of variance and permutation tests (999 permutations computed) using the R code source rdaTest and the R package Vegan 1.11-4 (http://www.vegan.r-forge.r-project.org/).

Analytical model

In the English Channel, currents are driven by tides, winds and density gradients (Salomon and Breton 1991). In our study, since the wind showed a mean speed of <0.5 m s^{-1} in July and August 2006, its influence on the hydrodynamics was considered negligible. As mentioned above (sampling section) the water column of the bay of Morlaix is well mixed, especially in its outer part, with some occasional thermal stratification (Conq et al. 1998; Rigal 2009). During our summer 2006 survey for example, the coastal site 0 showed a thermocline (about 2°C between bottom and surface waters) for only the 20 July and 21 August. The stratification, which can lead to strong effects on dispersal patterns (e.g. Thiébaut et al. 1992) was thus also considered negligible. According to these observations, we expected a strong influence of the tidal regime in the hydrodynamics of the bay of Morlaix. Since no hydrodynamical model at a fine spatial scale exists to allow the study of larval transport in the bay of Morlaix, we developed a simple analytical model inspired from Black et al. (1990). It allowed us to investigate the impact of the tide on the transport of larvae released at different sites in the bay, and in particular to test for larval retention processes (see "Appendix").

The bay was schematically divided into two regions differing by their hydrodynamic characteristics (see "Appendix" Fig. 6): (1) the inner part of the bay (B), only under the influence of a zonal tidal current $u(t)$, and where the spawning adults are located, and (2) the external part of the bay (E), under the influence of both the zonal tidal current $u(t)$ and a meridional offshore residual current U, perpendicular to $u(t)$. The size of the region E is determined by the maximum distance covered by a larva released in B during the tidal movement (maximal tidal amplitude x_T). Its width L thus depends on the location of the release site within B. See "Appendix" for more details on the definition of each region.

The numbers of larvae in regions B and E at time t are noticed $N_B(t)$ and $N_E(t)$, respectively. The volumes of regions B and E at time t are noticed $V_B(t)$ and $V_E(t)$, respectively. The larval concentrations are assumed to be homogeneous within each region. In this model only the advection is taken into account (i.e. the number of larvae in each region only varies under the effects of the currents $u(t)$ and U). During each time step Δt, the volume of water exchanged between the two regions by the tidal current $u(t)$ is noticed $V_1(t)$ and the volume of water removed from the region E by the current U is noticed $V_2(t)$. Detailed equations for $V_B(t)$, $V_E(t)$, $V_1(t)$ and $V_2(t)$ are given in the "Appendix".

At each time step Δt, a portion $V_2(t)/V_E(t)$ of the larvae of E is removed by the current U. During the ebbing tide, a portion $V_1(t)/V_B(t)$ of the larvae of B is transported to E. Hence the changes of $N_B(t)$ and $N_E(t)$ during ebb are given by the following equations:

$$N_B(t+\Delta t) = N_B(t) - \frac{V_1(t)}{V_B(t)} \times N_B(t) \quad (1)$$

$$N_E(t+\Delta t) = N_E(t) + \frac{V_1(t)}{V_B(t)} \times N_B(t) - \frac{V_2(t)}{V_E(t)} \times N_E(t) \quad (2)$$

During the rising tide, B receives a portion $V_1(t)/V_E(t)$ of the larvae from E. The changes of $N_B(t)$ and $N_E(t)$ during flow then follow:

$$N_B(t+\Delta t) = N_B(t) + \frac{V_1(t)}{V_E(t)} \times N_E(t) \quad (3)$$

$$N_E(t+\Delta t) = N_E(t) - \frac{V_1(t)}{V_E(t)} \times N_E(t) - \frac{V_2(t)}{V_E(t)} \times N_E(t) \quad (4)$$

According to these equations, we tested two scenarios, one at spring tide, one at neap tide. For each scenario, we used 5 values of U (1, 2, 3, 4 and 5 cm s^{-1}), corresponding to a range of values commonly reported in the literature (Salomon and Breton 1991), and 9 spawning locations. This lead to 90 simulations. A time step Δt of 1 h was chosen, since the values of the tidal current $u(t)$ and of the free surface elevation $\varepsilon(t)$ used in the volume calculations were obtained hourly from the SHOM (Service Hydrographique et Océanographique de la Marine, http://www.shom.fr). The simulations were performed for 15 days, which corresponds to the estimate of the larval life span at the temperatures prevailing in the bay in July and August 2006 (Rigal 2009).

Results

Spatial structure of larval abundance and mean larval size within the bay

Over the three sampling dates, 1,742 *C. fornicata* larvae were sampled and measured. Whatever the date and site, larval abundances ranged between less than 1 (site 5, 07/20/06) and 34 larvae m^{-3} (site 9, 08/04/06; Fig. 1). These values were not randomly distributed: the multiple regression analysis showed a significant correlation between the larval abundances and the latitudinal axis (1st sampling: $P = 0.003$ and 2nd sampling: $P = 0.007$), thus evidencing a spatial structure from the inner to the outer part of the bay.

