Influence of intermittent-upwelling on *Mytilus galloprovincialis* settlement patterns in the Ría de Ares-Betanzos

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ABSTRACT: Coastal upwelling systems can directly or indirectly affect the population dynamics of marine invertebrates due to their influence on residual circulation patterns and biological production cycles. In the present study we evaluated the influence of shelf winds and continental runoff on settlement patterns of *Mytilus galloprovincialis* at 2 contrasting locations in an embayment (Ría de Ares-Betanzos) located at the northern boundary of the Iberian–Canary current upwelling system. We quantified settlement at 2 depths (1 and 6 m) every 15 d for a period of 2 yr at an outer location (Miranda) with direct oceanic influence and at an estuarine dominated site in the inner ría (Arnela). We explored the instantaneous and delayed (15 and 30 d) effects of the forcing variables to infer their influence at different times in larval development. The results showed a coupling between mussel settlement and the upwelling favourable season. Wind stress and Ekman transport along the main axis of the ría affected mussel settlement patterns significantly. Instantaneous and delayed responses showed the relevance of shelf winds at different larval developmental stages. Inverse patterns were observed between the inner and outer location in response to instantaneous winds. Onshore transport caused a decrease in settlement at Miranda, while only intense offshore transport showed a detrimental effect on settlement at Arnela. With regard to the 15 d delayed effect, maximum settlement abundances matched at both locations with transport values around zero. The 30 d delayed effect on settlement abundance showed a positive linear relationship with wind stress and Ekman transport at both locations. These relationships might be directly related to physical transport processes or indirectly associated with food availability and larval survival.

KEY WORDS: Coastal upwelling · Mussel · Settlement · Galician rías · NW Spain

INTRODUCTION

The life cycle of many benthic marine invertebrates, such as *Mytilus galloprovincialis*, involve a pelagic larval stage, which in some cases can last over a month (Levin & Bridges 1995, Cáceres-Martínez & Figueras 1998a, Grantham et al. 2003). During this period, multiple physical and biological processes determine the balance between mortality, dispersal and retention within parental habitats

(Eckman 1996, Pineda et al. 2009). Settlement plays a strong role in the population dynamics of complex life cycle marine invertebrates as the process linking larval and benthic stages (Connell 1985, Menge 1992).

Survival during larval development and large-scale offshore oceanographic processes are usually considered main factors determining settlement abundance (Pineda et al. 2009). Thus, coastal upwelling systems have been studied recurrently

because of their high productivity and the physical mechanisms involved in along- and cross-shore transport (Roughgarden et al. 1988, Wing et al. 1995, Shanks et al. 2000, Guisande et al. 2001, Queiroga et al. 2007, Broitman et al. 2008, Otero et al. 2008, Morgan et al. 2009a).

In eastern-boundary upwelling systems, equatorward winds transport shelf surface waters to the adjacent ocean and promote the uplifting of the cold and nutrient-rich ocean waters from 150 to 200 m depth to the surface, fertilizing coastal waters and enhancing phytoplankton growth. When equatorward winds relax or rotate to poleward, circulation patterns reverse producing downwelling along the coast and warm, nutrient-poor surface ocean waters occupy the shelf (Wooster et al. 1976).

Due to limited larval swimming capacity (≤ 0.1 cm s^{-1} for bivalves; Chia et al. 1984, Young 1995), upwelling systems have traditionally been considered as dispersive ecosystems, where larvae are passively transported in the surface layer: offshore during upwelling events, and onshore during downwelling episodes (Roughgarden et al. 1988, Farrell et al. 1991). Larval retention in these regions is frequently associated with local areas where coastal and bottom topography interact with upwelling/downwelling transport events, favouring larval accumulation (Graham & Largier 1997, McCulloch & Shanks 2003, Mace & Morgan 2006). However, upwelling areas have been suggested as retentive environments for some species (Poulin et al. 2002, Shanks & Shearman 2009). Recent studies show that dispersion models assuming simple advection of larvae as inert particles overestimate larval exchange among locations (Cowen et al. 2000, Becker et al. 2007). Vertical migrations between layers flowing in opposite directions have been reported as a mechanism that enables larvae to regulate along- and cross-shore displacements (Poulin et al. 2002, Queiroga & Blanton 2004, Shanks & Brink 2005, Marta-Almeida et al. 2006). These mechanisms allow the maintenance of larvae close to parental habitats (Sponaugle et al. 2002) even in strong upwelling regions (Morgan et al. 2009b) and along the open coast (Shanks & Shearman 2009, Morgan & Fisher 2010).

