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

3

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14

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16 *fusiformis*, *Pectinaria koreni*, *Sabellaria alveolata*, Bay of Biscay.

17

18

19 **ABSTRACT**

20 The relationship between meroplankton distribution and spatio-temporal variability of coastal  
21 mesoscale hydrological structure was investigated in the northern Bay of Biscay, North-East  
22 Atlantic. For the three coastal polychaetes studied, i.e., *Pectinaria koreni*, *Owenia fusiformis*,  
23 *Sabellaria alveolata*, the highest larval abundances were sampled in low salinity, low density and  
24 high temperature river plume waters. For two species (*P. koreni* and *O. fusiformis*), maximal  
25 abundances were observed in the surface and thermocline layers due to ontogenic migrations.

26 Variance partitioning based on multiple regression and redundancy analyses were used to assess the  
27 relative roles played by the hydrological environment alone, the geographical space alone, and their  
28 interactions, i.e. the spatial structure of the hydrological environment. These analyses demonstrate  
29 the key role played by hydrological spatial structure in the distribution of larval abundances,  
30 indicating that larvae mainly act as passive particles. The hydrological environment alone was  
31 insignificant, whereas geographical space alone explained a significant part of the variability in  
32 meroplankton distribution, probably in conjunction with ecological processes. For species whose  
33 benthic populations are spatially structured, the distribution and the size of adult populations and  
34 the timing of spawning events can significantly affect larval distribution and dispersal.

## 1 INTRODUCTION

2 For marine benthic invertebrates with a complex life cycle, pelagic larval transport is a key process  
3 in dispersal and population connectivity and plays a major role in population establishment and  
4 persistence, biodiversity conservation, spread of alien species and species distributions (Cowen and  
5 Sponaugle, 2009). Larval transport results from complex interactions of biological traits (e.g.,  
6 spawning time and location, larval behaviour, planktonic larval duration) and hydrodynamic  
7 processes, and both vary at several spatial and temporal scales (Pineda *et al.*, 2007). In coastal  
8 environments, numerous and complex mesoscale hydrodynamic features can tightly control the  
9 transport of planktonic organisms (Largier, 2003). For example, coastal invertebrate larvae may be  
10 “trapped” and transported within estuarine plumes, which act as physical barriers to offshore  
11 transport (Thiébaud, 1996; Shanks *et al.*, 2002; Shanks *et al.*, 2003a). Biological species-specific  
12 traits may also modulate the role of this type of hydrodynamic feature on larval transport. In  
13 particular, the vertical behaviour of some larvae may ensure their retention in suitable habitats, even  
14 when local hydrodynamics is expected to induce offshore transport, as in estuaries or upwelling  
15 areas (Thiébaud *et al.*, 1992; Shanks *et al.*, 2003b; Queiroga *et al.*, 2007). In addition, spawning  
16 time and location may be more important than larval behaviour in determining larval dispersal  
17 (Edwards *et al.*, 2007; Ayata *et al.*, 2010; Carson *et al.*, 2010). Sorting out which factors control  
18 larval distribution and transport thus remains a challenging issue for better understanding marine  
19 population connectivity and metapopulation dynamics (Gawarkiewicz *et al.*, 2007; Pineda *et al.*,  
20 2007). Although new technological advances (e.g. biophysical models, molecular and geochemical  
21 markers) and the integration of different disciplines has fostered recent progress in assessing larval  
22 dispersal (Levin, 2006), mesoscale surveys are still needed to explicitly evaluate the role of most  
23 physical processes on larval populations.

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

1 In this general context, we focused on the horizontal and vertical larval distributions in three  
2 target species of coastal polychaetes for which complex phylogeographic patterns have been  
3 reported in the northern Bay of Biscay: *Pectinaria koreni*, *Owenia fusiformis* and *Sabellaria*  
4 *alveolata* (Jolly *et al.*, 2006; F. Rigal and F. Viard, Station Biologique de Roscoff, unpublished  
5 data). For these species, pelagic larvae can be morphologically identified at the species level and the  
6 extended spawning seasons increase the probability of successfully sampling larvae: (1) a major  
7 spawning period in spring (April-June) and an additional spawning period in late summer-autumn  
8 for *P. koreni* (Irlinger *et al.*, 1991); (2) a main spawning period in spring (April-June) for *O.*  
9 *fusiformis* (Gentil *et al.*, 1990) and (3) year-round reproduction with two main reproductive peaks  
10 in March-April and June-July for *S. alveolata* (Gruet and Lassus, 1983; Dubois *et al.*, 2007).  
11 Although these three species share the same general broadcast spawner life history, they differ in  
12 their adult benthic habitats, planktonic larval durations and larval behaviours, and all of these  
13 biological traits are known to significantly affect larval dispersal. *P. koreni* and *O. fusiformis*  
14 inhabit patches of fine sand and muddy fine sand in shallow coastal waters at about 10-20 m depth  
15 (Chassé and Glémarec, 1976; Fig. 1) whereas *S. alveolata* is a gregarious polychaete that builds  
16 intertidal biogenic reefs. Large *S. alveolata* reefs have been described on sandflats of the Bay of  
17 Bourgneuf south of the Loire estuary (Gruet and Lassus, 1983), while small groups of individuals  
18 adhering to rocks have also been reported all along southern Brittany coasts (F. Rigal and F. Viard,  
19 Station Biologique de Roscoff, unpublished data) (Fig. 1). From *in situ* observations, mean  
20 planktonic larval durations have been estimated at about two weeks for *P. koreni* (Lagadeuc and  
21 Retière, 1993), four weeks for *O. fusiformis* (Thiébaud *et al.*, 1992), and four to ten weeks for *S.*  
22 *alveolata* (Dubois *et al.*, 2007). Moreover, these species differ in their potential larval behaviour:  
23 vertical ontogenic migrations have been reported for *P. koreni* (Lagadeuc, 1992) and *O. fusiformis*  
24 (Thiébaud *et al.*, 1992), whereas complex short-term variations in *S. alveolata* vertical distribution  
25 have been reported in relation to the tidal cycle (Dubois *et al.*, 2007). Focusing on these three target  
26 species, the aim of the present study was to assess the relative role of coastal mesoscale  
27 hydrological structure and biological processes in meroplankton distribution, as well as larval  
28 dispersal and connectivity.