As observed for the abundance, the mean larval size (per date, per site) differed among sites ranging between 389 ± 25 µm (mean ± SD) on 20th July (site 0), and 572 ± 54 µm on 21st August (site 5). A multiple comparison Kruskal–Wallis test ($P < 0.0001$ for the three dates) followed by an a posteriori test revealed, for each sampling date, that the inner sites (in particular sites 8 and 9) displayed a significantly lower mean size. Interestingly, all the larvae had a size lower than the typical size at competence (i.e. 800–1,000 µm; Pechenik and Heyman 1987). Only 3 larvae out of the 1,270 that were sorted during the last sampling date could have reached competence, based on this sole size criterion. All were collected in the outer part of the bay, one at site 2 (800 µm) and two at site 3 (800 and 900 µm).

Adult characteristics and environmental descriptors

The distribution of adults showed a strong heterogeneity among sites (Table 1). Almost all adults were sampled in the inner sites with up to 304 individuals at site 8. Absence of adults was noticed only in the outer part of the bay at the four sites 2, 4, 5 and 6. The number of brooding females showed the same pattern with maximum values recorded in the inner part of the bay (Table 1).

Mean temperatures and chlorophyll *a* concentrations also differed between sites. In particular, the Penzé estuary (site 0) displayed the highest temperatures with a maximum value of 18.4°C in July while the lowest mean temperature (15.6°C) was recorded at site 5 at the end of August. Chlorophyll *a* concentrations displayed higher values in the Penzé estuary (2.33 µg l^{-1}, site 0, 1st and 2nd sampling dates) and in the outer sites (e.g. site 5, 2.47 µg l^{-1}, 1st sampling). Conversely, the salinity was homogeneous at the bay scale (between 35 and 35.5) with a weak decrease at site 0 for the third sampling (34.69). This absence of spatial structure for salinity evidenced an important oceanic influence within the bay.

Relationship between larval abundances, adult characteristics and environmental descriptors

This relationship was analysed with a PCA carried out on the first and second sampling dates. The first two PCA axes explained more than 75% of the dataset variation (53 and 30%, respectively, for the first sampling, Fig. 2; 52 and 24%, respectively, on the second dataset, Fig. S1). Larval abundances were positively and significantly correlated with the number of mature individuals (i.e. males and females) for the first sampling date but not for the second one. At both dates, the number of mature individuals and the number of brooding females were positively and significantly correlated. Both were negatively and significantly correlated with chlorophyll *a* concentration and depth.

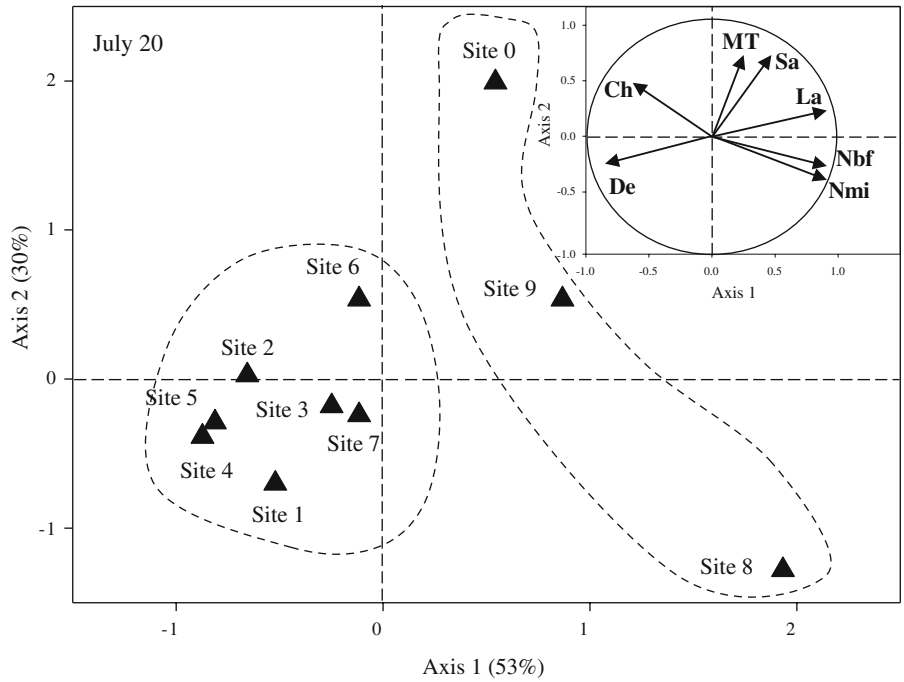

Fig. 2 Ordination of the 10 sites for the 1st sampling, the 20 July, based on the principal component analysis. Correlation circle is represented in the *upper part* of the figure in order to present the contribution of each variable to the first two axes. *La* larval abundance (larvae m^{-3}), *Nmi* number of mature individuals, *Nbf* number of brooding females, *Sa* salinity, *MT* mean temperature (°C), *Ch* Chlorophyll *a* (µg l^{-1}), *De* depth (m)

Depth and salinity were also negatively correlated (Table S1).