The study of spatial and temporal settlement patterns is a widely accepted indirect method for inferring pre-settlement processes (Wing et al. 1995, Ladah et al. 2005, Narváez et al. 2006, Pfaff et al. 2011) despite some limitations due to differences in the temporal span of both processes (Pineda et al. 2010, Pan et al. 2011). Combined studies of settlement

patterns and local oceanography are essential to infer larval dispersal patterns and potential connectivity pathways between populations (Dudas et al. 2009a). This information will help us to understand the population dynamics that would be the basis for the establishment of coastal marine reserves (Grantham et al. 2003, Mace & Morgan 2006) and, more generally, for the development of strategies for ecosystem-based management (Leslie & McLeod 2007). These strategies are especially important for the management of highly exploited species, such as the blue mussel in Galicia, which totals 40% of the European and 15% of the World production (Labarta 2004).

Galicia is located at the northern boundary of the Iberian–Canary current upwelling system, where upwelling-favourable northerly winds blow predominantly from March to September (Wooster et al. 1976, Arístegui et al. 2009). The upwelling season is characterized by intermittent northerly winds that relax or even reverse to southerly with frequencies from 10 to 20 d (Álvarez-Salgado et al. 1993). Coastal upwelling and downwelling episodes dictate the residual circulation patterns as well as the primary and secondary production cycles of the large coastal embayments located on the Galician coast, collectively known as 'rías' (Álvarez-Salgado et al. 2000, Figueiras et al. 2002). The typical residual circulation pattern of the rías is characterized by an outgoing surface current enriched in river water and a compensating ingoing bottom current enriched in shelf waters. This circulation pattern intensifies when northerly winds prevail and weakens when northerly winds relax, and can even reverse to an ingoing surface and an outgoing bottom current when southerly winds are predominant (Álvarez-Salgado et al. 2000). The wind-induced circulation of the rías can potentially determine larval dispersal patterns as a result of physical transport (Queiroga et al. 2007) or affect settlement abundance indirectly due to its influence on primary production and food availability during larval development (Otero et al. 2008).

The objective of the present study was to determine whether the settlement patterns of *Mytilus galloprovincialis* are influenced by shelf winds and continental runoff in different ways at 2 locations with different hydrographic characteristics in the Ría de Ares-Betanzos. We evaluated settlement every 15 d for a period of 2 yr at an outer location (Miranda) with direct oceanic influence and at an estuarine dominated site (Arnela) in the inner ría. Preferential settlement depth was evaluated to infer larval vertical distribution according to transport mechanisms. In addition, we investigated delayed effects (15 and 30 d

before settlement substrate deployment) of the forcing variables on settlement, to infer the relevance of these variables at different times of the planktonic life.

MATERIALS AND METHODS

Study area

The Ría de Ares–Betanzos is a complex embayment, formed by the estuaries of the Eume and Mandeo Rivers, which converge in an outer area with direct oceanic influence (Fig. 1). The surface area of the ría is 52 km^2 and its total volume is 0.65 km^3 (Álvarez-Salgado et al. 2011). The ría is characterized by a mesotidal and a semidiurnal tide (Sánchez-Mata et al. 1999). Commercial mussel production is intensive in this ría (~10 000 t yr^{-1}; Labarta 2004), but mussel cultivation farms are concentrated on the southern side of the ría (Arnela and Lorbé with 40 and 107 rafts respectively).

Between March 2006 and December 2007, larval settlement was monitored in the inner (Arnela) and outer (Miranda) Ría de Ares-Betanzos (Fig. 1). The sampling site at Arnela is located in the Mandeo River estuary area between the 5 and 10 m isobaths, while the sampling site at Miranda is located between the 20 and 25 m isobaths, in the area considered an extension of the continental shelf (Fig. 1).

