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Meroplankton distribution and its relationship to coastal mesoscale hydrological structure in the northern Bay of Biscay (NE Atlantic)

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The relationship between meroplankton distribution and spatio-temporal variability of coastal mesoscale hydrological structure was investigated in the northern Bay of Biscay, North-East Atlantic. For the three coastal polychaetes studied, i.e. *Pectinaria koreni*, *Owenia fusiformis* and *Sabellaria alveolata*, the highest larval abundances were sampled in low-salinity, low-density and high-temperature river plume waters. For two species (*P. koreni* and *O. fusiformis*), maximal abundances were observed in the surface and thermocline layers due to ontogenic migrations. Variance partitioning based on multiple regression and redundancy analyses was used to assess the relative roles played by the hydrological environment alone, the geographical space alone and their interactions, i.e. the spatial structure of the hydrological environment. These analyses demonstrate the key role played by the hydrological spatial structure in the distribution of larval abundances. The hydrological environment alone was insignificant, whereas geographical space alone explained a significant part of the variability in meroplankton distribution, probably in conjunction with ecological processes. For species whose benthic populations are spatially structured, the distribution and the size of adult populations and the timing of spawning events can significantly affect larval distribution and dispersal.

KEYWORDS: meroplankton; larval transport; mesoscale structures; river plume; fronts; *Owenia fusiformis*; *Pectinaria koreni*; *Sabellaria alveolata*; Bay of Biscay

INTRODUCTION

For marine benthic invertebrates with a complex life cycle, pelagic larval transport is a key process in dispersal and population connectivity and plays a major role in population establishment and persistence, biodiversity conservation, spread of alien species and species distributions (Cowen and Sponaugle, 2009). Larval transport results from complex interactions of biological traits (e.g. spawning time and location, larval behaviour, planktonic larval duration) and

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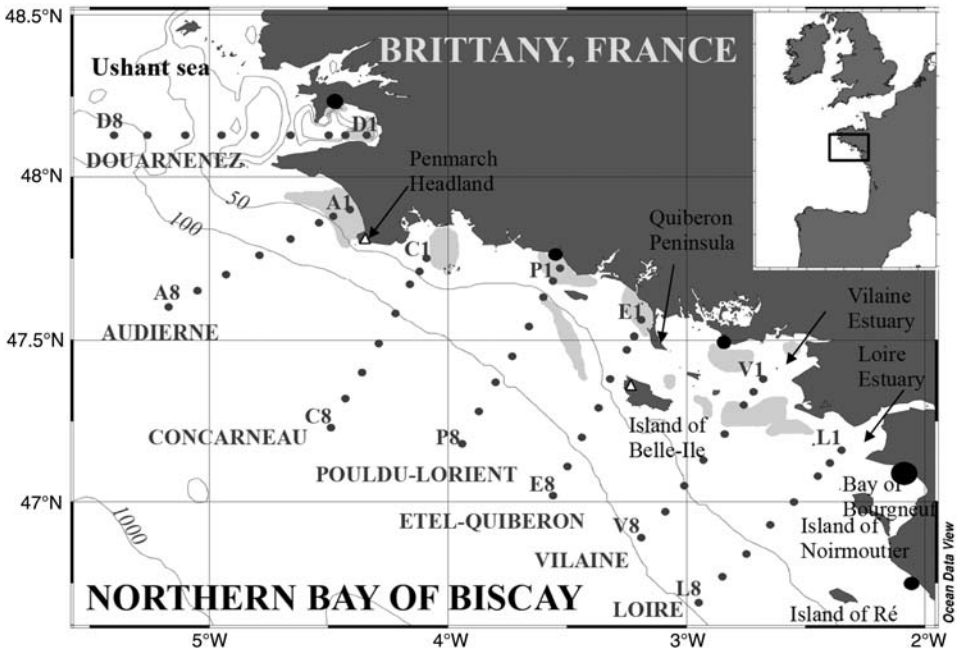

Fig. 1. Study area. The locations of the sampled stations are indicated by dark grey dots. The names of the seven transects and the codes of the first and last stations of each transect are indicated. Triangles indicate the locations of the semaphores at Penmarc'h and Belle-Ile where meteorological data were recorded. Light grey areas indicate patches of fine sand and muddy fine sand that form the preferential habitats of *P. koreni* and *O. fusiformis* (Chassé and Glémarec, 1976) and where adult populations have been recently reported (Jolly *et al.*, 2006). Black circles indicate locations where adult populations of *S. alveolata* have been reported (Gruet and Lassus, 1983; F. Rigal and F. Viard, unpublished data).

hydrodynamic processes, and both vary at several spatial and temporal scales (Pineda *et al.*, 2007). In coastal environments, numerous and complex mesoscale hydrodynamic features can tightly control the transport of planktonic organisms (Largier, 2003). For example, coastal invertebrate larvae may be "trapped" and transported within estuarine plumes, which act as physical barriers to offshore transport (Thiébaut, 1996; Shanks *et al.*, 2002, 2003b). Biological species-specific traits may also modulate the role of this type of hydrodynamic feature in larval transport. In particular, the vertical behaviour of some larvae may ensure their retention in suitable habitats, even when local hydrodynamics are expected to induce offshore transport, as in estuaries or upwelling areas (Thiébaut *et al.*, 1992; Shanks *et al.*, 2003a; Queiroga *et al.*, 2007). In addition, spawning time and location may be more important than larval behaviour in determining larval dispersal (Edwards *et al.*, 2007; Ayata *et al.*, 2010; Carson *et al.*, 2010). Sorting out which factors control larval distribution and transport thus remains a challenging issue for better understanding marine population connectivity and metapopulation dynamics (Gawarkiewicz *et al.*, 2007; Pineda *et al.*, 2007). Although new technological advances (e.g. biophysical models, molecular and geochemical markers) and the integration of different disciplines have fostered recent progress in assessing larval dispersal (Levin, 2006), mesoscale surveys are still needed to explicitly evaluate the role of most physical processes on larval populations.

In the Bay of Biscay (North-East Atlantic, Fig. 1), numerous mesoscale hydrological features, including frontal systems, river plumes, wind-induced coastal upwellings or low-salinity lenses, have been reported to occur simultaneously and to have large spatio-temporal variability at scales ranging from days to seasons (Koutsikopoulos and Le Cann, 1996; Puillat *et al.*, 2006). These features play a role in phytoplankton primary production (Morin *et al.*, 1991; Maguer *et al.*, 2009), zooplankton community structure (Albaina and Irigoien, 2007) and plankton biomass distribution (Zarauz *et al.*, 2007, 2008). Furthermore, the northern Bay of Biscay forms a transition area between the Boreal–Arctic and the Boreal–Lusitanian biogeographic provinces together with the occurrence of phylogeographic breaks in several marine taxa (Jolly *et al.*, 2006; Maggs *et al.*, 2008). Through their influence on larval transport and population connectivity, the contemporary complex hydrodynamics may participate in the maintenance of these genetic breaks (Ayata *et al.*, 2010).

In this general context, we focused on the horizontal and vertical larval distributions in three target species of coastal polychaetes for which complex phylogeographic

patterns have been reported in the northern Bay of Biscay: *Pectinaria koreni*, *Owenia fusiformis* and *Sabellaria alveolata* (Jolly *et al.*, 2006; F. Rigal and F. Viard, Station Biologique de Roscoff, unpublished results). For these species, pelagic larvae can be morphologically identified at the species level and the extended spawning seasons increase the probability of successfully sampling larvae: (i) a major spawning period in spring (April–June) and an additional spawning period in late summer–autumn for *P. koreni* (Irlinger *et al.*, 1991); (ii) a main spawning period in spring (April–June) for *O. fusiformis* (Gentil *et al.*, 1990) and (iii) year-round reproduction with two main reproductive peaks in March–April and June–July for *S. alveolata* (Gruet and Lassus, 1983; Dubois *et al.*, 2007). Although these three species share the same general broadcast spawner life history, they differ in their adult benthic habitats, planktonic larval durations and larval behaviours, and all of these biological traits are known to significantly affect larval dispersal. *P. koreni* and *O. fusiformis* inhabit patches of fine sand and muddy fine sand in shallow coastal waters at about 10–20 m depth (Chassé and Glémarec, 1976; Fig. 1), whereas *S. alveolata* is a gregarious polychaete that builds intertidal biogenic reefs. Large *S. alveolata* reefs have been described on sandflats of the Bay of Bourgneuf south of the Loire estuary (Gruet and Lassus, 1983), while small groups of individuals adhering to rocks have also been reported all along southern Brittany coasts (F. Rigal and F. Viard, Station Biologique de Roscoff, unpublished results; Fig. 1). From *in situ* observations, mean planktonic larval durations have been estimated to be about 2 weeks for *P. koreni* (Lagadeuc and Retière, 1993), 4 weeks for *O. fusiformis* (Thiébaut *et al.*, 1992) and 4–10 weeks for *S. alveolata* (Dubois *et al.*, 2007). Moreover, these species differ in their potential larval behaviour: vertical ontogenic migrations have been reported for *P. koreni* (Lagadeuc, 1992) and *O. fusiformis* (Thiébaut *et al.*, 1992), whereas complex short-term variations in *S. alveolata* vertical distribution have been reported in relation to the tidal cycle (Dubois *et al.*, 2007). Focusing on these three target species, the aim of the present study was to assess the relative role of coastal mesoscale hydrological structure and biological processes in meroplankton distribution, as well as larval dispersal and connectivity.