For the first (Fig. 2) and second (Fig. S1) sampling dates, PCA allowed to discriminate 2 clusters according to the first axis, opposing the inner (sites 0, 8 and 9) and outer (all other sites) sites of the bay. According to the contribution of environmental variables along the first axis, the inner sites were characterized by a higher number of adults and brooding females (which contribute for 21.9 and 21.6% to axis 1, respectively) and displayed higher larval abundances (which contribute for 19% to axis 1) for the first sampling. Outer sites were mainly characterized by higher depth (18%) and higher concentrations of chlorophyll *a* (10%). The second axis discriminated sites according to the temperature (34% contribution to axis 2) and opposed sites 0 and 8, site 0 (Penzé estuary), being the warmest location. Similar results were obtained for the second sampling date (Fig. S1).

Larval size structure

Length-frequency histograms generated for each site sampled during the last date differed according to their location (Fig. 3). Inner sites displayed significantly lower median values with a dominance of larvae in small size classes (sites 8 and 9). Site 0 shared the same characteristic but a higher proportion of larger larvae was also observed. In the outer sites, the smallest larvae were absent (site 4) or represented a low proportion of the total number of larvae (e.g. sites 2 and 7). This reflected a shift from small size classes to larger ones from the inner to the outer sites.

Taking advantage of the large sampling size obtained during the third sampling, the size structure has been examined in relation to the geographical coordinates using a canonical redundancy analysis (RDA). Using these two coordinates, the canonical regression performed by the RDA was significant (R^2 adjusted = 0.43; $F = 4.48$; $P = 0.001$). The two axes were significant (RDA1, $P = 0.001$; RDA2, $P = 0.001$) and contributed to 80 and 20% of the variance explained by the canonical regression, respectively (Fig. 4). Only the latitude contributed significantly to the variability of the overall larval dataset ($P = 0.004$), reflecting the size gradient between the inner and outer sites (for longitude, $P = 0.107$). Along RDA1, two clusters were