Larval settlement

Settlement was monitored at each location at 1 and 6 m depths using 3 collecting ropes covered with jute. Prior to their deployment in the field, collecting ropes were kept for 30 d in seawater filtered through a 100 µm mesh, renewing the water every 2 d to allow for the development of an adequate biofilm but preventing the occurrence of larval settlement (Porri et al. 2006). Conditioned ropes were suspended from a long-line where they remained for 15 d until they were sampled and replaced by new collecting ropes. Sampling consisted of the collection of 3 sub-samples of known area (6 × 2 cm) from the jute covering each collecting rope (3 replicates) at both depths (1 and 6 m). Samples were preserved in 70 % ethanol until their processing in the laboratory. Sample processing consisted of the detachment of settled individuals using a 20 % bleach dilution (Davies 1974), and an ultrasound bath for 5 min. Detached individuals were then sorted using a sieve kit with mesh openings between 125 and 355 µm, in order to facilitate their counting on a binocular microscope. The average size of individuals retained was calculated by measuring the length of the ante-posterior axis of 100 to 150 individuals for each replicate and sieve size. Individuals retained above 355 µm sieve size showed a great variability in length, which prevented distinction between primary and secondary settlement (Cáceres-Martínez & Figueras 1998a). Therefore settlement magnitude (S) was calculated as the number of settlers on a <355 µm sieve per collector (ind. col.$^{-1}$).

Settlement synchrony among locations and depths was assessed through cross-correlation ($\rho_{xy}(j)$). Given the autocorrelation structure of the time series, the significance of cross-
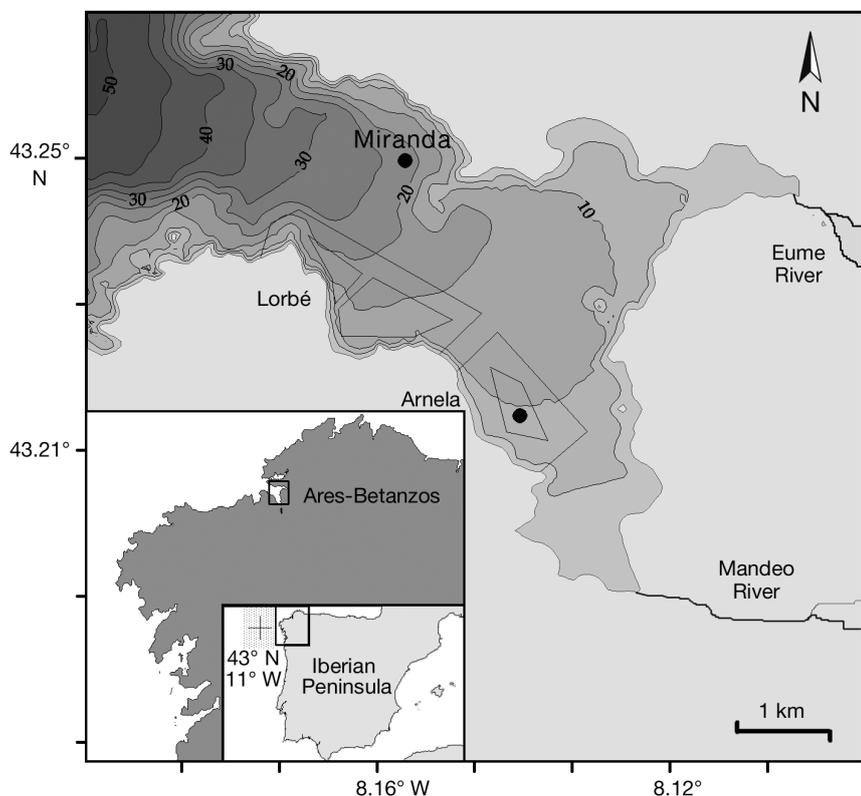

Fig. 1. The Ría de Ares-Betanzos. (●) = sampling stations at Arnela and Miranda; polygons = commercial mussel culture areas at Arnela and Lorbé. The shaded area in the smallest inset is the 2° × 2° cell where the geostrophic winds where calculated. Contour lines: depth (m). Modified from Álvarez-Salgado et al. (2011)

correlations was assessed based on 95% CI calculated for the 'effective' df (N^*; Pyper & Peterman 1998), estimated through the equation:

$$\frac{1}{N^*} = \frac{1}{N} + \frac{2}{N}\sum_{j=1}^{\infty}\frac{(N-j)}{N}\rho_{xx}(j)\cdot\rho_{yy}(j) \qquad (1)$$

where N is size of the time series and $\rho_{xx}(j)$, $\rho_{yy}(j)$ are autocorrelation coefficients of settlement in locations x and y for a delay j.