29 Several statistical methods that model spatial and temporal relationships in ecological data  
30 have been recently developed to describe the distribution of zooplankton in relation to their  
31 environment (e.g., generalized linear models, generalized additive models, clustering or ordination)  
32 (e.g. Zarauz *et al.*, 2008), but these methods neglect the spatial structure of the environmental  
33 variables. However, the spatial patterns of a response variable such as larval distribution depend on  
34 (1) the hydrological environment alone (i.e. non-spatial environmental variation); (2) the  
35 geographical space alone (i.e. spatial variations not shared by the environmental variables); (3) the

1 interactions between space and environment, i.e., the spatial structure of the hydrological  
2 environment and (4) other undetermined factors such as organism behaviour (Borcard *et al.*, 1992).  
3 Hence, the spatial structure of the environment should be taken into account when describing spatial  
4 patterns of zooplankton (Belgrano *et al.*, 1995), for example by using variance partitioning, a  
5 recently developed quantitative statistical method.

6 The application of a variance partitioning method to mesoscale samples of larval horizontal  
7 distribution in two different oceanographic conditions provided the opportunity to test a set of  
8 hypotheses on the main factors affecting the meroplankton distributions and larval dispersal in the  
9 northern Bay of Biscay and to quantify their relative roles. Under our first hypothesis, larval  
10 distributions would mainly depend on the hydrological properties of the water masses (e.g. salinity,  
11 temperature, stratification of the water column) that may affect larval development and survival.  
12 According to the second hypothesis, it is assumed that larvae are advected passively by currents and  
13 trapped by mesoscale hydrodynamic structures within typical water masses. Consequently,  
14 spatially-structured hydrodynamic processes would be the major factor affecting the meroplankton  
15 distribution and similar larval distributions would be observed for the different larval stages of  
16 target species and for the different target species. Finally, under the third hypothesis, biological  
17 traits such as spawning, settlement location and swimming larval behaviour would be the major  
18 factors determining larval distributions and significant differences would be observed between the  
19 species characterised by different biological traits. To test this last hypothesis, variance partitioning  
20 was completed by an analysis of larval vertical distribution in relation to water column stratification  
21 in a few stations where larval densities were high.

22

## 23 **METHODS**

### 24 **Study area**

25 In coastal areas of the Bay of Biscay, strong freshwater inputs combined with relatively low vertical  
26 mixing cause strong haline stratification. Thermal stratification superimposes on haline  
27 stratification, not necessarily at the same depth, from spring to mid-September. Vertical temperature  
28 gradients reach a maximum of 9 to 10°C between surface and bottom layers. In the vicinity of the  
29 Loire and Vilaine estuaries (Fig. 1), the presence of low salinity surface waters in spring induces  
30 significant density gradients responsible for strong density currents over the continental shelf (2 to  
31 20 cm s<sup>-1</sup>) generally oriented northwards. The wind-induced currents are highly variable both in  
32 direction and speed at temporal scales ranging from days to seasons, and typically reach 10 to 30  
33 cm s<sup>-1</sup> in the north of the bay. During thermal stratification, W to NW winds induce local transitory  
34 upwellings in the north of the Loire estuary and result in the formation and offshore transport of  
35 lenses of low salinity surface waters about 50-80 km wide and 30 m thick (Puillat *et al.*, 2006). In

1 the north, the Bay of Biscay is connected to the English Channel at the tip of Brittany through the  
 2 Ushant Sea, a transitional area between well-mixed (English Channel) and stratified (Bay of  
 3 Biscay) waters where strong thermal fronts are caused by tidal mixing in spring and summer  
 4 (Pingree *et al.*, 1975; Morin *et al.*, 1991). Low salinity waters from the Loire and Vilaine Rivers  
 5 have been reported from March to April in the Ushant Sea and at the entrance of the English  
 6 Channel following strong river run-offs and periods of NE winds (Kelly-Gerreyn *et al.*, 2006).

7

## 8 **Sampling and laboratory procedures**

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

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

$$21 \hat{S} = (\sum_{i=1}^{i=n} \Delta\sigma_{ti} \cdot \Delta z_i) / n$$

22 where  $n$  is the number of pairs of adjacent measurements,  $\Delta\sigma_{ti}$  the difference in water density  
 23 between the  $i^{\text{th}}$  pair of measurements and  $\Delta z_i$  the depth interval between the  $i^{\text{th}}$  pair of measurements  
 24 fixed at 1 m in the present case.