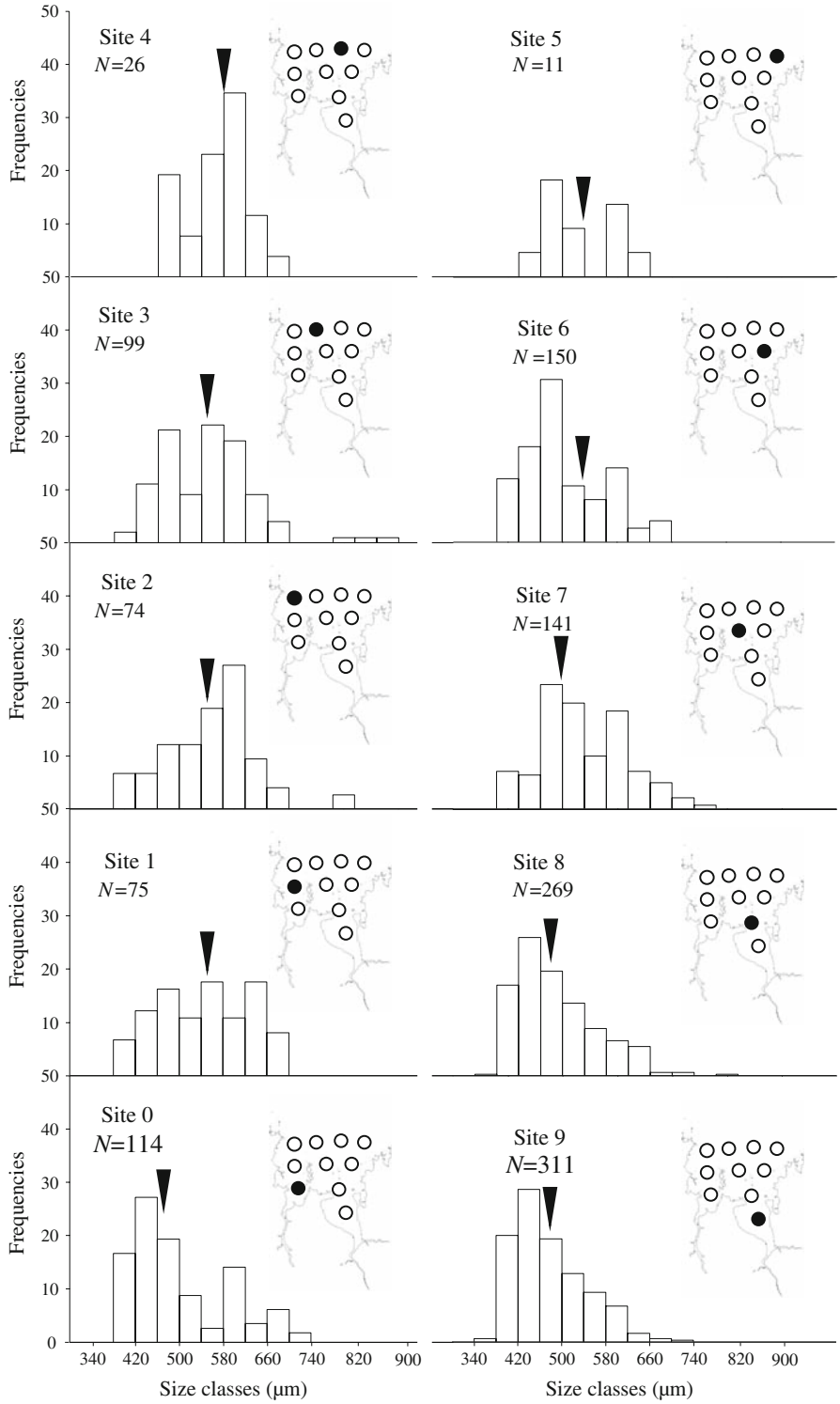

Fig. 3 Length-frequency histograms of larvae collected at the ten sites sampled during the 21 August sampling (3rd date). *Arrows* indicate the median of the distributions. *Inserted maps* indicate site location. *N* is the number of larvae measured

separated. The cluster composed of the inner sites (0, 6, 8 and 9) was characterized by the lowest latitude and was dominated by small size classes. In the opposite, the cluster composed of the outer sites (1–5 and 7) was characterized by larger size classes and highest latitude (Fig. 4).

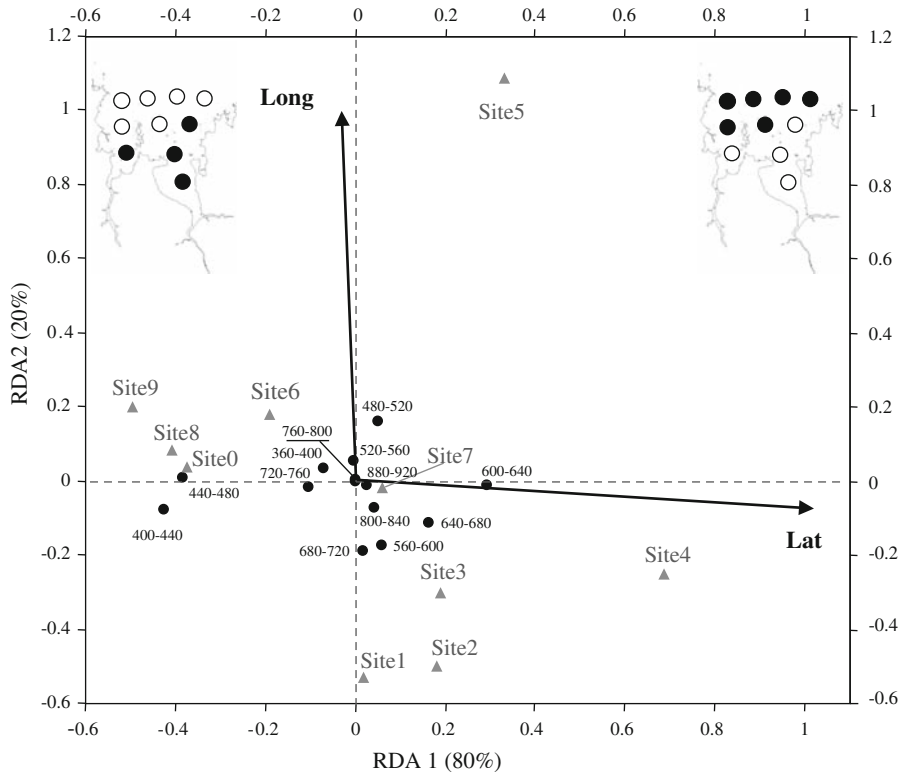

Fig. 4 RDA ordination biplot based on the RDA analysis. *Maps* indicate the location of the sites included in each group discriminated after the analysis. *Arrows* indicate the two geographical variables used in the analysis (*Lat* latitude, *Long* longitude), *triangles* indicate sites and *dots* the size classes (40 µm interval)

Tidal influence on the larval transport

Our analytical model took into account both the instantaneous tidal current within the bay and an offshore residual current to simulate the larval transport, and allowed us to calculate the larval retention rate within the bay for several spawning locations and hydrodynamic scenarios. In all simulations, the number of larvae retained within the bay oscillated according to the tidal cycle and decreased due to the loss of a proportion of larvae by the offshore residual current (Fig. 5a). As an example, with $U = 3$ cm s^{-1}, 91% of the larvae released from the main adult population (site 8) were lost after 15 days of simulation (Fig. 5a). Figure 5b illustrated that, for a given offshore residual current, larvae released more upstream (i.e. higher values of distance within the bay) were more likely to be retained within the bay. However, for a realistic residual current in this area ($U = 3$ cm s^{-1}), the retention rate never exceeded 20%, whatever the spawning site.