Cumulative settlement per year was calculated as the sum of the annual counts per replicate (collector rope) to estimate average and standard deviation (SD) at each location and depth. A factorial repeated measures ANOVA was performed to assess the effect of the factors location (Arnela and Miranda), depth (1 and 6 m) and year (2006 and 2007) on the accumulated settlement. Fisher's LSD test was used as a post-hoc test.

Environmental variables

Continental runoff to the Ría de Ares–Betanzos is mostly a combination of the discharges of rivers Eume and Mandeo (Fig. 1). The flow at the mouth of the Mandeo River (with a total drainage basin of 456.97 km^2) was estimated from the volume at the nearby gauge station of Irixoa (that controls 248.21 km^2 of the drainage basin) provided by Augas de Galicia (Galician Government), by applying Horton's proportional law (Strahler 1963). The volume of the Eume River is a combination of regulated and natural flows. Daily volumes of the Eume reservoir, which regulates 376.20 km^2 (80% of the drainage basin), were provided by ENDESA S.A., the company in charge of its management. The natural component of the Eume River flow was estimated from the flow of the Mandeo River by again applying Horton's Law, considering that the drainage basin not regulated by the reservoir is only 94.04 km^2. Daily continental runoff to the Ría de Ares-Betanzos (Q_R; m^3 s^{-1}) was calculated as the sum of the Eume and Mandeo flows.

Wind stress (τ_x, τ_y) and Ekman transport ($-Q_x$, Q_y) due to regional shelf winds were roughly estimated from wind speed and direction according to the methodology described by Bakun (1973) adapted for the Iberian Peninsula by Lavín et al. (1991):

$$\tau_x = \rho_A \cdot C_D \cdot |V| \cdot V_x \qquad \tau_y = \rho_A \cdot C_D \cdot |V| \cdot V_y \qquad (2, 3)$$

$$-Q_x = -\frac{\tau_y}{\rho_W \cdot f} \qquad Q_y = \frac{\tau_x}{\rho_W \cdot f} \qquad (4, 5)$$

where ρ_A is air density (1.22 kg m^{-3} at 15°C), C_D is an empirical dimensionless drag coefficient (1.4×10^{-3}),

f is the Coriolis parameter (9.946×10^{-5} s^{-1} at 43° latitude), ρ_W is sea water density (~1025 kg m^{-3}), $|V|$, V_x and V_y are the average daily modules, westerly and southerly components of the geostrophic wind in a $2° \times 2°$ cell centred at 43°N, 11°W, representative of the study area. Average daily winds were estimated from atmospheric surface pressure charts, provided at 6 h intervals by the Spanish Institute of Meteorology.

τ_x, τ_y were rotated 30° clockwise to produce longitudinal (τ_L) and transversal (τ_T) components of the wind stress to the main axis of the Ría de Ares–Betanzos (Fig. 1). Longitudinal ($-Q_L$) and transversal (Q_T) components of the Ekman transport were also obtained from τ_T and τ_L, respectively. Positive values of $-Q_L$ indicate an offshore Ekman transport and negative values an onshore Ekman transport, while positive and negative values of Q_T indicate displacement of the surface layer towards NE and SW respectively. Given that $-Q_L$ is proportional to τ_T and Q_T is proportional to τ_L, only $-Q_L$ and Q_T will be used as explanatory variables. Therefore, $-Q_L$ will be a proxy to both the effect of a transversal wind stress and a longitudinal Ekman transport and Q_T a proxy to the effect of a longitudinal wind stress and a transversal Ekman transport.

Daily values of Q_R, $-Q_L$ and Q_T were condensed to 15 d averages to match settlement sampling frequency (15 d). Seasonal patterns in these environmental variables were analyzed by means of general additive models (GAMs), as implemented in the mgcv library of R (R Development Core Team 2010).

GAMs allow the exploration of non-linear functional relationships between dependent and explanatory variables, fitting predictor variables by smooth functions (Guisan et al. 2002). The general model form of a GAM is:

$$E(Y) = \alpha + \sum_{j=1}^{p} f_j(X_j) + \varepsilon \qquad (6)$$

where $E(Y)$ is the estimated value of the response variable, α is the population intercept, X_j are the covariates and f_j are the smooth unknown functions estimated for each covariate (Wood 2006).