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

$$29 z_x = z_b |X_m - X_b| / |X_s - X_b|$$

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

34 In addition to *in situ* data, satellite images of sea surface chlorophyll *a* concentrations during  
 35 the two cruises were obtained from CERSAT (French Centre for European Remote-Sensing

1 Satellite Processing and Archiving Facility). Wind data in spring 2008 were provided by the French  
2 Office of Meteorology (Météo France) and were recorded at two locations in the north (i.e.  
3 Penmarc'h headland) and in the centre of the study area (i.e. Belle-Ile Island) (Fig. 1). Since wind  
4 data recorded at the two semaphores were very close, indicating homogeneous wind conditions all  
5 over the study area, only data collected at Penmarc'h will be presented. Daily records of the Vilaine  
6 and Loire River flows were provided by the French Freshwater Office database.

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

13 To determine the larval vertical distribution in relation to water column stratification,  
14 zooplankton samples were also collected at fixed depths using a pumping system. A 5 cm diameter  
15 collection pipe was attached to the CTD armature and to an immersed pump. CTD records provided  
16 real-time data on the depth and the water properties from which samples were collected. Three to  
17 four depths were selected per station: the surface mixed-layer (about 3-5 m), the halocline and/or  
18 thermocline layers (about 10-15 m), and the bottom layer (about 20-40 m). With a pumping rate of  
19 300  $\text{L min}^{-1}$ , a volume of 1.5  $\text{m}^3$  of water was filtered through an 80  $\mu\text{m}$  mesh net at each sampled  
20 depth for 5 min. Samples were preserved immediately after collection in 3% buffered formalin.  
21 Owing to the time required to sort samples, larval vertical distributions were described for only a  
22 few stations with high larval abundances (i.e., higher than a few hundreds of  $\text{ind.m}^{-3}$ ) (i.e., stations  
23 D2, C1, P2, and V2 in May and stations D2, P1, and V1 in June, see Fig. 1).

24 In the laboratory, each sample was rinsed and completed to 200 mL with filtered seawater.  
25 Samples were then homogenized by vigorous random stirring and a subsample of 5 mL was  
26 pipetted. The larvae of the three target species were enumerated in 3 to 5 subsamples under a  
27 dissecting stereomicroscope, to reach a count of at least 100 larvae per sample and species  
28 (Frontier, 1972). When total zooplankton concentration was low, the sample was completed to 100  
29 mL only. Conversely, when concentration was high, the subsample volume was decreased to 3 mL.  
30 By this procedure, 3% to 20% of each sample was analysed. Larval abundances were expressed as  
31 number of larvae per  $\text{m}^3$ . For each species, the four larval developmental stages were distinguished  
32 using morphological characters (*P. koreni*: Lagadeuc and Retière, 1993; *O. fusiformis*: Wilson,  
33 1932; *S. alveolata*: Wilson, 1968; Dubois et al, 2007).

34

### 35 **Statistical analyses**

1 All statistical analyses were performed using R software, version 2.7 (R Development Core Team,  
2 2005; <http://www.r-project.org>) and the *vegan* library.

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

11 The horizontal depth-integrated larval abundances of each species were analysed using a  
12 variance partitioning method based on three partial multiple regressions (Borcard *et al.*, 1992;  
13 Legendre and Legendre, 1998). For these analyses, three vectors or matrices were used: (1) the  
14 response vector  $Y$  of the  $\log_{10}$ -transformed horizontal larval abundances; (2) the explanatory matrix  
15  $X$  of the hydrological variables and (3) the explanatory matrix  $W$  of the spatial variables. To ensure  
16 the extraction of the more complex structures, spatial variables were described as the different terms  
17 of a cubic polynomial function of the centred geographical coordinates ( $x,y$ ) of the stations such that  
18  $W = f(x,y,x^2,xy,y^2,x^3,xy^2,x^2y,y^3)$ . In the first partial multiple regression step, larval abundances were  
19 analysed as a function of the hydrological data, through a multiple regression between the response  
20 vector  $Y$  and the environmental matrix  $X$ . Since multiple regression is sensitive to colinearity among  
21 the explanatory variables, variables were selected prior to the regression to avoid redundancy  
22 between the ten hydrological variables. The matrix of Pearson's product-moment correlation  
23 coefficients was calculated between each pair of hydrological variables and only variables with a  
24 correlation coefficient lower than 0.75 were chosen for the analysis so that one variable was omitted  
25 for each pair of highly correlated variables. Hence, four hydrological variables covering the spatial  
26 variations of salinity and temperature and the vertical structure of the water column were selected in  
27 May ( $T_s, S_s, z_S, z_{st}$ ) and in June ( $T_s, S_s, z_{st}, \hat{S}$ ). In the second step, a multiple regression was  
28 performed between  $Y$  and the spatial matrix  $W$ . Finally, in the third step, a multiple regression was  
29 performed between  $Y$  and both the hydrological and spatial matrix  $XW$ . From these three successive  
30 steps, variance in total larval abundances was partitioned: the first regression provided the  
31 proportion of variance explained by the hydrological environment ( $a+b$ : hydrological environment  
32 alone and interaction between hydrological environment and geographical space), while the second  
33 regression indicated the proportion of variance explained by the geographical space ( $c+b$ :  
34 geographical space alone and interaction between hydrological environment and geographical  
35 space). The third regression provided the proportion of variance explained by the hydrological



1 environment, the geographical space, and their interaction ( $a+c+b$ ) and allows the calculation of the  
2 unexplained variance ( $d = 1-a-b-c$ ).