Discussion

Larval supply is known to play a major role in the structure and dynamics of populations of species with a bentho-pelagic life cycle (e.g. Gaines and Roughgarden 1985) and is expected to be involved in the success or failure of invasions by non-indigenous species (e.g. Cameron and Metaxas 2005; Byers and Pringle 2006; deRivera et al. 2007). In particular, the amount of larvae produced and their further dispersal or retention have been shown to be crucial for the establishment and spread of introduced populations in coastal ecosystems (Byers and Pringle 2006).

In the bay of Morlaix, the abundances of the introduced *Crepidula fornicata* larvae were low, ranging from <1–34 larvae m^{-3}, as compared to the concentrations that had been observed in other bays or estuaries of its European distribution range. These abundances measured in summer 2006 are not unusual in the bay, and a three-year survey of *C. fornicata* larval abundances conducted at site 8

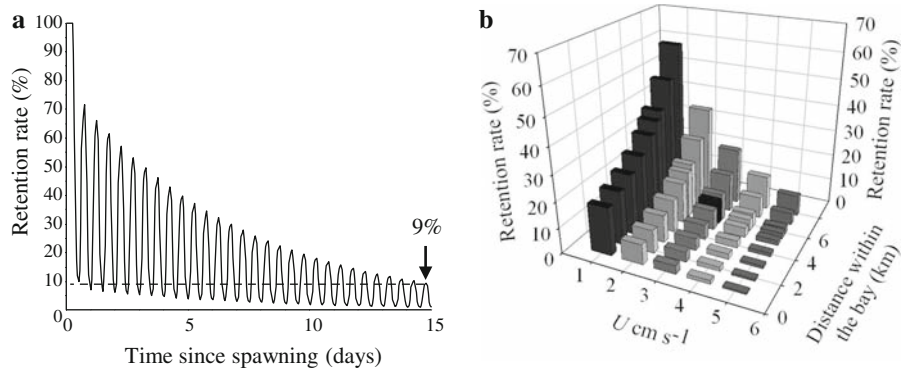

Fig. 5 **a** Retention rate (%) within the region **B** calculated with $U = 3$ cm s^{-1} and larvae released above the main adult population. **b** Retention rate (%) in the bay calculated as a function of the offshore current U and the spawning location (distance within the bay, i.e. x in Fig. 6). *Black bar* represents retention rate for the case shown in **a**. Results are presented for a spring tide

showed only little inter and intra-annual variations (with a maximum number of 83 larvae m^{-3}; Rigal 2009). This low larval abundance might be related to the overall low adult abundance in the bay (mean: 20 individuals m^{-2}, maximum: 200 individuals m^{-2}; Dupont 2004). As a comparison, from vertical plankton net tows, high concentrations of *C. fornicata* larvae (up to 3,000 larvae m^{-3}) were reported in the summer months in other European bays such as the bay of Mont Saint Michel (Quiniou and Blanchard 1987) where the local adult densities reached 2,000 individuals m^{-2} (mean: 200 individuals m^{-2}; Viard et al. 2006). Similarly, in the bay of Brest where adult densities reached 500 individuals m^{-2}, Coum (1979) reported larval concentrations of more than 500 larvae m^{-3} in summer. In the Northern part of its European distribution range, *C. fornicata* showed an average benthic density of 141 individuals m^{-2} and larval abundances varied between a few larvae m^{-3} up to 2,000 larvae m^{-3} (Thieltges et al. 2004). However in this latter study, larvae were collected by sampling 10 l of surface water, which makes the direct comparison with data based on net tows difficult. At a regional scale, our observations thus suggested the occurrence of a positive relationship between summer larval abundances and the adult stock.

Despite such low concentrations, our results clearly showed that the abundance and size structure of *C. fornicata* larvae were spatially heterogeneous at the bay scale, exhibiting a gradient from the inner to the outer sites. In the inner sites, characterized by lower depths, higher temperatures and lower chlorophyll *a* concentrations, larval abundances were higher and small size classes were dominant, while in the outer sites, deeper, colder and with higher chlorophyll *a* concentrations, lower abundances were observed and larger larvae occurred. Adults, and especially brooding females, were mainly located in the inner part of the bay (84% of the adults and 83% of the brooding females were sampled at sites 8 and 9, Table 1), where higher larval abundances were observed. In addition, mean larval size was positively related to the distance from the major spawning area (sites 8 and 9), with the smallest larvae collected close to the adults. The mean larval size and lower size classes at these locations were close to the size-at-hatching (ca. 400 µm; Pechenik and Lima 1984) which suggested that larvae were probably recently released by the reproductive females. The high abundance of small larvae in the innermost sites might thus reflect the location of the release sites.