To test the influence of the environmental variables (Q_R, $-Q_L$ and Q_T), seasonal cycles (day of the year) and depth on settlement GAMs were built. Depth was included as a factor (1 and 6 m). Continuous variables were considered as smoothed terms in the model and estimated with thin plate regression splines. Settlement data were characterized by many zero-valued observations and a long right tail. Zero-inflated data is a common feature in species abundance studies, which prevents the use of com-
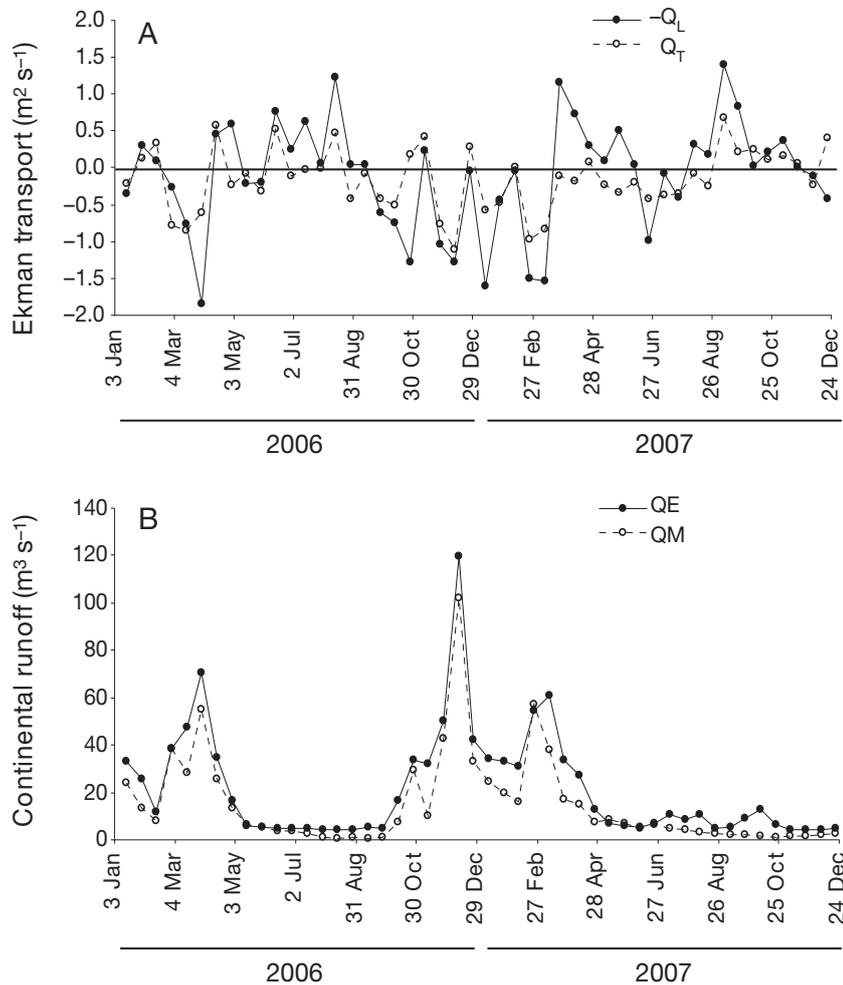
Fig. 2. Time series of (A) Ekman transport longitudinal ($-Q_L$) and transversal (Q_T) to the main axis of the ría and (B) continental runoff of rivers Eume (QE) and Mandeo (QM) during years 2006 and 2007 in the Ría de Ares-Betanzos

The model selection protocol was repeated using explicative variables lagged by 1 and 2 sampling intervals, in order to investigate delayed effects of the forcing variables on settlement. The instantaneous response (lag 0) and time-lagged response (lag 1 and 2 sampling intervals) models were compared by percentage of variability explained and their BICs, to select the most explicative effects on settlement magnitude.