Several statistical methods that model spatial and temporal relationships in ecological data have been recently developed to describe the distribution of zooplankton in relation to their environment (e.g. generalized linear models, generalized additive models, clustering or ordination) (e.g. Zarauz *et al.*, 2008), but these methods neglect the spatial structure of the environmental variables. However, the spatial patterns of a response variable such as larval distribution depend on (i) the hydrological environment alone (i.e. non-spatial environmental variation); (ii) the geographical space alone (i.e. spatial variations not shared by the environmental variables); (iii) the interactions between space and environment, i.e. the spatial structure of the hydrological environment and (iv) other undetermined factors such as organism behaviour (Borcard *et al.*, 1992). Hence, the spatial structure of the environment should be taken into account when describing spatial patterns of zooplankton (Belgrano *et al.*, 1995), for example by using variance partitioning, a recently developed quantitative statistical method.

The application of a variance partitioning method to mesoscale samples of larval horizontal distribution in two different oceanographic conditions provided the opportunity to test a set of hypotheses on the main factors affecting the meroplankton distributions and larval dispersal in the northern Bay of Biscay and to quantify their relative roles. Under our first hypothesis, larval distributions would mainly depend on the hydrological properties of the water masses (e.g. salinity, temperature, stratification of the water column) that may affect larval development and survival. According to the second hypothesis, it is assumed that larvae are advected passively by currents and trapped by mesoscale hydrodynamic structures within typical water masses. Consequently, spatially structured hydrodynamic processes would be the major factor affecting the meroplankton distribution, and similar larval distributions would be observed for the different larval stages of target species and for the different target species. Finally, under the third hypothesis, biological traits, such as spawning, settlement location and larval swimming, behaviour would be the major factors determining larval distributions, and significant differences would be observed between the species characterized by different biological traits. We tested these hypotheses by doing variance partitioning analysis on larval horizontal distributions and by describing larval vertical distribution in relation to water column stratification at a few stations.

METHOD

Study area

In coastal areas of the Bay of Biscay, strong freshwater inputs combined with relatively low vertical mixing cause strong haline stratification. Thermal stratification superimposes on haline stratification, not necessarily at the same depth, from spring to mid-September. Vertical temperature gradients reach a maximum of 9–10°C between surface and bottom layers. In the vicinity of the Loire and Vilaine estuaries

(Fig. 1), the presence of low-salinity surface waters in spring induces significant density gradients responsible for strong density currents over the continental shelf ($2-20\ cm\ s^{-1}$) generally oriented northwards. The wind-induced currents are highly variable both in direction and speed at temporal scales ranging from days to seasons, and typically reach $10-30\ cm\ s^{-1}$ in the north of the bay. During thermal stratification, W to NW winds induce local transitory upwellings in the north of the Loire estuary and result in the formation and offshore transport of lenses of low-salinity surface waters about 50–80 km wide and 30 m thick (Puillat *et al.*, 2006). In the north, the Bay of Biscay is connected to the English Channel at the tip of Brittany through the Ushant Sea, a transitional area between well-mixed (English Channel) and stratified (Bay of Biscay) waters where strong thermal fronts are caused by tidal mixing in spring and summer (Pingree *et al.*, 1975; Morin *et al.*, 1991). Low-salinity waters from the Loire and Vilaine Rivers have been reported from March to April in the Ushant Sea and at the entrance of the English Channel following strong river run-offs and periods of NE winds (Kelly-Gerreyn *et al.*, 2006).

Sampling and laboratory procedures

Data were collected in the northern Bay of Biscay in spring 2008 during two oceanographic cruises (from 10 to 18 May and from 9 to 13 June). Cruises were separated by an interval of 3 weeks to increase the probability of sampling larvae of the three target species and to cover different oceanographic conditions during the main reproductive season. Along seven inshore–offshore transects localized in front of the main coastal bays and estuaries, eight stations distributed from the 20 m isobath to the open sea were sampled during the daytime (Fig. 1). The first three stations were separated by 3 nautical miles and then four stations 6 nautical miles apart, so that transects extended about 40 nautical miles offshore.

At each sampling station, vertical profiles of hydrological parameters were obtained from the surface to the bottom (or to a maximum of 50 m depth) using a conductivity, temperature, depth (CTD) probe (Seabird SBE 19). A stratification index $\hat{S}$ of the water column was defined by integrating the vertical density profile as the mean of the density differences along the water column (Fortier and Leggett, 1982):

$$\hat{S} = \frac{\sum_{i=1}^{i=n} \Delta\sigma_{ti}.\Delta z_i}{n},$$

where n is the number of pairs of adjacent measurements, $\Delta\sigma_{ti}$ the difference in water density between the ith pair of measurements and Δz_i the depth interval between the ith pair of measurements fixed at 1 m in the present case.

The thermocline, halocline and pycnocline depths were calculated using a theoretical two-layer model of the water column (Planque *et al.*, 2006). For a given hydrological variable X, the water column is assumed to be composed of two homogeneous layers, a surface layer of width z_x and a bottom layer of width $z_b - z_x$. The cline depth z_x is

$$z_x = z_b|X_m - X_b|/|X_s - X_b|,$$

where z_b is the water column height, X_m the mean value of variable X from surface to bottom, X_b the value of variable X in the bottom layer and X_s the value of variable X in the surface layer. The variable X stands for temperature T, salinity S or density σ_t to calculate the thermocline, halocline or pycnocline depth, respectively.

In addition to *in situ* data, satellite images of sea surface chlorophyll *a* concentrations during the two cruises were obtained from CERSAT (French Centre for European Remote-Sensing Satellite Processing and Archiving Facility). Wind data in spring 2008 were provided by the French Office of Meteorology (Météo France) and were recorded at two locations in the north (i.e. Penmarc'h headland) and in the centre of the study area (i.e. Belle-Ile Island) (Fig. 1). Since wind data recorded at the two stations were very close, indicating homogeneous wind conditions all over the study area, only data collected at Penmarc'h will be presented. Daily records of the Vilaine and Loire River flows were provided by the French Freshwater Office database.

To describe the horizontal larval distribution, zooplankton samples were collected at each station using a vertical haul from the bottom (or a maximum depth of 50 m) to the surface with a triple WP2 plankton net with a mesh size of 80 μm and a mouth area of $0.25\ m^2$. A TSK flow meter (Tsurumi Seiki Co., Ltd., Yokohama, Japan) was fixed to one of the net apertures to determine the volume of water filtered (range: 2.6–$19.9\ m^3$, average: $10.0\ m^3$). The samples collected by one of the three nets were preserved in 3% buffered formalin and analysed.

To determine the larval vertical distribution in relation to water column stratification, zooplankton samples were also collected at fixed depths using a pumping system. A 5 cm diameter collection pipe was attached to the CTD and to a submersible pump. CTD records provided real-time data on the depth and the water properties from which samples were collected. Three to four depths were selected per station: the

surface mixed-layer (about 3–5 m), the halocline and/or thermocline layers (about 10–15 m) and the bottom layer (about 20–40 m). With a pumping rate of 300 L min^{-1}, a volume of 1.5 m^3 of water was filtered through an 80 μm mesh net at each sampled depth for 5 min. Samples were preserved immediately after collection in 3% buffered formalin. Owing to the time required to sort samples, larval vertical distributions were described for only a few stations with high larval abundances (i.e. higher than a few hundreds of ind m^{-3}) (i.e. stations D2, C1, P2 and V2 in May and stations D2, P1 and V1 in June, see Fig. 1).

In the laboratory, each sample was rinsed and completed to 200 mL with filtered seawater. Samples were then homogenized by vigorous random stirring and a subsample of 5 mL was pipetted. The larvae of the three target species were enumerated in three to five subsamples under a dissecting stereomicroscope, to reach a count of at least 100 larvae per sample and species. This method leads to an error of about 30% in larval counting (Frontier, 1972), which is relatively small in comparison with the order of magnitude observed in the larval concentration differences between stations. When total zooplankton concentration was low, the sample was completed to 100 mL only. Conversely, when concentration was high, the subsample volume was decreased to 3 mL. By this procedure, 3–20% of each sample was analysed. Larval abundances were expressed as number of larvae per m^3. For each species, the four larval developmental stages were distinguished using morphological characters (*P. koreni*: Lagadeuc and Retière, 1993; *O. fusiformis*: Wilson, 1932; *S. alveolata*: Wilson, 1968; Dubois *et al.*, 2007).

Statistical analyses

All statistical analyses were performed using R software, version 2.7 (R Development Core Team, 2005; http://www.r-project.org) and the *vegan* library.

For each cruise, the hydrological typology of the water masses was based on 10 variables: the sea surface temperature (T_s), the temperature gradient from surface to bottom or a 50 m depth (ΔT), the thermocline depth (z_T), the sea surface salinity (S_S), the salinity gradient from surface to bottom or at 50 m (ΔS), the halocline depth (z_S), the surface density (σ_{tS}), the density gradient from surface to bottom or at 50 m ($\Delta\sigma_t$), the pycnocline depth ($z_{\sigma t}$) and the stratification index ($\hat{S}$). A cluster analysis was carried out using Ward's method on the Euclidean distance matrix calculated between stations to group stations according to their physico-chemical properties and to identify hydrological regions.