Crepidula fornicata settles gregariously by responding to ecologically relevant cues which may be released by sessile conspecific adults (Pechenik and Heyman 1987; McGee and Targett 1989). Due to such aggregative behaviour towards adults we expected to sample large larvae (close to the size at competence, i.e. 800–1,000 µm; Pechenik and Heyman 1987) above adult beds. This was not what we observed, only 3 larvae (out of 1,270 collected larvae) at this size were sampled and none of them were above the main adult beds (sites 8 and 9). However, the observation of newly recruited benthic individuals (i.e. early juveniles) every year between July and September during a four-year survey (2005–2008) of the benthic population (Le Cam 2009), suggested that the low number of

settlement-stage larvae that we observed is sufficient to ensure recruitment. Given the occurrence of young-stage larvae at all three sampling occasions (from 20 July to 21 August), and especially on 20 July, and the estimated larval life duration of *C. fornicata* (about 2 weeks at the temperatures prevailing in the bay in July and August 2006; Rigal 2009), settlement-stage larvae should have occurred during our sampling period. Several hypotheses might explain this low number of late-stage larvae. Late developmental stages are expected to be found close to the bottom, looking for available substrate, which makes these larvae more difficult to sample with vertical tows. Moreover, when larvae find a suitable habitat (e.g. conspecific adults for *C. fornicata*), settlement processes run fast (Todd 1998), decreasing the opportunity to sample large larvae in the field. But more likely, the low number of large larvae resulted from both larval mortality and larval exportation outside the bay (see below). Our data did not allow to estimate larval mortality but it is usually considered to be high (Rumrill 1990; Pechenik 1999; Pedersen et al. 2008), leading to a strong developmental bottleneck (Schneider et al. 2003).

If larval supply depends in part on the location of spawning adults, it is also influenced by local hydrodynamics and their interactions (e.g. Dunstan and Bax 2007). The presence of the largest larvae in low abundance at sites distant from the main broodstock, as well as the overall low larval abundances, might be explained by the transport of larvae outside the bay, which might be expected from the shape of the bay (V-shaped, gradually deeper and widening towards the mouth; Dame and Allen 1996). As suggested by Geyer and Signell (1992) in other bays and estuaries, larval exportation might be due to tidal currents, known to be a major component of the prevailing hydrodynamics regime in the English Channel (Salomon and Breton 1991). Outputs of our analytical model agreed with this assumption, and showed that retention rates after 15 days were low for larvae released from the main known spawning locations (sites 8 and 9). For a residual current typical of this area ($U = 3$ cm s^{-1}; Salomon and Breton 1991), the retention rate never exceeded 20% after 15 days, whatever the spawning site. This approach however suggested that higher retention rates might be observed in some cases with larvae released more upstream in the estuary (Fig. 5). However, although larvae were collected upstream (authors' personal observations), it is still not known if spawning adults live there. These results evidenced the importance of the interactions between spawning location and hydrodynamics at a fine scale ($\sim$1 km), thus extending the results of Edwards et al. (2007) who investigated the role of such interactions in shaping dispersal kernels at a broader, regional scale. In the future, more complex bio-physical models have to be specifically designed to ascertain our hypothesis of larval exportation. In particular, our fine-scale analytical model did not address the potential effects of wind speed and direction. If wind speed was very low during the period under study (less than 0.5 m s^{-1}), it might not be the case during other periods of the reproductive season of *C. fornicata*, which is known to last several months (Chipperfield 1951; Richard et al. 2006). Several studies, carried out in the English Channel, have emphasised the major role played by wind on dispersal patterns. In particular, Barnay et al. (2003), by using a lagrangian hydrodynamic model at the English Channel scale, studied the wind effect on larval dispersal of the polychaete *Owenia fusiformis*, and showed that larval retention in the bay of Morlaix remained unchanged with or without wind. More specifically, they showed that the retention rate would be twice higher under a moderate constant NE wind (6 m s^{-1}), and twice lower under a moderate constant SW wind (6 m s^{-1}), as compared to a situation with no wind.

Despite the strong tidal export of its larvae, *C. fornicata* is now well established in the bay, which implies that efficient recruitment occurs in the population. The size-frequency analysis done on the whole dataset revealed 2 groups of larvae (with a mean size of 474 $\pm$ 40 and 602 $\pm$ 60 µm, respectively; Fig. S2), whose mean ages can be calculated according to a relationship between size, growth rate and temperature (Rigal 2009). These mean ages were estimated to be 2.5–3.8 days old at high temperature (maximum field temperature: 18.4°C) and 5.2–8.2 days old at low temperature (minimum field temperature: 15.6°C) and suggested that rather old larvae (1-week-old) may be found in the bay. However, whether these larvae were produced locally or came from adjacent bays is not known. Due to the low retention rates we estimated, self-recruitment would probably be limited and recruitment from larvae originating from distant populations might be involved in population maintenance. This assumption is supported by previous genetic assignments between

6 bays of the English Channel which suggested that the bay of Morlaix displayed the lowest levels of self-recruitment (less than 30% of individuals from the bay were assigned to this bay), which further suggested that this population might also rely on exchanges with other populations (Dupont et al. 2007).