RESULTS

Environmental parameters

Fig. 2A shows the time series of the fortnightly-averaged Ekman transport longitudinal and transversal to the main axis of the ría ($-Q_L$ and Q_T). Seasonality explained 15.3% of the total variance of $-Q_L$, defining an upwelling-favourable season ($-Q_L > 0$) between day of the year 100 and 300 (April 9th and October 26th), and a downwelling-favourable season ($-Q_L < 0$) for the rest of the year (Fig. 3A). There were no significant differences (Student's t-test, p = 0.109) between the average (± SD) $-Q_L$ values for the upwelling seasons of 2006 (0.07 ± 1.09 $m^2 s^{-1}$) and 2007 (0.20 ± 0.94 $m^2 s^{-1}$). In addition, the coefficient of variation of $-Q_L$ (Fig. 2A) was larger for the upwelling season of 2006 (1600%) than for 2007 (480%). The parallel time course of the fortnight-average longitudinal and transversal components of the Ekman transport (Fig. 2A) does not allow differentiation between the effect of the longitudinal wind stress (proportional to Q_T) and the longitudinal Ekman transport ($-Q_L$) on the residual circulation of the ría.

River discharge showed a marked seasonal pattern that explained 38.0% of total variance (Figs. 2B & 3B). The pattern of Q_R was opposite to that of $-Q_L$, showing minimum values during the upwelling-favourable season (Fig. 3). Continental runoff was significantly higher (Student's t-test, p < 0.005) and more variable in 2006 (average ± SD = 15.81 ± 20.15 $m^3 s^{-1}$) than in 2007 (12.59 ± 5.98 $m^3 s^{-1}$).

mon assumptions on data distribution for modelling (Barry & Welsh 2002). Therefore, data were modelled in 2 steps; first the association between the presence and absence of settlement and the available covariates was modelled and second the relationship between abundance and the covariates, conditionally on the presence of the organism, was modelled (Barry & Welsh 2002). The presence-absence data were modelled using a binomial distribution with a logit-link. Over-dispersion on settlement abundance data was accounted for using a negative binomial distribution with a log-link function. Bayesian's information criterion (BIC) was used to select the optimal set of variables for inclusion in the models. Model validation included the verification of homogeneity, normality and independence assumptions (Zuur et al. 2009).
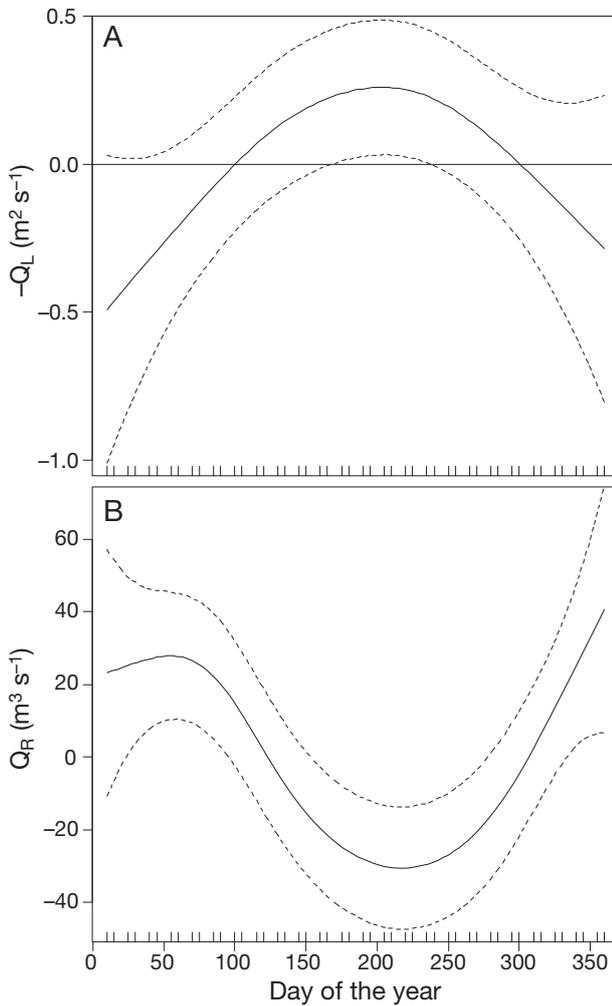
Fig. 3. Seasonal patterns of environmental variables. Results of general additive models showing the effect of variable 'Day of year' on (A) longitudinal component of Ekman transport (−Q_L) and (B) continental runoff (Q_R). Dashed lines show 95% CI, and tick marks along the x-axis below each curve represent effect values where observations occurred
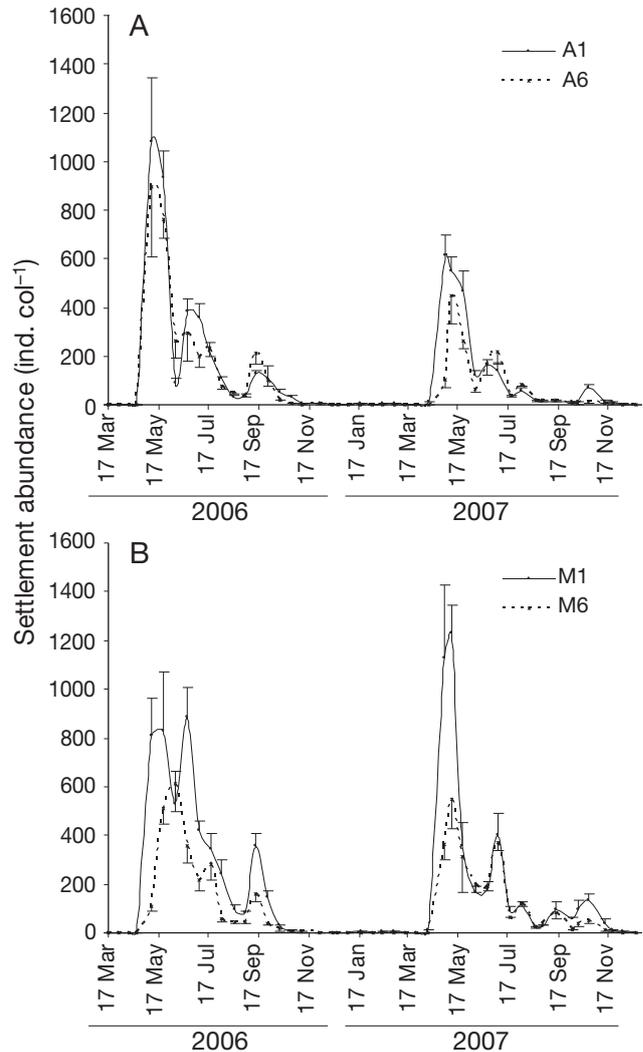