The horizontal depth-integrated larval abundances of each species were analysed using a variance partitioning method based on three partial multiple regressions (Borcard *et al.*, 1992; Legendre and Legendre, 1998). For these analyses, three vectors or matrices were used: (i) the response vector Y of the $\log_{10}$-transformed horizontal larval abundances; (ii) the explanatory matrix X of the hydrological variables and (iii) the explanatory matrix W of the spatial variables. To ensure the extraction of the more complex structures, spatial variables were described as the different terms of a cubic polynomial function of the centred geographical coordinates (x,y) of the stations such that $W = f(x,y,x^2,xy,y^2,x^3,xy^2,x^2y,y^3)$. In the first partial multiple regression step, larval abundances were analysed as a function of the hydrological data, through a multiple regression between the response vector Y and the environmental matrix X. Since multiple regression is sensitive to colinearity among the explanatory variables, variables were selected prior to the regression to avoid redundancy between the 10 hydrological variables. The matrix of Pearson's product–moment correlation coefficients was calculated between each pair of hydrological variables and only variables with a correlation coefficient lower than 0.75 were chosen for the analysis so that one variable was omitted for each pair of highly correlated variables. Hence, four hydrological variables covering the spatial variations of salinity and temperature and the vertical structure of the water column were selected in May (T_s, S_S, z_S, $z_{\sigma t}$) and in June (T_s, S_S, $z_{\sigma t}$, $\hat{S}$). In the second step, a multiple regression was performed between Y and the spatial matrix W. Finally, in the third step, a multiple regression was performed between Y and both the hydrological and spatial matrix XW. From these three successive steps, variance in total larval abundances was partitioned: the first regression provided the proportion of variance explained by the hydrological environment ($a + b$: hydrological environment alone and interaction between hydrological environment and geographical space), while the second regression indicated the proportion of variance explained by the geographical space ($c + b$: geographical space alone and interaction between hydrological environment and geographical space). The third regression provided the proportion of variance explained by the hydrological environment, the geographical space and their interaction ($a + c + b$) and allows the calculation of the unexplained variance ($d = 1 - a - b - c$).

To analyse the horizontal distributions of the different larval stages, redundancy analyses (RDA), which are a direct extension of multiple regressions to multivariate response data, were performed and variance partitioning was conducted as previously described (Legendre and Legendre, 1998).

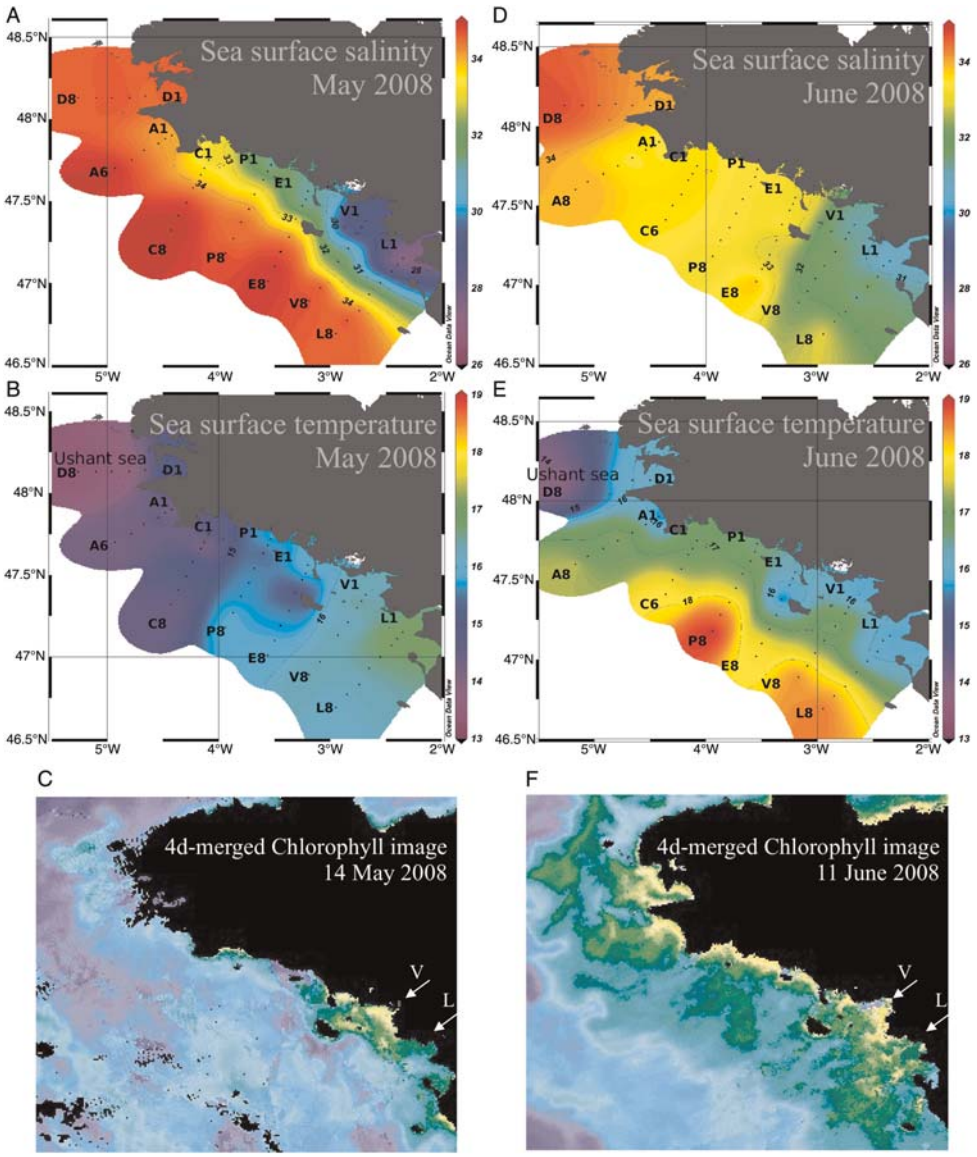

Fig. 2. Surface hydrological conditions in May (**A**–**C**) and June (**D**–**F**) 2008 in the northern Bay of Biscay: horizontal distribution of sea surface values of (A) salinity in May, (B) temperature (in °C) in May, (C) chlorophyll *a* concentrations in May, (D) salinity in June, (E) temperature (in °C) in June and (F) chlorophyll *a* concentrations in June. Sampling transects (with the codes of the first and last stations) are indicated for surface salinity and temperature maps. The Vilaine (V) and the Loire (L) estuaries are indicated on the chlorophyll maps. To minimize cloud coverage, 4-day merged satellite images of surface chlorophyll *a* concentrations are presented; light-coloured coastal areas indicate higher concentrations (CERSAT data, MORIS/MODIS images). The hydrological maps have been performed using ODV (http://odv.awi.de/) with the *jetplus* colour palette proposed by S. Haddock in *L&O Bulletin* [2010 Vol. 19(2)]. A colour version of this figure can be found online.

RESULTS

Meteorological and run-off conditions in spring 2008

Wind conditions were mainly from W to NW during spring 2008, with decreasing average speed over time, from 8.5 m s^{-1} in March to 5.6 m s^{-1} in April and 3.3 m s^{-1} in May (Supplementary data, Fig. S1A). In June, average wind speed increased slightly to 4.8 m s^{-1}. The May and June cruises occurred under low to moderate wind speeds of 2.6 and 6.0 m s^{-1}, respectively. After the May cruise, low winds of various directions (average speed, 3.9 m s^{-1}) were recorded over 10 days. The week before the second cruise was characterized by stronger NW winds (average speed, 6.4 m s^{-1}), with maximal speed of 8–9 m s^{-1}. Two peaks in Loire River run-off were observed in March and April 2008, with run-offs exceeding 1800 and