Occurring since more than 50 years along the European coasts, *C. fornicata* has particularly proliferated in sheltered areas such as bays or estuaries, with some noticeable exceptions as failure or low success (Blanchard 1997). For instance, *C. fornicata* failed to invade the bay of Arcachon, which was explained by the scarcity of suitable habitats and the absence of bottom-trawl fishing (known to disperse individuals through both transport in trawl gears and outboard throwing of adult stacks during catch sorting; de Montaudouin et al. 2001). In the bay of Arcachon, only 30% of the water mass is removed after 15 days in the inner part of the bay where *C. fornicata* population occurs (Plus et al. 2006), which suggests that the hypothesis of larval exportation could not be responsible for the failure. The non-proliferation of *C. fornicata* in the bay of Morlaix can not be explained by the lack of suitable habitats. This species is indeed found over a wide range of substrata, from muddy sediments to gravels and pebbles, both subtidally (up to 50 m depth) and intertidally (e.g. Barnes et al. 1973; Deslous-Paoli 1985; Loomis and Van Nieuwenhuyze 1985; Ehrhold et al. 1998; Sauriau et al. 1998; de Montaudouin and Sauriau 1999), all being found in the bay of Morlaix (Cabioch 1968). In the Northern part of the *C. fornicata* European introduction range, temperature, and especially low winter temperature, has also been demonstrated to limit population increase through both adult mortality and limitation of reproductive output during freezing winters (Thieltges et al. 2004). Such a scenario could not be applied to the bay of Morlaix as winter water temperatures never fell below 7°C (Conq et al. 1998; Rigal 2009). This lack of high mortality during winter was also observed during a four-year (2005–2008) survey of the size-structure of *C. fornicata* in the Bay of Morlaix (Le Cam 2009). Finally, *C. fornicata* lives over a wide range of salinities (from 10‰ in the Baltic Sea to 35,6‰ in the bay of Brest; Paavola et al. 2005; Martin et al. 2006), encompassing the salinities observed in the bay of Morlaix (Conq et al. 1998; Rigal 2009), further suggesting that local salinity does not prevent *C. fornicata* from proliferating. Our study did not allow us to search for other unknown environmental factors that could limit adult proliferation (e.g. biotic control through parasitism). Acknowledging such a limitation, our results nevertheless support the hypothesis of an important role of (1) adult distribution together with (2) local hydrodynamics as key factors modulating larval supply and, consequently, proliferation of the species. In addition to laboratory experiments, comparisons with bays where *C. fornicata* became highly proliferative may further highlight the role of larval supply in the invasion success. Thus, the bay of Mont Saint-Michel displays high adult biomasses with 170,000 tons estimated in the western part of the bay where tidal residual currents may promote larval retention in a large and permanent anticyclonic gyre (Dubois et al. 2007). Similarly, the bay of Brest (10,000 tons of *C. fornicata* estimated in the inner part; Blanchard 1995) is a semi-enclosed marine system favouring larval retention.

Managing non-indigenous species requires understanding the factors which lead to the success or failure of each step of the invasion process. Nevertheless, causes of failure remain rarely studied in literature and are likely to be complex and multiple (e.g. Simberloff and Gibbons 2004; Drake and Lodge 2006). Our study suggested that, among other factors, limitation in larval supply due to local hydrodynamics features may impede the proliferation of an introduced species which has nevertheless been well established for more than 50 years.

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Appendix

The descriptions and the values of the parameters used in the analytical model are given in Table 2. Figure 6 gives the schematic representation of the study bay

used in the analytical model. Two regions are considered. The region **B** is delimited in the north by a section of surface $s_1(t)$. The adult population is located within the region **B** at a distance x of the section $s_1(t)$. The region **E** is defined as the area outside the bay where the larvae released from the adult population can be exported by the tide: its width L is equal to $x_T - x$, where x_T is the maximal tidal excursion. The surface $s_1(t)$ of the section separating the regions **B** and **E** varies with the tidal cycle and is given by:

$$s_1(t) = W \times (h + \varepsilon(t)) \tag{5}$$

with W the length of the region **E**, h the mean depth of the bay, and $\varepsilon(t)$ the free surface elevation.