Fig. 4. *Mytilus galloprovincialis*. Average settlement abundance (ind. collector⁻¹) and SD in locations (A) Arnela at 1 and 6 m depth (A1 and A6) and (B) Miranda at 1 and 6 m depth (M1 and M6) during 2006 and 2007

Settlement patterns

Settlement abundance showed a similar seasonal pattern in 2006 and 2007, characterized by an initial major peak followed by 2 to 4 peaks of smaller amplitude during the upwelling-favourable season and absence or residual settlement during the rest of the year (Fig. 4). The regression model for settlement presence–absence supported the strong seasonal component of settlement (Table 1, Fig. 5). Seasonality explained 64.1% of the total deviance. Only the inclusion of the factor depth, which showed a settlement probability reduction of 0.18 at 6 m, improved the fit (67% of deviance explained).

Maximum cross-correlation coefficients between locations showed settlement synchrony (r ≥ 0.77 for lag 0; Table 2) except in the case of Miranda at 6 m depth, which showed higher correlations at lag −1, indicating some delay in settlement (Table 2).

The repeated measures ANOVA showed significantly higher settlement abundances in the outermost location, Miranda (Tables 3 & 4). Differences in settlement magnitude between years were detected only at Arnela, with a significant decrease in settlement during 2007 (Tables 3 & 4). Both locations showed higher settlement at 1 m depth, but the significant interaction between depth and location revealed greater differences

Table 1. *Mytilus galloprovincialis*. Structure of the model selected to describe settlement presence–absence. The inverse of the logit function has been applied to get the estimated values and SE on the scale of actual probability. edf: estimated degrees of freedom