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

7

## 8 **RESULTS**

### 9 **Meteorological and run-offs conditions in spring 2008**

10 Wind conditions were mainly from W to NW during spring 2008, with decreasing average speed  
11 over time, from  $8.5 \text{ m}\cdot\text{s}^{-1}$  in March to  $5.6 \text{ m}\cdot\text{s}^{-1}$  in April and  $3.3 \text{ m}\cdot\text{s}^{-1}$  in May (Fig. S1A). In June,  
12 average wind speed increased slightly to  $4.8 \text{ m}\cdot\text{s}^{-1}$ . The May and June cruises occurred under low to  
13 moderate wind speeds of  $2.6$  and  $6.0 \text{ m}\cdot\text{s}^{-1}$ , respectively. After the May cruise, low winds of various  
14 directions (average speed,  $3.9 \text{ m}\cdot\text{s}^{-1}$ ) were recorded over ten days. The week before the second  
15 cruise was characterized by stronger NW winds (average speed,  $6.4 \text{ m}\cdot\text{s}^{-1}$ ), with maximal speed of 8  
16 to  $9 \text{ m}\cdot\text{s}^{-1}$ . Two peaks in Loire River run-offs were observed in March and April 2008, with run-offs  
17 exceeding  $1,800$  and  $2,500 \text{ m}^3\cdot\text{s}^{-1}$ , respectively (Fig. S1B). The May cruise occurred during a period  
18 of low river run-offs, about 3 weeks after the last flood. Just before the June cruise, a peak in the  
19 river outputs of both the Vilaine and the Loire Rivers was recorded ( $> 2,000 \text{ m}^3\cdot\text{s}^{-1}$  for the Loire).

20

### 21 **Environmental variables during the May cruise**

22 In May 2008, a large low salinity plume ( $S_S < 32$ ) was observed along the southern Brittany coasts  
23 from the Loire estuary to the entrance of the Bay of Concarneau (Fig. 2A). Surface salinities were  
24 minimal at the most inshore stations of the Loire transect ( $S_S = 26.5$  at station L1) and maximal  
25 along the two transects of Douarnenez and Audierne and at the more offshore stations of the other  
26 transects ( $S_S > 34$ ). Sea surface temperatures followed a latitudinal gradient with the lowest  
27 temperatures in the north ( $T_S < 13.5^\circ\text{C}$  at stations D8 and D7) and the highest temperatures in the  
28 south ( $T_S > 16.7^\circ\text{C}$  at stations L2 and L3) (Fig. 2B). Cross-shore thermal gradients were weak,  
29 except along the Douarnenez transect where a thermal front was observed at the entrance of the bay  
30 and along the Loire transect. The highest chlorophyll *a* concentrations were localized in river plume  
31 waters (Fig. 2C). Vertical stratification was low ( $\hat{S} < 0.1$ ), except for the coastal stations located in  
32 the river plumes (Fig. S2). Weak thermal stratification was observed along most transects. When  
33 observed, the depths of the thermocline and the halocline differed, and varied between 5 and 10 m  
34 and between 10 and 15 m, respectively. The distribution of water density was mainly governed by  
35 variation in salinity as illustrated by the similarity of the salinity and density profiles (Fig. S2B,

1 S2C).

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

9

### 10 **Horizontal larval distribution during the May cruise**

11 Inshore-offshore and latitudinal gradients were observed in larval distributions of all three species,  
12 with higher abundances ( $> 100 \text{ ind. m}^{-3}$ ) close to the shore and in the southern part of the study area  
13 (Fig. 4). *P. koreni* and *O. fusiformis* larvae were sampled along each transect, but *S. alveolata*  
14 larvae were only observed along the five southernmost transects, from the Bay of Concarneau to the  
15 Loire estuary. The *P. koreni* larval population was mainly composed of the first three larval  
16 developmental stages (Fig. 5A), which were homogeneously distributed over the study area (data  
17 not shown). In contrast, the fourth aulophore stage was only reported in a few stations. The larval  
18 population of *O. fusiformis* was largely dominated by stage-3 larvae and to a lesser extent by stage-  
19 4 larvae (Fig. 5B). While these two larval stages were evenly distributed, the two youngest stages  
20 were restricted to the more coastal stations. The *S. alveolata* larval population was also largely  
21 dominated by a single larval developmental stage: stage 2 (Fig. 5C).

22 For all three species, multiple regressions showed significant relationships between total  
23 larval abundances and the four selected hydrological variables: sea surface temperature, sea surface  
24 salinity, halocline depth and pycnocline depth (*P. koreni*:  $R^2 = 0.5669$ ,  $p < 10^{-3}$ ; *O. fusiformis*:  $R^2 =$   
25  $0.4486$ ,  $p < 10^{-3}$ ; *S. alveolata*:  $R^2 = 0.6960$ ,  $p < 10^{-3}$ ). Larval abundances were significantly  
26 negatively correlated with surface salinity and either surface temperature or halocline depth,  
27 indicating that larvae were mainly located in the river plume stations (Table II). Variance  
28 partitioning highlighted that variation in larval abundances was mainly explained by the spatial  
29 structure of the hydrological environment (56% for *P. koreni*, 44% for *O. fusiformis* and 68% for *S.*  
30 *alveolata*) (Fig. 6A). For all three species, geographical space alone accounted for 26%, 27% and  
31 16% of the variance, respectively, whereas the non-spatial hydrological environment explained less  
32 than 1% of the variance. The remaining unexplained variance ranged between 14% and 28%.