The section of surface $s_2(t)$ is the other section of the region **E**. By this section, larvae are exported outside **E** by the offshore residual current U. $s_2(t)$ also varies with the tidal cycle following:

$$s_2(t) = L \times (h + \varepsilon(t)) = (x_T - x) \times (h + \varepsilon(t)) \tag{6}$$

The volume $V_B(t)$ of the region **B** is calculated from the surface of the bay S, the mean depth of the bay h, and the free surface elevation $\varepsilon(t)$ following the equation:

$$V_B(t) = S \times (h + \varepsilon(t)) \tag{7}$$

and the volume $V_E(t)$ of the region **E** is calculated from:

$$V_E(t) = W \times s_2(t) \tag{8}$$

The volume $V_1(t)$ exchanged between the regions **B** and **E** according to the tidal current $u(t)$ through the section of surface $s_1(t)$ and during a time step Δt is defined by:

$$V_1(t) = u(t) \times s_1(t) \times \Delta t \tag{9}$$

and the volume $V_2(t)$ removed from region **E** by the residual current U through the section of surface $s_2(t)$ during a time step Δt is defined by:

$$V_2(t) = U \times s_2(t) \times \Delta t \tag{10}$$

Using those equations, the final equations of the analytical model are:

During ebb:

$$N_B(t + \Delta t) = N_B(t) \times \left(1 - \frac{u(t) \times W \times \Delta t}{S}\right) \tag{11}$$

$$N_E(t + \Delta t) = N_E(t) \times \left(1 - \frac{U \times \Delta t}{W}\right) + \frac{u(t) \times W \times \Delta t}{S} \times N_B(t) \tag{12}$$

During flow:

$$N_B(t + \Delta t) = N_B(t) + \frac{u(t) \times \Delta t}{(x_T - x)} \times N_E(t) \tag{13}$$

$$N_E(t + \Delta t) = N_E(t) \times \left(1 - \frac{U \times \Delta t}{W} - \frac{u(t) \times \Delta t}{(x_T - x)}\right) \tag{14}$$

Table 2 Values used to parameterize the analytical model

Parameter	Description	Values	Source
L	Width of the region **E**	$x_T - x$	
x_T	Maximal tidal excursion	10,000 m	Cabioch and Douvillé (1979)
x	Distance between the release location and the boundary between regions **E** and **B**	From 1,000 to 8,000 m	
W	Length of the region **E** and **B**	10,813 m	SHOM[a]
h	Mean depth of the regions **B** and **E**	15 m	SHOM[a]
$\varepsilon(t)$	Free surface elevation	Hourly values, range from 2.15 to 7.94 m	SHOM[a]
S	Surface of the bay (under the hydrographic zero)	38,421,300 m^2	SHOM[a]
Δt	Time step of the simulation	1 h	
$u(t)$	Tidal current	Hourly values, range from 5.14 to 51.39 cm s^{-1}	Map of the bay (SHOM)[a]
U	Tidal residual current	From 1 to 5 cm s^{-1}	Salomon and Breton (1991)

[a] SHOM 2007: Service Hydrographique et Océanographique de la Marine. Data communicated by the SHOM (contract no 115/2007). http://www.shom.fr

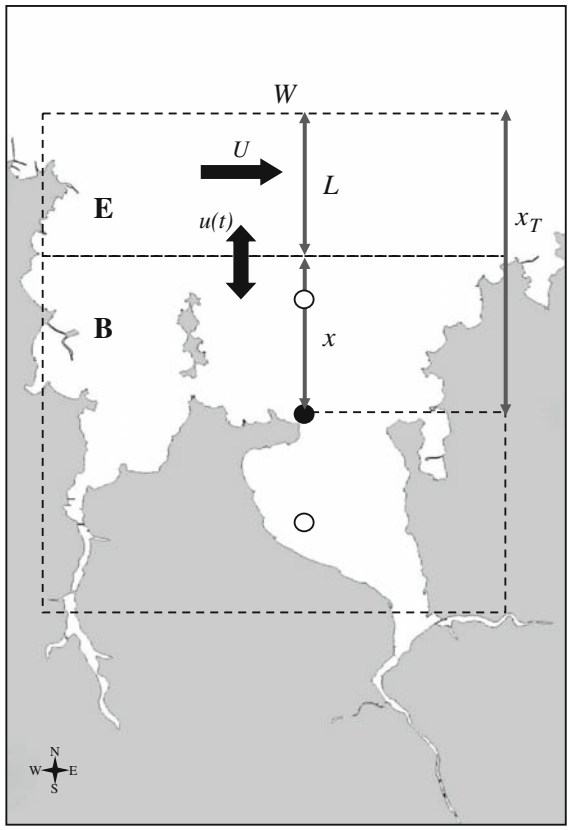

Fig. 6 Schematic view of the bay used to construct the analytical model. Meaning of the letters are presented in Table 2. The *two white dots* indicate the innermost and outermost spawning locations which were used in the model, with a distance within the bay of 8 and 1 km, respectively

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