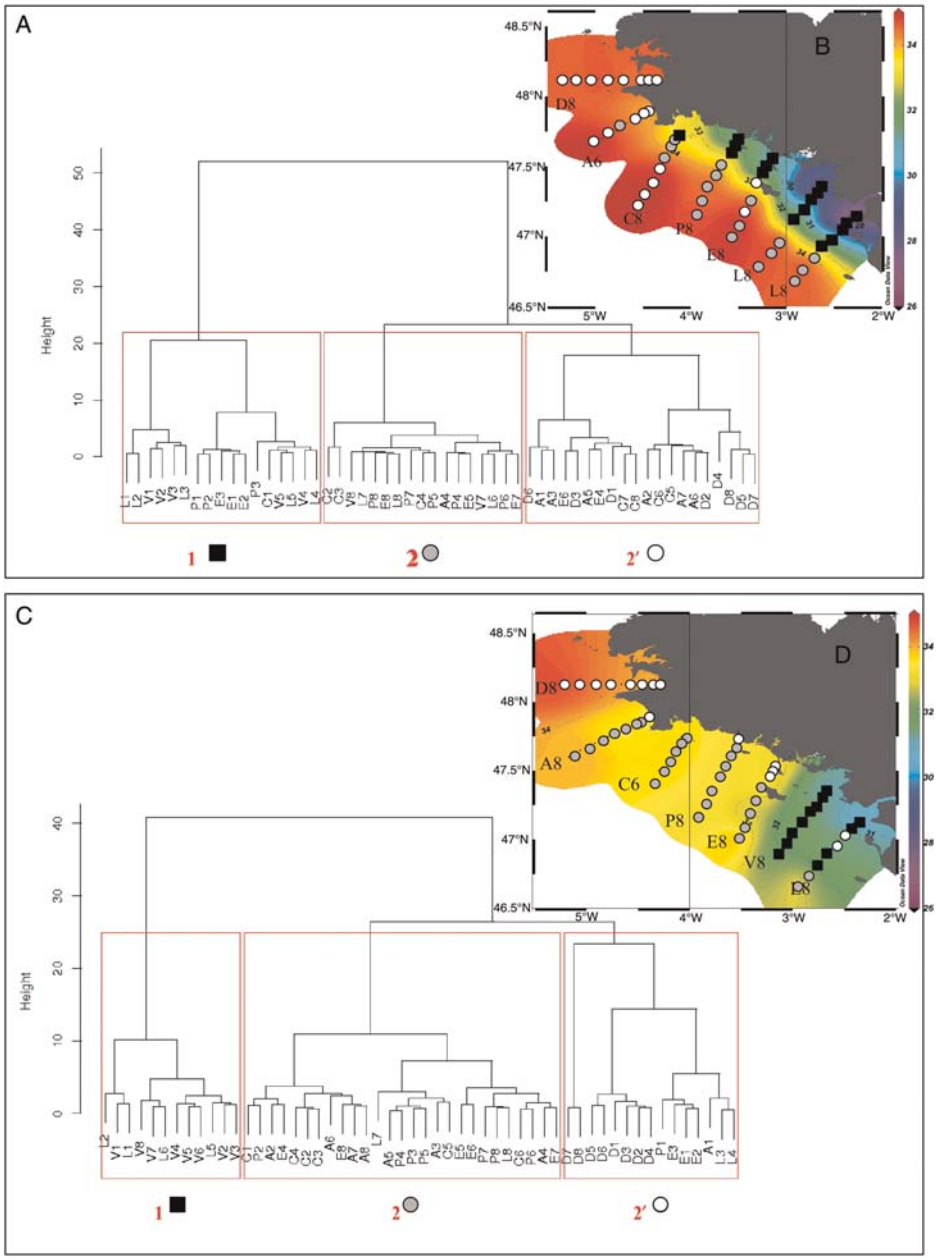

Fig. 3. Hydrological typology in the northern Bay of Biscay in May (**A** and **B**) and June (**C** and **D**) 2008: (A) Cluster analysis performed on the hydrological data and (B) spatial distribution of the three clusters according to the surface salinity distribution in May 2008, (C) cluster analysis performed on the hydrological data and (D) spatial distribution of the three clusters according to the surface salinity distribution in June 2008. For each cruise, black squares indicate the stations belonging to cluster 1, grey circles the stations of cluster 2 and white circles the stations of cluster 2′. The hydrological maps have been performed using ODV (http://odv.awi.de/) with the *jetplus* colour palette proposed by S. Haddock in *L&O Bulletin* [2010 Vol. 19(2)]. A colour version of this figure can be found online.

$2500\ m^3\ s^{-1}$, respectively (Supplementary data, Fig. S1B). The May cruise occurred during a period of low river run-off, about 3 weeks after the last flood. Just before the June cruise, a peak in the river outputs of both the Vilaine and the Loire Rivers was recorded ($>2000\ m^3\ s^{-1}$ for the Loire).

Environmental variables during the May cruise

In May 2008, a large low-salinity plume ($S_S < 32$) was observed along the southern Brittany coasts from the Loire estuary to the entrance of the Bay of Concarneau (Fig. 2A). Surface salinities were minimal at the most

inshore stations of the Loire transect ($S_S = 26.5$ at station L1) and maximal along the two transects of Douarnenez and Audierne and at the more offshore stations of the other transects ($S_S > 34$). Sea surface temperatures followed a latitudinal gradient with the lowest temperatures in the north ($T_S < 13.5°C$ at stations D8 and D7) and the highest temperatures in the south ($T_S > 16.7°C$ at stations L2 and L3) (Fig. 2B). Cross-shore thermal gradients were weak, except along the Douarnenez transect where a thermal front was observed at the entrance of the bay and along the Loire transect. The highest chlorophyll *a* concentrations were localized in river plume waters (Fig. 2C). Vertical stratification was low ($\hat{S} < 0.1$), except for the coastal stations located in the river plumes (Supplementary data, Fig. S2). Weak thermal stratification was observed along most transects. When observed, the depths of the thermocline and the halocline differed, and varied between 5 and 10 m and between 10 and 15 m, respectively. The distribution of water density was mainly governed by variation in salinity as illustrated by the similarity of the salinity and density profiles (Supplementary data, Fig. S2B and S2C).

The cluster analysis distinguished two main regions according to their hydrological properties (Fig. 3A and 3B). The first cluster grouped the inshore stations of the southern transects, located in river plumes and characterized by higher stratification, lower surface salinities and densities and shallower thermoclines, haloclines and pycnoclines (Table I). The second cluster was composed of the stations along the northern transects and of the offshore stations along the southern transects. It could be further separated into two subgroups that differed by their surface temperatures (Table I).

Table I: Typology of water masses in the northern Bay of Biscay in May and June 2008

Hydrological variables	Cluster 1	Clusters 2 and 2′	
		Cluster 2	Cluster 2′
Stratification index $\hat{S}$	0.16 ± 0.09	0.03 ± 0.01	
Surface temperature T_s	16.20 ± 0.45°C	16.00 ± 0.52°C	14.34 ± 0.71°C
Surface salinity S_s	30.54 ± 1.92	34.39 ± 1.07	
Surface density σ_{tS}	22.37 ± 1.52	25.58 ± 0.88	
Thermocline depth z_T	12.22 ± 3.99 m	15.19 ± 4.83 m	
Halocline depth z_S	10.58 ± 4.32 m	19.94 ± 7.49 m	
Pycnocline depth $z_{\sigma\tau}$	10.80 ± 4.19 m	17.64 ± 6.85 m	
Stratification index $\hat{S}$	0.12 ± 0.04	0.05 ± 0.03	
Surface temperature T_s	17.02 ± 1.06°C	17.37 ± 0.86°C	15.59 ± 0.92°C
Surface salinity S_s	31.24 ± 0.67	33.53 ± 0.65	
Surface density σ_{tS}	22.74 ± 0.38	24.56 ± 0.61	
Thermocline depth z_T	11.64 ± 3.04 m	14.58 ± 5.57 m	
Halocline depth z_S	8.07 ± 2.10 m	11.73 ± 5.35 m	
Pycnocline depth $z_{\sigma\tau}$	9.01 ± 2.37 m	12.89 ± 5.23 m	

Mean values ± standard deviations of the hydrological variables are indicated for the clusters identified among the sampled stations. Clusters are defined in Fig. 3.

Horizontal larval distribution during the May cruise

Inshore–offshore and latitudinal gradients were observed in larval distributions of all three species, with higher abundances (>100 ind m^{-3}) close to the shore and in the southern part of the study area (Fig. 4). *P. koreni* and *O. fusiformis* larvae were sampled along each transect, but *S. alveolata* larvae were only observed along the five southernmost transects, from the Bay of Concarneau to the Loire estuary. The *P. koreni* larval population was mainly composed of the first three larval developmental stages (Fig. 5A), which were homogeneously distributed over the study area (data not shown). In contrast, the fourth aulophore stage was only reported in a few stations. The larval population of *O. fusiformis* was largely dominated by stage-3 larvae and, to a lesser extent, by stage-4 larvae (Fig. 5B). While these two larval stages were evenly distributed, the two youngest stages were restricted to the more coastal stations. The *S. alveolata* larval population was also largely dominated by a single larval developmental stage: stage 2 (Fig. 5C).

For all three species, multiple regressions showed significant relationships between total larval abundances and the four selected hydrological variables: sea surface temperature, sea surface salinity, halocline depth and pycnocline depth (*P. koreni*: $R^2 = 0.5669$, $P < 10^{-3}$; *O. fusiformis*: $R^2 = 0.4486$, $P < 10^{-3}$; *S. alveolata*: $R^2 = 0.6960$, $P < 10^{-3}$). Larval abundances were significantly negatively correlated with surface salinity and either surface temperature or halocline depth, indicating that larvae were mainly located in the river plume stations (Table II). Variance partitioning highlighted that variation in larval abundances was mainly explained by the spatial structure of the hydrological environment (56% for *P. koreni*, 44% for *O. fusiformis* and 68% for *S. alveolata*) (Fig. 6A). For all three species, geographical space alone accounted for 26, 27 and 16% of the variance, respectively, whereas the non-spatial hydrological environment explained <1% of the variance. The remaining unexplained variance ranged between 14 and 28%.

The RDA computed on the abundances of the different larval stages and the hydrological variables indicated that the hydrological variables significantly influenced larval stage distribution (*P. koreni*: $R^2 = 0.5278$, $P < 10^{-3}$; *O. fusiformis*: $R^2 = 0.3072$, $P < 10^{-3}$; *S. alveolata*: $R^2 = 0.5582$, $P < 10^{-3}$). For example, for the RDA performed on *P. koreni* larvae, only one canonical axis, which

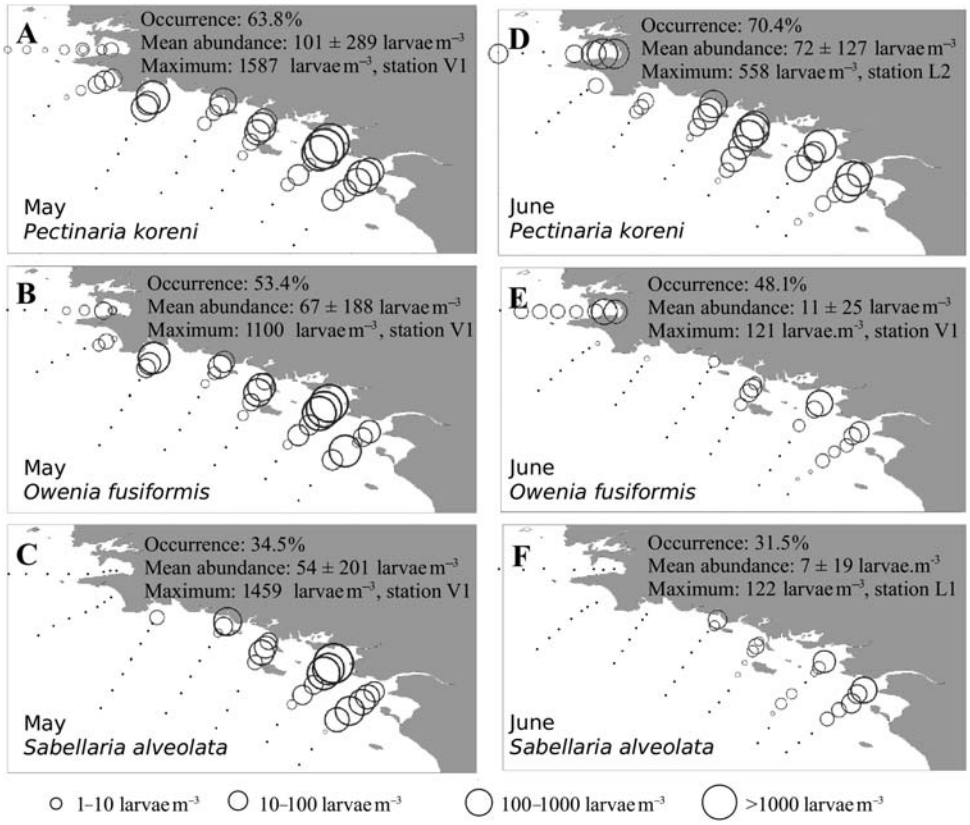

Fig. 4. Horizontal distribution in May (**A**–**C**) and June (**D**–**F**) 2008 of *P. koreni* (A and D), *O. fusiformis* (B and E) and *S. alveolata* (C and F) larvae in the northern Bay of Biscay. Percentage of occurrence, mean ± standard deviation of larval abundances calculated over all samples ($n = 54$), and maximal larval abundance are indicated for each species.