33 The RDA computed on the abundances of the different larval stages and the hydrological  
34 variables indicated that the hydrological variables significantly influenced larval stage distribution  
35 (*P. koreni*:  $R^2 = 0.5278$ ,  $p < 10^{-3}$ ; *O. fusiformis*:  $R^2 = 0.3072$ ,  $p < 10^{-3}$ ; *S. alveolata*:  $R^2 = 0.5582$ ,  $p <$

1  $10^{-3}$ ). For example, for the RDA performed on *P. koreni* larvae, only one canonical axis, which  
2 explained 94.2% of the constrained variance, was significant ( $p < 0.001$ ) and was related to the  
3 surface salinity and the pycnocline/halocline depths (Fig. 7A). The scores of the first three  
4 developmental stages on the RDA biplot diagram were grouped together, suggesting similar  
5 horizontal distributions according to the hydrological environment in the plume waters. Only the  
6 score of stage 4 differed slightly, which may be partly explained by its very low occurrence.  
7 Variance partitioning from the successive redundancy analyses showed that the spatial structure of  
8 the hydrological environment accounted for 52%, 30% and 55% of the variation in larval stage  
9 distributions for *P. koreni*, *O. fusiformis* and *S. alveolata*, respectively (Fig. 6B). Geographical  
10 space alone explained respectively 22%, 25% and 22% of the variance in stage abundances,  
11 whereas the hydrological environment alone explained less than 1% of the variance. The  
12 unexplained variance varied between 22% and 44%.

13

#### 14 **Environmental variables during the June cruise**

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

27 The cluster analysis again separated two main hydrological regions (Fig. 3C-D). The  
28 stations of the first cluster were located off the Vilaine and Loire estuaries, and were characterised  
29 by stronger vertical stratification, lower surface salinities, lower surface densities and shallower  
30 thermoclines, haloclines and pycnoclines (Table I). The second cluster, which included all the other  
31 stations, could be divided in two subclusters according to surface temperature (Fig. 3C-D, Table I).  
32 The first subcluster characterized by higher surface temperatures and deeper thermoclines was  
33 composed of most of the stations in the transects from Audierne to Etel-Quiberon. Conversely, the  
34 second subcluster, characterized by lower surface temperatures and shallower thermoclines,  
35 included all the stations of the Douarnenez transect and some inshore stations of other transects.

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## Horizontal larval distribution during the cruise of June

The general horizontal larval distributions observed in June for all three species, resembled those 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 occurring at the end of May, assuming a planktonic larval duration of about two 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, 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, negative significant 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% to 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%.

1 For all three species, the RDA indicated significant relationships between larval stage  
2 abundances and hydrological variables (*P. koreni*:  $R^2 = 0.4624$ ,  $p < 10^{-3}$ ; *O. fusiformis*:  $R^2 = 0.3507$ ,  
3  $p < 10^{-3}$ ; *S. alveolata*:  $R^2 = 0.5383$ ,  $p < 10^{-3}$ ). For each species, the RDA biplot diagram showed that  
4 the first canonical axis, which was the only significant axis ( $p < 0.001$ ), was positively correlated to  
5 surface salinity, surface temperature and pycnocline depth, and negatively correlated to the  
6 stratification index as illustrated, for instance, for *P. koreni* larvae (Fig. 7B). The scores of the  
7 different larval stages were grouped together on the biplot diagram, indicating that they were all  
8 located preferentially in stations with higher stratification and lower surface salinity and  
9 temperature. Variance partitioning indicated that variation in larval stage distributions were mainly  
10 due to the spatial structure of the hydrological environment which accounted for 39% of the total  
11 variation for *P. koreni*, 28% for *O. fusiformis* and 39% for *S. alveolata* (Fig. 6D). For these three  
12 species, geographical space alone explained 18%, 7% and 19% of the variations in larval stage  
13 abundances respectively. The fraction of the variance explained by the non-spatial hydrological  
14 environment reached 7%, 7% and 14%, respectively, and the fraction of unexplained variance  
15 varied from 27% to 58%. Hence, the importance of the spatial structure of the hydrological  
16 environment in explaining the variations in the distribution of the different larval stages decreased  
17 in June, whereas the fraction due to the hydrological environment and the proportion of unexplained  
18 variance both increased.

19

## 20 Larval vertical distributions

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

27

## 28 DISCUSSION

### 29 Meroplankton distribution in relation to hydrological structure

30 Previous descriptions of the mesoscale hydrodynamic features of the Bay of Biscay have  
31 highlighted the importance of short temporal variation at scales ranging from a few days to one  
32 week (Puillat *et al.*, 2006), which may preclude obtaining a synoptic view of the hydrological  
33 conditions from oceanographic cruises (Planque *et al.*, 2006). However, although sampling was  
34 performed over five to nine consecutive days in the present study, satellite data indicated that at  
35 least sea surface temperatures were similar at the beginning and the end of each cruise (Fig. S4A-C

1 for May cruise and Fig. S4D-F for June cruise), indicating that our data provided a synoptic view of  
2 the hydrological environment for each cruise. In addition, no abrupt change in wind direction or  
3 intensity was reported during sampling, further suggesting that the spatial distribution of  
4 hydrological characteristics was not biased by short-term temporal changes. Two of the six  
5 hydrological regions previously described by Planque *et al.* (2006) in spring in the Bay of Biscay  
6 were then identified both in May and June 2008, i.e. oceanic waters and river plume waters,  
7 although their location and hydrological properties changed sharply between the two cruises with  
8 consequences on larval distribution.