explained 94.2% of the constrained variance, was significant ($P < 0.001$) and was related to the surface salinity and the pycnocline/halocline depths (Fig. 7A). The scores of the first three developmental stages on the RDA biplot diagram were grouped together, suggesting similar horizontal distributions according to the hydrological environment in the plume waters. Only the score of stage 4 differed slightly, which may be partly explained by its very low occurrence. Variance partitioning from the successive RDA showed that the spatial structure of the hydrological environment accounted for 52, 30 and 55% of the variation in larval stage distributions for *P. koreni*, *O. fusiformis* and *S. alveolata*, respectively (Fig. 6B). Geographical space alone explained, respectively, 22, 25 and 22% of the variance in stage abundances, whereas the hydrological environment alone explained <1% of the variance. The unexplained variance varied between 22 and 44%.

Environmental variables during the June cruise

Similar to what was observed in May, surface waters showed the lowest salinities off the Vilaine and Loire estuaries ($S_S < 32$; Fig. 2D). However, although the river plume was less salty (minimal salinity: 29.8), a northern and offshore extension of low-salinity waters was observed ($S_s < 34$). Surface waters were generally warmer than in May ($T_S > 14.5°C$), except at stations D7 and D8 separated from the other stations of the Douarnenez transect by the Ushant thermal front (Fig. 2E). Maximal sea surface temperatures were observed offshore from the Bay of Concarneau to the Loire estuary ($T_S > 17.9°C$). Chlorophyll *a* concentrations were high all along the continental shelf with maximal values in inshore waters in response to the spring phytoplankton bloom (Fig. 2F). Compared with data obtained in May, a stronger vertical stratification was observed ($0.03 < \hat{S} < 0.19$) except at the offshore stations of the Douarnenez transect (Supplementary data, Fig. S3). Along the Vilaine and Loire transects, spatial variation in density varied primarily with salinity, whereas spatial variation was mainly related to temperature along the other transects.

The cluster analysis again separated two main hydrological regions (Fig. 3C and 3D). The stations of the first cluster were located off the Vilaine and Loire

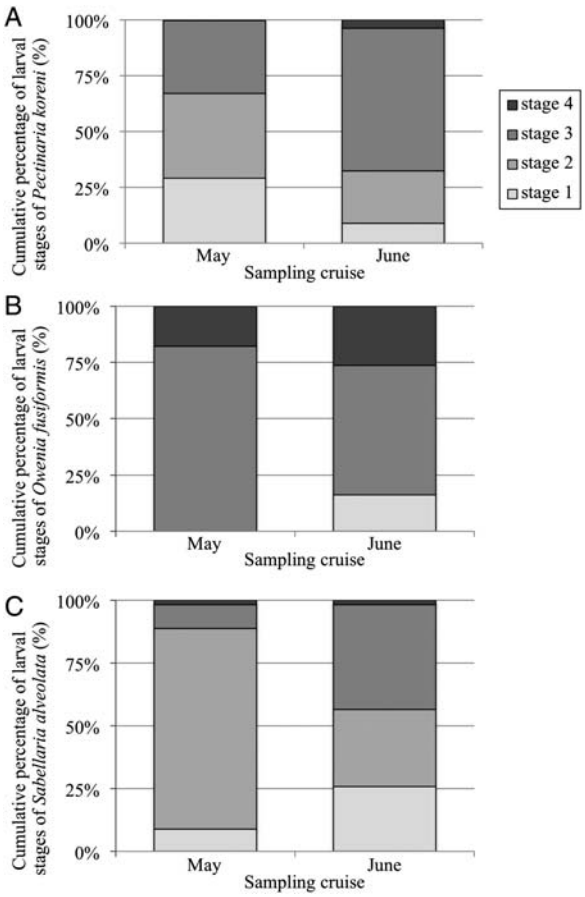

Fig. 5. Composition of the larval populations: cumulative percentage of the four main larval stages of (**A**) *P. koreni*, (**B**) O. *fusiformis* and (**C**) *S. alveolata* in May and June 2008 in the northern Bay of Biscay.

estuaries, and were characterized by stronger vertical stratification, lower surface salinities, lower surface densities and shallower thermoclines, haloclines and pycnoclines (Table I). The second cluster, which included all the other stations, could be divided in two subclusters according to surface temperature (Fig. 3C and 3D, Table I). The first subcluster characterized by higher surface temperatures and deeper thermoclines was composed of most of the stations on the transects from Audierne to Etel-Quiberon. Conversely, the second subcluster, characterized by lower surface temperatures and shallower thermoclines, included all the stations of the Douarnenez transect and some inshore stations of other transects.

Horizontal larval distribution during the June cruise

The general horizontal larval distributions, observed in June for all three species, resembled those

Table II: Results from multiple regressions on larval abundances and hydrological variables in May 2008

Species	Tested factor	Regression coefficient b	*P*-value
P. koreni	T_S	−0.244	0.036*
	S_S	−0.283	5.19E−06***
	z_S	−0.040	0.069
	$z_{\sigma t}$	0.009	0.706
	(Intercept)	(−14.717)	(−1.03E−05)***
O. fusiformis	T_S	−0.061	0.619
	S_S	−0.211	8.80E−04***
	z_S	−0.049	0.040*
	$z_{\sigma t}$	0.023	0.387
	(Intercept)	(9.279)	(0.006)**
S. alveolata	T_S	0.122	0.177
	S_S	−0.255	4.16E−07***
	z_S	−0.044	0.012*
	$z_{\sigma t}$	0.023	0.242
	(Intercept)	(7.598)	(2.35E−03)**

The regression coefficients *b* are given with their associated *P*-value for each tested factor. The intercept with its associated *P*-value is indicated in italics and in parentheses. The multiple regression was significant for all three species (*P. koreni*: $R^2 = 0.5669$, $P = 1.863 \times 10^{-8}$; *O. fusiformis*: $R^2 = 0.4486$, $P = 5.548 \times 10^{-6}$; *S. alveolata*: $R^2 = 0.696$, $P = 3.868 \times 10^{-12}$). ***, $P < 0.0001$, **, $P < 0.001$; *, $P < 0.05$.

described in May: the percentages of larval occurrence were similar and higher larval abundances were recorded in coastal and/or southern stations (Fig. 4). However, mean larval abundances were lower in June than in May, especially for *O. fusiformis* and *S. alveolata*. Other slight differences were observed for *P. koreni* and *O. fusiformis*. For *P. koreni* larvae, a more offshore larval distribution was observed at two southern transects (i.e. Etel-Quiberon and Loire), while higher densities were sampled in the Bay of Douarnenez. The distribution of *O. fusiformis* larvae was more variable between transects in June than in May, with larvae mainly sampled along the northernmost transect (Douarnenez), and the three southernmost transects. The *P. koreni* larval population was composed of older stages in June (mainly larvae of stage 3) than in May, while the larval populations of *O. fusiformis* and *S. alveolata* were composed of younger stages than in May (Fig. 5). Given the planktonic larval duration of the three target species and the temporal variation in the relative proportions of the different developmental stages, it seems unlikely that larvae sampled in June originated from the same spawning events as those sampled in May. For *O. fusiformis* and *S. alveolata*, younger larvae were collected in June, indicating that at least one spawning event occurred between the two cruises. For *P. koreni*, although older larvae were observed in June, they would have originated from a spawning event

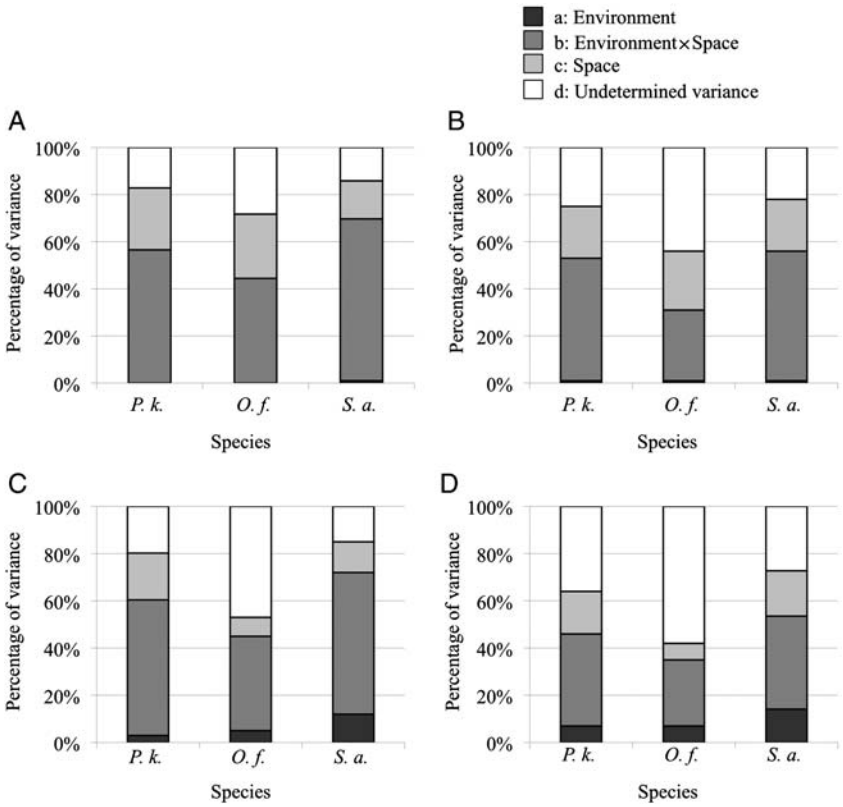

Fig. 6. Variance partitioning of (**A**) total larval abundances in May, (**B**) larval stage abundances in May, (**C**) total larval abundances in June and (**D**) larval stage abundances in June. The whole variance of the response matrix (total abundance or larval stages abundances) was partitioned into four fractions a, b, c and d attributed to the hydrological environment alone, the spatial structure of the hydrological environment, the geographical space alone and undetermined factors, respectively. Variance partitioning on total larval abundances was performed through partial multiple regressions. Variance partitioning on larval stage abundances was performed through RDA (see Methods section). P.k., *Pectinaria koreni*; O.f., *Owenia fusiformis*; S.a., *Sabellaria alveolata*.

occurring at the end of May, assuming a planktonic larval duration of about 2 weeks.