9         The hydrological environment may influence larval distribution through two components,  
10 the hydrological environment itself and/or its spatial organisation. The spatial structure of  
11 hydrological variables can lead to the overestimation of a strictly hydrological role due to high  
12 spatial autocorrelation (Legendre and Trousselier, 1988). However, the use of variance partitioning  
13 avoids this problem by isolating (1) the non-spatial component of the hydrological environment, (2)  
14 the spatially structured component of the hydrological environment, and (3) the non-hydrological  
15 spatial component of the total variance in species distribution or community structure (Borcard *et*  
16 *al.*, 1992). By using this approach, our results reveal that the hydrological environment alone  
17 explains only a small portion of the total variance in larval abundances, hence refuting our first  
18 hypothesis, even though parameters such as salinity or temperature are known to directly influence  
19 larval mortality or development (Anger *et al.*, 1998; O'Connor *et al.*, 2007). In contrast, and in  
20 accordance with our second hypothesis, the interactions between hydrological environment and  
21 geographical space generally explained most of the variation in larval distribution for the three  
22 polychaete species (i.e. from 40% to 68% of the total variance). A similar result has been reported  
23 for the meroplankton distribution along the coasts of the North Sea, a region that is also  
24 characterised by the presence of a front separating coastal and offshore waters (Belgrano *et al.*  
25 1995).

26         In our study, the maximal larval abundances of all three coastal polychaete species were  
27 mostly sampled in river plume waters, thus confirming their important role in concentrating and  
28 transporting coastal invertebrate larvae as reported in various nearshore environments (Thiébaud,  
29 1996; Shanks *et al.*, 2002). The spatial patterns in the horizontal larval distribution of each species  
30 were explained by the same set of spatially organised hydrological variables despite different  
31 spawning locations, planktonic larval durations and larval behaviour, highlighting the dominant role  
32 of spatially structured hydrodynamic processes over specific biological traits. Furthermore, while a  
33 spatial gradient in larval abundance according to developmental stage is expected in a homogeneous  
34 environment — with older larvae located offshore and younger larvae in the vicinity of their  
35 spawning location (i.e., close to the coast) — no clear pattern of spatial distribution of the different

1 larval development stages was observed here, suggesting that larvae of various ages are mixed  
2 within the river plume waters. River plumes and associated fronts may act as physical barriers for  
3 the dispersal of pelagic larvae, retaining them in the vicinity of their spawning location, or  
4 transporting them alongshore, thus limiting their offshore export and allowing connectivity between  
5 neighbouring populations (Thiébaud, 1996; Largier, 2003). In addition to this role on larval  
6 transport, river plume waters in the Bay of Biscay have been shown to sustain a phytoplankton  
7 biomass — predominantly composed of large phytoplankton cells — higher than in offshore waters  
8 (Morin *et al.*, 1991; Maguer *et al.*, 2009). This phytoplankton biomass may thus provide  
9 planktotrophic polychaete larvae with abundant food resources.

10 The importance of the river plume fronts as physical boundaries will also depend on their  
11 temporal variability with regard to planktonic larval duration. As an example, transitory wind  
12 events are likely to disrupt the plume frontal systems and induce large-scale dispersal in response to  
13 upwelling events (Thiébaud, 1996; Shanks *et al.*, 2003b). However, in areas characterized by a  
14 strong seasonal and intra-seasonal variation in hydrodynamic conditions, the timing of the spawning  
15 events in relation to the establishment of mesoscale structure is crucial for meroplankton  
16 distribution and a change in reproductive phenology would significantly alter larval transport,  
17 connectivity and metapopulation dynamics (Ayata *et al.*, 2010; Carson *et al.*, 2010). In the present  
18 study, the extent of the river plumes differed between the two sampling dates with consequences on  
19 larval distribution. Larvae were retained close to the shoreline in May due to the limited spatial  
20 extension of river plumes. Given alongshore density currents of about  $10 \text{ cm.s}^{-1}$  along the southern  
21 coasts of Brittany (Lazure and Jégou, 1998), an alongshore average advective transport of larvae of  
22 about  $8.64 \text{ km d}^{-1}$  is likely. However, this rough estimate can be largely influenced by the spatial  
23 variability in alongshore currents due to the local topography and the short-term effects of wind-  
24 induced currents. Such hydrological structuring can limit cross-shore export of larvae but may  
25 promote larval connectivity between neighbouring populations along the coasts of southern  
26 Brittany. Conversely, in June, strong N to NW winds recorded the week before the sampling survey  
27 could have favoured coastal upwelling and offshore export of plume waters. Although larvae  
28 remained mainly confined within plume waters, larval retention close to adult populations, and thus  
29 larval connectivity among neighbouring populations, were lower in June than in May, which may  
30 greatly affect larval settlement potential. On the other hand, variation in the hydrological  
31 environment can alter the relative role of river plumes in controlling larval distribution: the  
32 variation attributed to the interactions between hydrological environment and geographical space  
33 was lower in June than in May, for the total larval distribution of *O. fusiformis* and *S. alveolata* and  
34 larval stage distribution of all three species, compared to the temporal variation in the degree of the  
35 spatial organisation of the hydrological environment. Accordingly, the fraction of unexplained

1 variance was higher in June, i.e. when hydrological structuring was less contrasted due to the  
2 dilution of plume waters.