Multiple regressions indicated significant relationships between larval concentrations and the four hydrological variables selected in June (sea surface temperature, sea surface salinity, pycnocline depth and stratification index) (*P. koreni*: $R^2 = 0.6031$, $P < 10^{-3}$; *O. fusiformis*: $R^2 = 0.4513$, $P < 10^{-3}$; *S. alveolata*: $R^2 = 0.7212$, $P < 10^{-3}$) (Table III). Significant negative correlations were observed between larval abundances and surface temperature for all three species, but other significant correlations varied among species. Positive significant correlations were observed between larval abundances and stratification index for *P. koreni* and *S. alveolata*, and between larval abundances and surface salinity for *P. koreni*. Conversely, significant negative correlations were observed between larval abundances and pycnocline depth for *P. koreni* and *O. fusiformis*. However, as observed in May, variance partitioning indicated that larval horizontal distributions were mainly explained by the spatial structure of the hydrological environment, which accounted for 58% of the variability in total abundances for *P. koreni*, 40% for *O. fusiformis* and 60% for *S. alveolata* (Fig. 6C). For these species, geographical space alone explained 8–20% of the variation in the larval abundances, whereas the hydrological environment alone only explained from 3 to 12% of their variation. Unexplained variance varied from 15 to 47%.

For all three species, the RDA indicated significant relationships between larval stage abundances and hydrological variables (*P. koreni*: $R^2 = 0.4624$, $P < 10^{-3}$; *O. fusiformis*: $R^2 = 0.3507$, $P < 10^{-3}$; *S. alveolata*: $R^2 = 0.5383$, $P < 10^{-3}$). For each species, the RDA biplot diagram showed that the first canonical axis, which was the only significant axis ($P < 0.001$), was positively correlated to surface salinity, surface temperature and pycnocline depth, and negatively correlated to the stratification index as illustrated, for instance, for *P. koreni* larvae (Fig. 7B). The scores of the different larval stages were grouped together on the biplot diagram, indicating that they were all located preferentially at stations with

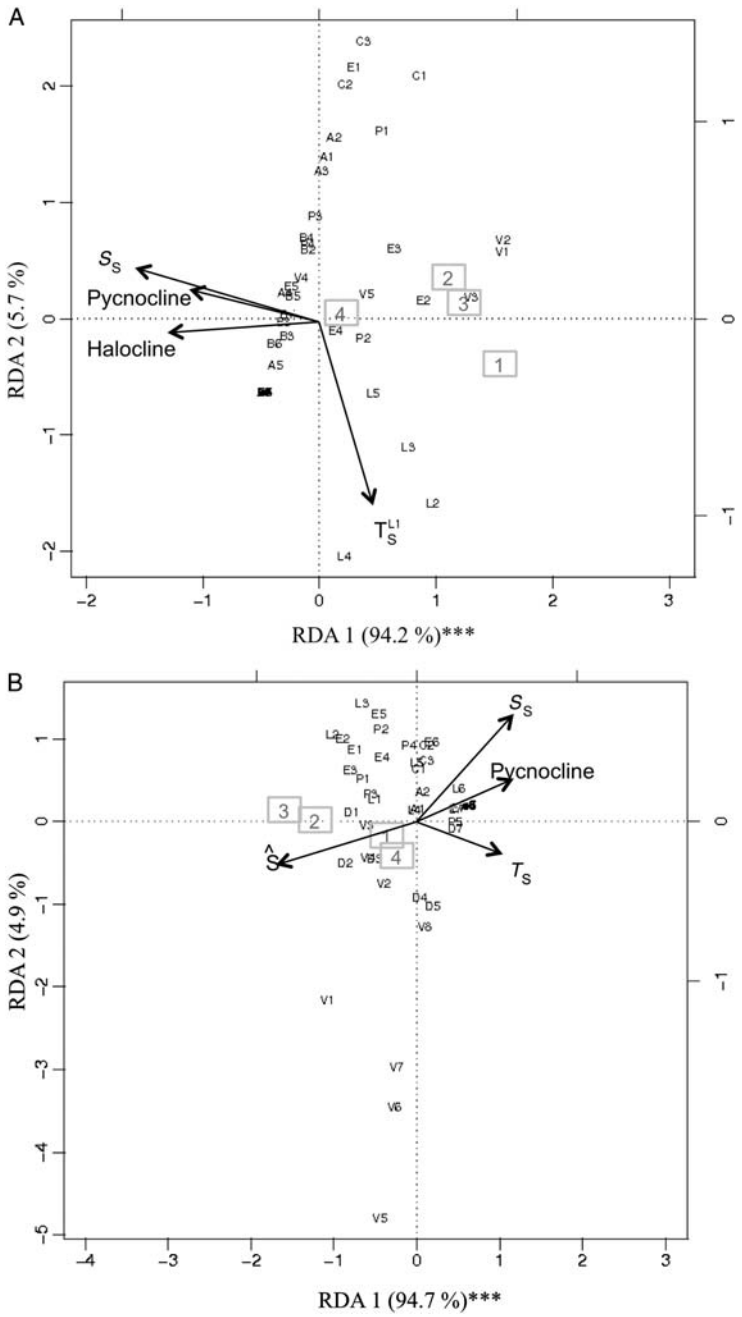

Fig. 7. RDA biplot diagrams of the abundances of the different larval stages of *P. koreni* in the northern Bay of Biscay: (**A**) in May and (**B**) June 2008. Arrows represent the plot scores of hydrological variables. Sampling sites and larval stages (indicated in grey boxes) are positioned according to their scores along the two axes RDA1 and RDA2. Asterisks indicate significant canonical axes ($P < 0.001$).

higher stratification and lower surface salinity and temperature. Variance partitioning indicated that variation in larval stage distributions was mainly due to the spatial structure of the hydrological environment which accounted for 39% of the total variation for *P. koreni*, 28% for *O. fusiformis* and 39% for *S. alveolata* (Fig. 6D). For these three species, geographical space alone explained 18, 7 and 19% of the variations in larval stage abundances, respectively. The fraction of the variance explained by the non-spatial hydrological environment reached 7, 7 and 14%, respectively, and the fraction of unexplained variance varied from 27 to 58%. Hence, the importance of the spatial structure of the hydrological environment in explaining the

Table III: Results from multiple regressions on larval abundances and hydrological variables in June 2008

Species	Tested factor	Regression coefficient b	*P*-value
P. koreni	T_S	−0.250	4.89E−3**
	S_S	0.560	3.32E−3**
	$z_{\sigma t}$	−0.047	0.034*
	$\hat{S}$	23.626	4.88E−5***
	(Intercept)	(−14.287)	(0.048)*
O. fusiformis	T_S	−0.276	1.24E−4***
	S_S	0.152	0.287
	$z_{\sigma t}$	−0.034	0.049*
	$\hat{S}$	6.618	0.116
	(Intercept)	(0.092)	(0.986)
S. alveolata	T_S	−0.150	5.93E−4***
	S_S	−0.058	0.506
	$z_{\sigma t}$	−0.012	0.261
	$\hat{S}$	8.311	2.18E−3**
	(Intercept)	(4.432)	(0.200)

The regression coefficients *b* are given with their associated *P*-value for each tested factor. The intercept with its associated *P*-value is indicated in italic and in brackets. The multiple regression was significant for all three species (*P. koreni*: $R^2 = 0.6031$, $P = 2.325 \times 10^{-9}$; *O. fusiformis*: $R^2 = 0.4513$, $P = 4.945 \times 10^{-6}$; *S. alveolata*: $R^2 = 0.7212$, $P = 4.791 \times 10^{-13}$). ***, $P < 0.0001$, **, $P < 0.001$; *, $P < 0.05$.

variations in the distribution of the different larval stages decreased in June, whereas the fraction due to the hydrological environment and the proportion of unexplained variance both increased.

Larval vertical distributions

Average vertical distributions indicated that young larvae (stages 1 and 2) of *P. koreni* and *O. fusiformis* were mainly restricted to the surface and halocline/thermocline layers (Fig. 8A and 8B), suggesting a preferential distribution within river plume waters. For these two species, ontogenic vertical migration was also observed, with a deeper distribution of the oldest larvae (stage 4). In contrast, *S. alveolata* larvae were not restricted to surface river plume waters but tended to be evenly distributed over the whole water column (Fig. 8C).