#### 4 **The relative role of specific biological traits**

5 In addition to the spatial organisation of the hydrological environment, variance partitioning  
6 showed that geographical space alone contributed to a significant proportion of the variation in  
7 larval distributions for each species (from 13% to 34% of the total variance). This variance can be  
8 attributed to spatial patterns in environmental variables that were not considered here or to  
9 ecological processes (Legendre and Fortin, 1989). Key spatial parameters to consider when  
10 describing larval distributions are thus the spatially structured characteristics of the species: (1) the  
11 location and the size of adult populations that determine potential spawning locations and the  
12 amount of released larvae, (2) the characteristics of larval release (e.g., date, intensity, synchrony at  
13 the scale of the study area), especially for species with several successive spawning events during  
14 an extended reproductive period and (3) the location of the potential sites for settlement.  
15 Asynchronous spawning events at the scale of the study area or settlement events can blur the  
16 relationships between larval densities and local adult densities.

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



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

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

32 For the three study species, the analysis of vertical larval distributions revealed contrasting  
33 results that can influence their larval horizontal distribution and dispersal and generate species-  
34 specific differences. *P. koreni* and *O. fusiformis* larvae were mainly distributed above and/or at the  
35 thermocline, i.e., within river plume waters, suggesting that their transport may be predominantly

1 determined by the displacement of plume waters by surface currents, as previously observed in the  
2 Seine river plume (eastern English Channel) (Thiébaud *et al.*, 1992). Nevertheless, the oldest larval  
3 stages of these two species were preferentially sampled in bottom layer waters in response to  
4 ontogenic vertical migrations. This deeper vertical distribution of old larvae could increase larval  
5 retention above adult populations of *P. koreni* and *O. fusiformis* in a stratified environment with  
6 strong density- or wind-induced currents, such as in estuaries (Lagadeuc, 1992; Thiébaud *et al.*,  
7 1992). On the contrary, *S. alveolata* larvae were evenly distributed over the whole water column  
8 even though the different larval developmental stages exhibited a patchy vertical distribution. A  
9 previous study in the non-stratified macrotidal environment of the Bay of Mont-Saint-Michel  
10 (English Channel) concluded that there is no ontogenic migration for this species, but highlighted  
11 short-term variation in relation to the tidal cycle with shallower distribution during flood tides and  
12 deeper distribution during ebb tides (Dubois *et al.*, 2007). This type of variation may promote  
13 selective tidal-stream transport and therefore inshore larval transport. Moreover, competent *S.*  
14 *alveolata* larvae have the ability to perceive adult chemical cues to actively select their habitat or  
15 delay their metamorphosis if suitable environment for settlement is not encountered (Pawlik, 1988).

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

33

## 34 **CONCLUSION**

35 Here, we described the horizontal and vertical distributions of larvae of three coastal polychaetes

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

18

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## 28 TABLE LEGENDS

29 Table I: Typology of water masses in the northern Bay of Biscay in May and June 2008. Mean  
30 values  $\pm$  standard deviations of the hydrological variables are indicated for the clusters identified  
31 among the sampled stations. Clusters are defined in Fig. 3.

32

33 Table II: Results from multiple regressions on larval abundances and hydrological variables in May  
34 2008. The regression coefficients *b* are given with their associated p-value for each tested factor.  
35 The intercept with its associated p-value is indicated in italics and in parentheses. The multiple

1 regression was significant for all three species (*Pectinaria koreni*:  $R^2 = 0.5669$ ,  $p = 1.863 \cdot 10^{-8}$ ;  
2 *Owenia fusiformis*:  $R^2 = 0.4486$ ,  $p = 5.548 \cdot 10^{-6}$ ; *Sabellaria alveolata*:  $R^2 = 0.696$ ,  $p = 3.868 \cdot 10^{-12}$ ).  
3 \*\*\*,  $p < 0.0001$ , \*\*,  $p < 0.001$ ; \*,  $p < 0.05$ .

4  
5 Table III: Results from multiple regressions on larval abundances and hydrological variables in  
6 June 2008. The regression coefficients  $b$  are given with their associated p-value for each tested  
7 factor. The intercept with its associated p-value is indicated in italic and in brackets. The multiple  
8 regression was significant for all three species (*Pectinaria koreni*:  $R^2 = 0.6031$ ,  $p = 2.325 \cdot 10^{-9}$ ;  
9 *Owenia fusiformis*:  $R^2 = 0.4513$ ,  $p = 4.945 \cdot 10^{-6}$ ; *Sabellaria alveolata*:  $R^2 = 0.7212$ ,  $p = 4.791 \cdot 10^{-13}$ ).  
10 \*\*\*,  $p < 0.0001$ , \*\*,  $p < 0.001$ ; \*,  $p < 0.05$ .

11  
12 Table IV: Adult densities (ind.m<sup>-2</sup>) of *Pectinaria koreni* and *Owenia fusiformis* in different bays  
13 along the coasts of southern Brittany. Within each bay, density was estimated as the average of the  
14 densities measured at three stations located a few hundred meters apart, and at each station three  
15 replicates of 0.1 m<sup>2</sup> were collected (C. Broudin and F. Gentil, Station Biologique de Roscoff,  
16 unpublished data). na: not available.