DISCUSSION

Meroplankton distribution in relation to hydrological structure

In our study, the maximal larval abundances of all three coastal polychaete species were mostly observed in river plume waters, thus confirming their important role in concentrating and transporting coastal invertebrate larvae as reported in various nearshore environments (Thiébaut, 1996; Shanks *et al.*, 2002). The spatial patterns in the horizontal larval distribution of each species were explained by the same set of spatially organized hydrological variables despite different spawning locations, planktonic larval durations and larval behaviour, highlighting the dominant role of spatially structured hydrodynamic processes over specific biological traits. Furthermore, while a spatial gradient in larval abundance according to developmental stage is expected in a homogeneous environment, with older larvae located offshore and younger larvae in the vicinity of their spawning location (i.e. close to the coast), no clear pattern of spatial distribution of the different larval development stages was observed here, suggesting that larvae of various ages are mixed within the river plume waters. River plumes and associated fronts may act as physical barriers for the dispersal of pelagic larvae, retaining them in the vicinity of their spawning location, or transporting them alongshore, thus limiting their offshore export and allowing connectivity between neighbouring populations (Thiébaut, 1996; Largier, 2003). In addition to this role in larval transport, river plume waters in the Bay of Biscay have been shown to sustain a phytoplankton biomass, predominantly composed of large phytoplankton cells, higher than in offshore waters (Morin *et al.*, 1991; Maguer *et al.*, 2009). This phytoplankton biomass may thus provide planktotrophic polychaete larvae with abundant food resources.

The importance of the river plume fronts as physical boundaries will also depend on their temporal variability with regard to planktonic larval duration. As an example, transitory wind events are likely to disrupt the plume frontal systems and induce large-scale dispersal in response to upwelling events (Thiébaut, 1996; Shanks *et al.*, 2003a). However, in areas characterized by a strong seasonal and intra-seasonal variation in hydrodynamic conditions, the timing of the spawning events in relation to the establishment of mesoscale structure is crucial for meroplankton distribution and a change in reproductive phenology would significantly alter larval transport, connectivity and metapopulation dynamics (Ayata *et al.*, 2010; Carson *et al.*, 2010). In the present study, the extent of the river plumes differed between the two sampling dates with consequences on larval distribution. Larvae were retained close to the shoreline in May due to the limited spatial extension of river plumes. Given alongshore density currents of about 10 cm s^{-1} along the southern coasts of Brittany (Lazure and Jégou, 1998), an alongshore average advective transport of larvae of about 8.64 km day^{-1} is likely. However, this rough estimate can be largely influenced by the spatial variability in alongshore currents due to the local topography and the short-term effects of wind-induced currents. Such hydrological structuring can

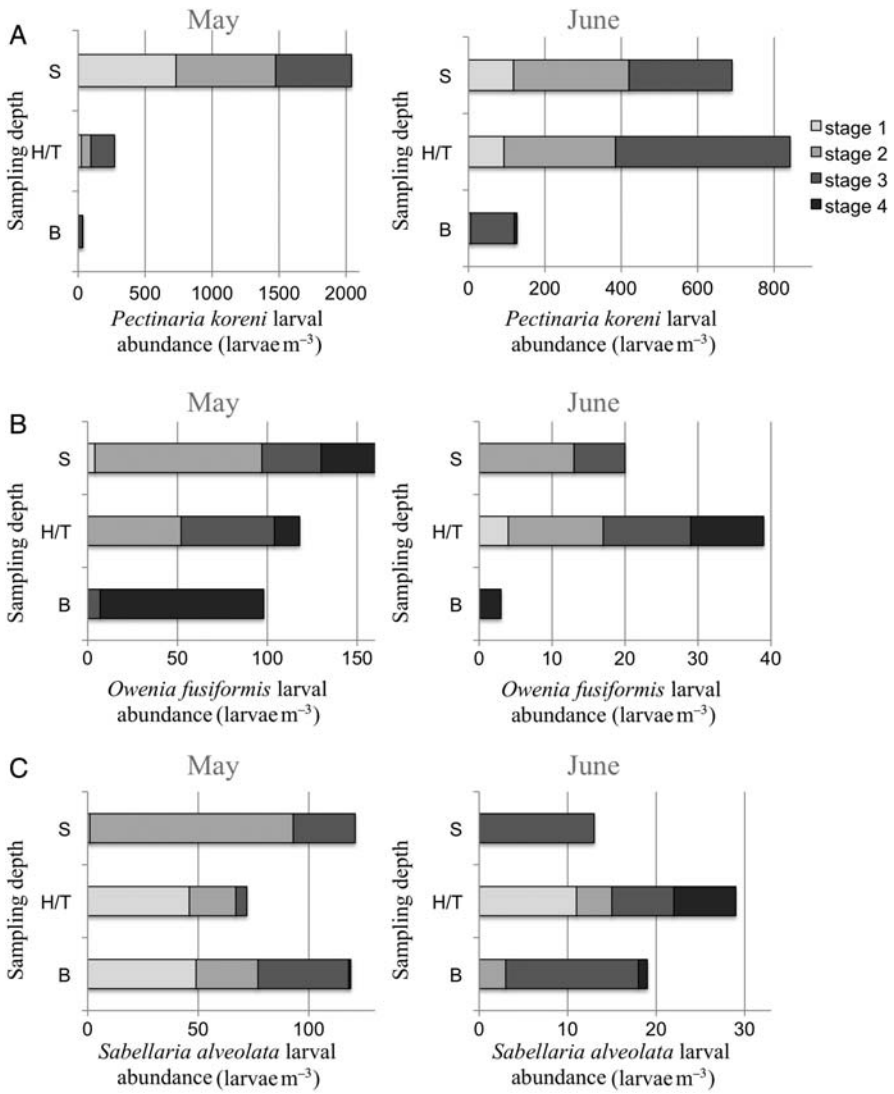

Fig. 8. Vertical distribution of the different larval stages of (**A**) *P. koreni*, (**B**) *O. fusiformis* and (**C**) *S. alveolata* in the northern Bay of Biscay. Larval abundances per sampling depth are given as larvae m^{-3}. S, surface layer; H/T, halocline and/or thermocline; B, bottom layer. The results are the means obtained for four stations (D2, C1, P2 and V2) sampled in May 2008, and for three stations (D2, P1 and V1) sampled in June 2008.

limit cross-shore export of larvae but may promote larval connectivity between neighbouring populations along the coasts of southern Brittany. Conversely, in June, strong N to NW winds recorded the week before the sampling survey could have favoured coastal upwelling and offshore export of plume waters. Although larvae remained mainly confined within plume waters, larval retention close to adult populations, and thus larval connectivity among neighbouring populations, was lower in June than in May, which may greatly affect larval settlement potential. On the other hand, variation in the hydrological environment can alter the relative role of river plumes in controlling larval distribution: the variation attributed to the interactions between hydrological environment and geographical space was lower in June than in May, for the total larval distribution of *O. fusiformis* and *S. alveolata* and larval stage distribution of all three species, compared with the temporal variation in the degree of the spatial organization of the hydrological environment. Accordingly, the fraction of unexplained variance was higher in June, i.e. when hydrological structuring was less contrasted due to the dilution of plume waters.

Previous descriptions of the mesoscale hydrodynamic features of the Bay of Biscay have highlighted the importance of short temporal variation at scales ranging from a few days to 1 week (Puillat *et al.*, 2006), which may preclude obtaining a synoptic view of the hydrological

conditions from oceanographic cruises (Planque *et al.*, 2006). However, although sampling was performed over five to nine consecutive days in the present study, satellite data indicated that at least sea surface temperatures were similar at the beginning and the end of each cruise (Supplementary data, Fig. S4A–C for the May cruise and Fig. S4D–F for the June cruise), indicating that our data provided a synoptic view of the hydrological environment for each cruise. In addition, no abrupt change in wind direction or intensity was reported during sampling, further suggesting that the spatial distribution of hydrological characteristics was not biased by short-term temporal changes. Two of the six hydrological regions previously described by Planque *et al.* (2006) in spring in the Bay of Biscay were then identified both in May and June 2008, i.e. oceanic waters and river plume waters, although their location and hydrological properties changed sharply between the two cruises with consequences for larval distribution.

The hydrological environment may influence larval distribution through two components, the hydrological environment itself and/or its spatial organization. The spatial structure of hydrological variables can lead to the overestimation of a strictly hydrological role due to high spatial autocorrelation (Legendre and Trousselier, 1988). However, the use of variance partitioning avoids this problem by isolating (i) the non-spatial component of the hydrological environment, (ii) the spatially structured component of the hydrological environment and (iii) the non-hydrological spatial component of the total variance in species distribution or community structure (Borcard *et al.*, 1992). By using this approach, our results reveal that the hydrological environment alone explains only a small portion of the total variance in larval abundances, hence refuting our first hypothesis, even though parameters such as salinity or temperature are known to directly influence larval mortality or development (Anger *et al.*, 1998; O'Connor *et al.*, 2007). In contrast, and in accordance with our second hypothesis, the interactions between hydrological environment and geographical space generally explained most of the variation in larval distribution for the three polychaete species (i.e. from 40 to 68% of the total variance). A similar result has been reported for the meroplankton distribution along the coasts of the North Sea, a region that is also characterized by the presence of a front separating coastal and offshore waters (Belgrano *et al.*, 1995).

The relative role of specific biological traits

In addition to the spatial organization of the hydrological environment, variance partitioning showed that geographical space alone contributed to a significant proportion of the variation in larval distributions for each species (from 13 to 34% of the total variance). This variance can be attributed to spatial patterns in environmental variables that were not considered here or to ecological processes (Legendre and Fortin, 1989). Key spatial parameters to consider when describing larval distributions are thus the spatially structured characteristics of the species: (i) the location and the size of adult populations that determine potential spawning locations and the amount of released larvae, (ii) the characteristics of larval release (e.g. date, intensity, synchrony at the scale of the study area), especially for species with several successive spawning events during an extended reproductive period and (iii) the location of the potential sites for settlement. Asynchronous spawning events at the scale of the study area or settlement events can blur the relationships between larval densities and local adult densities.

For *P. koreni* and *O. fusiformis*, which inhabit subtidal patches of fine sand and muddy fine sand, the locations of adult populations are not exhaustively known and are based on historical data on the distribution of benthic communities (Chassé and Glémarec, 1976). However, annual quantitative samples of benthic macrofauna have been taken since 2004 at one or two sites in the main coastal embayments along the coasts of the northern Bay of Biscay as part of the REBENT monitoring network (www.rebent.org). Although these samples provide only a very crude estimate of stock size, they indicate that densities of both species are highly variable in space at the scale of the surveyed area with large year-to-year fluctuations (Table IV). On average, adult densities of *O. fusiformis* are higher in the southern part of the study area, in the Vilaine estuary and off Quiberon, and to a lesser extent, in the Bay of Concarneau and in the Bay of Douarnenez, whereas *P. koreni* is more abundant in the Vilaine estuary and in the Bay of Douarnenez, and to a lesser extent, off Quiberon and in the Bay of Concarneau. A larval distribution more similar to the adult distribution was observed for *P. koreni*, the study species with the shortest larval planktonic duration (2 weeks), with highest densities reported either off the Vilaine estuary and Concarneau in May, or off the Vilaine estuary, Quiberon and Douarnenez in June. For *O. fusiformis* with a planktonic larval duration of four weeks, high concentrations of old larvae have been reported in the vicinity of both low-abundance and high-abundance adult populations in May, although our results cannot discriminate between locally spawned and transported larvae. In contrast, the observation in June of younger larvae in proximity to high-abundance adult

populations suggested that local spawning heavily influences larval distribution. For both species, temporal variation in larval distribution between the two surveys depended on both intra-seasonal variation in hydrodynamics and the distribution of spawning events. In the case of *S. alveolata*, the highest larval concentrations observed in the southern part of the study area with a decreasing gradient to the north may be related to the location of the major adult population within the study area in the Bay of Bourgneuf, south of the Loire estuary (Gruet and Lassus, 1983). Interestingly for this species, larval distributions are less governed by geographical space alone than *P. koreni* and *O. fusiformis*, while interactions between hydrological environment and geographical space have a greater influence, probably because the spatial distribution of adults partly overlaps the spatial structure of the hydrological environment.

Finally, despite the major role played by hydrodynamics, a large proportion of variation in larval distributions, ranging from 14 to 47% was still unexplained and varied among species. Two major processes can contribute to this unexplained portion of the variance: stochastic processes driven by the interaction between coastal circulation and organism life histories (e.g. planktonic larval duration, reproductive events) and biotic factors such as active swimming and vertical migration (Siegel *et al.*, 2008). The stochastic nature of larval dispersal results mainly from the chaotic nature of coastal circulation at the relevant larval time scales and induces patchiness in larval distribution at local spatial scales. Nevertheless, some planktonic larvae can partly regulate their vertical position, either to feed or to avoid predators, in response to environmental cues (e.g. light, tide) or simply because of ontogenic migration. For polychaete larvae, including *O. fusiformis* larvae, vertical swimming speeds of $1-2\ mm\ s^{-1}$ have been measured (Chia *et al.*, 1984; Guizien *et al.*, 2006). These swimming behaviours are thought to greatly influence the horizontal distribution and dispersal of meroplankton through interaction with stratified circulation or tidal currents (Chia *et al.*, 1984; Thiébaut *et al.*, 1992; Hsieh *et al.*, 2010) and create discrepancies between the observed distribution of larvae and the expected distributions for inert particles. For example, in a subtropical estuary, Hsieh *et al.* (2010) report distributional differences between two groups of polychaete larvae (sabellid larvae versus spionid larvae) according to their swimming ability. In contrast, if larvae behave as passive particles, their distributions would be expected to be linked to a specific water mass, as has been reported for some echinoderm and polychaete larvae in Kiel Bay (Banse, 1986) or for some mollusc and polychaete larvae in the estuarine plume of the Chesapeake Bay (Shanks *et al.*, 2002).

Table IV: Adult densities (ind m^{-2}) of P. koreni and O. fusiformis in different bays along the coasts of southern Brittany

	2004	2005	2006	2007	2008	Mean
P. koreni						
Douarnenez North	3.3	1.1	0	2.2	0	1.3
Douarnenez South	na	na	na	20	2.2	11.1
Audierne	0	0	0	0	0	0
Concarneau	1.1	7.8	11.1	1.1	2.2	4.7
Etel	1.1	2.2	1.1	0	4.4	1.8
Quiberon	11.1	3.3	3.3	0	2.2	4.0
Vilaine Estuary	13.3	25.6	12.2	4.4	4.4	12.0
Vilaine Bay 1	na	na	na	1.1	1.1	1.1
Vilaine Bay 2	na	na	na	1.1	0	0.6
O. fusiformis						
Douarnenez North	17.8	4.4	3.3	4.4	3.3	6.6
Douarnenez South	na	na	na	24.4	23.3	23.9
Audierne	1.1	0	0	0	0	0.2
Concarneau	17.8	16.7	15.6	12.2	4.4	13.3
Etel	3.3	12.2	1.1	0	0	3.3
Quiberon	214.4	61.1	64.4	75.6	78.9	98.9
Vilaine Estuary	57.8	41.1	40	2.2	1100	248.2
Vilaine Bay 1	na	na	na	1.1	3.3	2.2
Vilaine Bay 2	na	na	na	106.7	0	53.4

Within each bay, density was estimated as the average of the densities measured at three stations located a few hundred meters apart, and at each station three replicates of $0.1\ m^2$ were collected (C. Broudin and F. Gentil, Station Biologique de Roscoff, unpublished data). na, not available.

For the three study species, the analysis of vertical larval distributions revealed contrasting results that can influence their larval horizontal distribution and dispersal and generate species-specific differences. *P. koreni* and *O. fusiformis* larvae were mainly distributed above and/or at the thermocline, i.e. within river plume waters, suggesting that their transport may be predominantly determined by the displacement of plume waters by surface currents, as previously observed in the Seine river plume (eastern English Channel) (Thiébaut *et al.*, 1992). Nevertheless, the oldest larval stages of these two species were preferentially sampled in bottom layer waters in response to ontogenic vertical migrations. This deeper vertical distribution of old larvae could increase larval retention above adult populations of *P. koreni* and *O. fusiformis* in a stratified environment with strong density- or wind-induced currents, such as in estuaries (Lagadeuc, 1992; Thiébaut *et al.*, 1992). On the contrary, *S. alveolata* larvae were evenly distributed over the whole water column even though the different larval developmental stages exhibited a patchy vertical distribution. A previous study in the non-stratified macrotidal environment of the Bay of Mont-Saint-Michel (English Channel) concluded that there is no ontogenic migration for this species, but

highlighted short-term variation in relation to the tidal cycle with shallower distribution during flood tides and deeper distribution during ebb tides (Dubois *et al.*, 2007). This type of variation may promote selective tidal-stream transport and therefore inshore larval transport. Moreover, competent *S. alveolata* larvae have the ability to perceive adult chemical cues to actively select their habitat or delay their metamorphosis if suitable environment for settlement is not encountered (Pawlik, 1988).

The influence of vertical migration on larval distribution and dispersal is commonly inferred from variation in the vertical structure of currents or explicitly estimated from biophysical dispersal modelling. However, for weak-swimming larvae such as bivalve or polychaete larvae, this latter approach has given divergent results in different oceanographic environments. In the Chesapeake Bay, North *et al.* (2008) argue that larval behaviour of two oyster species has greater influence on spatial patterns of larval dispersal than temporal variation in water circulation patterns. In the western Mediterranean Sea, Guizien *et al.* (2006) highlight that vertical settling of *O. fusiformis* larvae, which results from a balance between passive settling and active swimming behaviours, is a key parameter in larval dispersal. Conversely, a recent modelling study in the northern Bay of Biscay shows that ontogenic or diel vertical migrations have only a limited impact on the general patterns of larval transport, but decrease the spatial variance of larval dispersal by reducing inter-individual variability in the larval trajectories (Ayata *et al.*, 2010). On the basis of the present study, disentangling the relative role of stochastic processes and vertical migration on the unexplained variance in larval distribution of the three target species is not possible. However, the fact that the unexplained variance in larval distribution was about twice as high for *O. fusiformis* as for *P. koreni* although both species exhibited similar vertical distributions, may suggest a predominant role of stochastic events at local scales.

CONCLUSION

Here, we described the horizontal and vertical distributions of larvae of three coastal polychaetes inhabiting patchy subtidal and intertidal environments in relation to the spatial and temporal variability in hydrological mesoscale features recorded in spring in the northern Bay of Biscay. A typological description of the water masses over the continental shelf in spring discriminated high-salinity oceanic waters from low-salinity river plume waters. The spatial distribution of the hydrological environment was responsible for most of the spatial variation observed in the larval abundances of the three species. Larvae were mainly observed within plume waters, suggesting that the river plume fronts may act as a physical barrier to offshore larval dispersal of coastal invertebrates and favour alongshore transport in the complex and highly variable environment of the northern Bay of Biscay. Cross-shore transport of larvae was mainly governed by wind-induced currents, which influence the location of the river plumes. The spatio-temporal variation in the hydrological environment is thus a key parameter in determining larval dispersal and connectivity and metapopulation dynamics. Our results also underline the role of spatially structured ecological processes, such as the distribution of benthic populations, their size and the timing of spawning or settlement events. Most of the unexplained variability in the larval distributions of each species seemed to be related to stochastic processes in the coastal circulation rather than to larval vertical migrations, although ontogenic vertical behaviours were reported for two of the three species (i.e. *P. koreni* and *O. fusiformis*).

SUPPLEMENTARY DATA

Supplementary data can be found online at http://plankt.oxfordjournals.org

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