## 17 18 **FIGURE LEGENDS**

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

27  
28 Fig. 2: Surface hydrological conditions in May (A-C) and June (D-F) 2008 in the northern Bay of  
29 Biscay: horizontal distribution of sea surface values of (A) salinity in May, (B) temperature (in °C)  
30 in May, (C) chlorophyll *a* concentrations in May, (D) salinity in June, (E) temperature (in °C) in  
31 June, (F) chlorophyll *a* concentrations in June. Sampling transects (with the codes of the first and  
32 last stations) are indicated for surface salinity and temperature maps. The Vilaine (V) and the Loire  
33 (L) estuaries are indicated on the chlorophyll maps. To minimize cloud coverage, 4-day merged  
34 satellite images of surface chlorophyll *a* concentrations are presented; light-coloured coastal areas  
35 indicate higher concentrations (CERSAT data, MORIS/MODIS images). The hydrological maps



1 have been performed using ODV (<http://odv.awi.de/>) with the *jetplus* color palette proposed by S.  
2 Haddock in *L&O Bulletin* (2010 Vol. 19(2)).

3  
4 Fig. 3: Hydrological typology in the northern Bay of Biscay in May (A-B) and June (C-D) 2008:  
5 (A) Cluster analysis performed on the hydrological data and (B) spatial distribution of the three  
6 clusters according to the surface salinity distribution in May 2008, (C) cluster analysis performed  
7 on the hydrological data and (D) spatial distribution of the three clusters according to the surface  
8 salinity distribution in June 2008. For each cruise, black squares indicate the stations belonging to  
9 cluster 1, grey circles the stations of cluster 2, and white circles the stations of cluster 2'. The  
10 hydrological maps have been performed using ODV (<http://odv.awi.de/>) with the *jetplus* color  
11 palette proposed by S. Haddock in *L&O Bulletin* (2010 Vol. 19(2)).

12  
13 Fig. 4: Horizontal distribution in May (A-C) and June (D-F) 2008 of *Pectinaria koreni* (A and D),  
14 *Owenia fusiformis* (B and E), and *Sabellaria alveolata* (C and F) larvae in the northern Bay of  
15 Biscay. Percentage of occurrence, mean  $\pm$  standard deviation of larval abundances calculated over  
16 all samples (n = 54), and maximal larval abundance are indicated for each species.

17  
18 Fig. 5: Composition of the larval populations: cumulative percentage of the four main larval stages  
19 of (A) *Pectinaria koreni*, (B) *Owenia fusiformis*, and (C) *Sabellaria alveolata* in May and June  
20 2008 in the northern Bay of Biscay.

21  
22 Fig. 6: Variance partitioning of (A) total larval abundances in May, (B) larval stage abundances in  
23 May, (C) total larval abundances in June, and (D) larval stage abundances in June. The whole  
24 variance of the response matrix (total abundance or larval stages abundances) was partitioned into  
25 four fractions *a*, *b*, *c*, and *d* attributed to the hydrological environment alone, the spatial structure of  
26 the hydrological environment, the geographical space alone, and undetermined factors, respectively.  
27 Variance partitioning on total larval abundances was performed through partial multiple  
28 regressions. Variance partitioning on larval stage abundances was performed through redundancy  
29 analyses (see Materials and Methods section). P.k.; *Pectinaria koreni*; O.f.: *Owenia fusiformis*; S.a.:  
30 *Sabellaria alveolata*.

31  
32 Fig. 7: RDA biplot diagrams of the abundances of the different larval stages of *Pectinaria koreni* in  
33 the northern Bay of Biscay: (A) in May and (B) June 2008. Arrows represent the plot scores of  
34 hydrological variables. Sampling sites and larval stages (indicated in grey boxes) are positioned  
35 according to their scores along the two axes RDA1 and RDA2. Asterisks indicate significant

1 canonical axes ( $p < 0.001$ ).

2

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

8

### 9 **SUPPLEMENTARY FIGURE LEGENDS**

10 Fig. S1: Hydroclimatic conditions in spring 2008 in the northern Bay of Biscay. (A) Wind  
11 conditions at Penmarc'h headland (Météo France data). Daily-averaged zonal (solid line) and  
12 meridional (dashed line) wind components are calculated from hourly raw data. Positive zonal and  
13 meridional components indicate SW winds. (B) Daily run-offs of the two main rivers of the  
14 northern Bay of Biscay from January to September 2008: Vilaine (dashed line) and Loire (solid  
15 line). Black arrows indicate the dates of the May and June cruises.

16

17 Fig. S2: Vertical hydrological structures along the transects of Douarnenez, Pouldu-Lorient, and  
18 Vilaine in May 2008: (A) temperature, (B) salinity and (C) density profiles. Note that the colour  
19 scales differ from those in Fig. 2.

20

21 Fig. S3: Vertical hydrological structures along the transects of Douarnenez, Pouldu-Lorient, and  
22 Vilaine in June 2008: (A) temperature, (B) salinity and (C) density profiles. Note that the colour  
23 scales differ from those in Fig. 2.

24

25 Fig. S4: Satellite images of the sea surface temperatures in the Bay of Biscay recorded by the  
26 NOAA-17 satellite during the two sampling cruises: (A) May 11 20:00 UTC, (B) May 14 20:00  
27 UTC, (C) May 18 20:00 UTC, (D) June 09 20:00 UTC, (E) June 11 20:00 UTC, (F) June 18 20:00  
28 UTC. Data provided by IFREMER.

29

1 **TABLE**

2

3 **Table I**

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

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1 **Table II**

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

2

1 **Table III**

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

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1 **Table IV**

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	<i>Pectinaria koreni</i>					Mean
	2004	2005	2006	2007	2008	
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

	<i>Owenia fusiformis</i>					Mean
	2004	2005	2006	2007	2008	
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

3

4