Parametric coefficients				
Parameter	Estimate	SE	Z	p
Depth: 6m	−0.184	0.066	−3.803	0.0001
Smooth terms (non-parametric)				
Parameter	edf	χ^2	p	
Date	1.975	101.9	$<2 \times 10^{-16}$	
R^2 adjusted: 0.661		% Deviance explained: 67.0%		
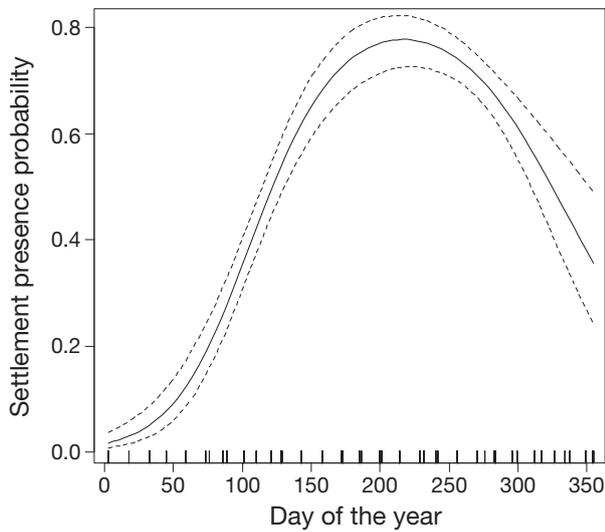
Fig. 5. *Mytilus galloprovincialis*. Results of the generalized additive models showing the partial effect of the variable 'day of the year' on settlement presence probability. Dashed lines show 95% CI, and tick marks along the *x*-axis below the curve represent effect values where observations occurred

Table 2. *Mytilus galloprovincialis*. Cross-correlation coefficients showing settlement synchrony and delays between locations and depths of study (Arnela and Miranda at 1 and 6 m depth; A1, A6, M1 and M6, respectively). Only the significant correlation coefficients are detailed. The specific lag for each coefficient is given in brackets

	A1	A6	M1
A6	0.59 (lag −1) 0.93 (lag 0)		
M1	0.54 (lag −1) 0.85 (lag 0) 0.51 (lag +1)	0.77 (lag 0) 0.53 (lag +1)	
M6	0.56 (lag −2) 0.81 (lag −1) 0.64 (lag 0)	0.53 (lag −2) 0.74 (lag −1) 0.67 (lag 0)	0.76 (lag −1) 0.85 (lag 0) 0.51 (lag +1)

Table 3. *Mytilus galloprovincialis*. Accumulated settlement (average ± SD) (ind. collector⁻¹) through 2006 and 2007 in each study location and depth

Site	Depth (m)	2006	2007
Arnela	1	3582.0 ± 303.7	2365.7 ± 133.2
	6	3154.3 ± 375.5	1478.7 ± 175.6
Miranda	1	4784.7 ± 339.9	4182.0 ± 380.1
	6	2594.0 ± 116.9	2309.3 ± 250.4

Table 4. *Mytilus galloprovincialis*. Repeated measures ANOVA assessing the effect of factors Location (Loc; Arnela and Miranda), Depth (1 and 6 m) and Year (2006 and 2007) on accumulated settlement magnitude (ind. collector⁻¹)

Model		Accumulated settlement		
	df	SS	F	p
Loc	1	4 057 393	70.39	<0.001
Depth	1	10 846 081	252.77	<0.001
Year	1	4 627 060	47.59	<0.01
Loc × Depth	1	2 833 188	66.03	<0.01
Loc × Year	1	1 934 608	19.90	<0.05
Year × Depth	1	5 891	0.053	0.829
Loc × Year × Depth	1	408 726	3.671	0.128

in settlement density between depths at Miranda (Tables 3 & 4).

Regression models for settlement abundance were performed for each sampling site because of the interactions detected by the ANOVA analysis (Table 4). They showed a strong seasonal pattern in settlement abundances in both locations (77.7% and 76.4% of the total variability explained at Arnela and Miranda, respectively; Table 5). The inclusion of the factor depth in the model decreased BIC values and increased the variance explained at both study areas, but again a greater increase in the amount of variance explained was observed at Miranda (Tables 5 & 6). None of the

models revealed a significant relationship between continental runoff and settlement density using instantaneous (lag 0) or lagged responses (lag 1 and 2 sampling periods). The longitudinal and transversal components of the Ekman transport to the main axis of the ría both showed a significant effect on settlement abundances for instantaneous and lagged responses, similar percentages of variance explained, BIC values (Table 5) and analogous partial effects on settlement abundance. As
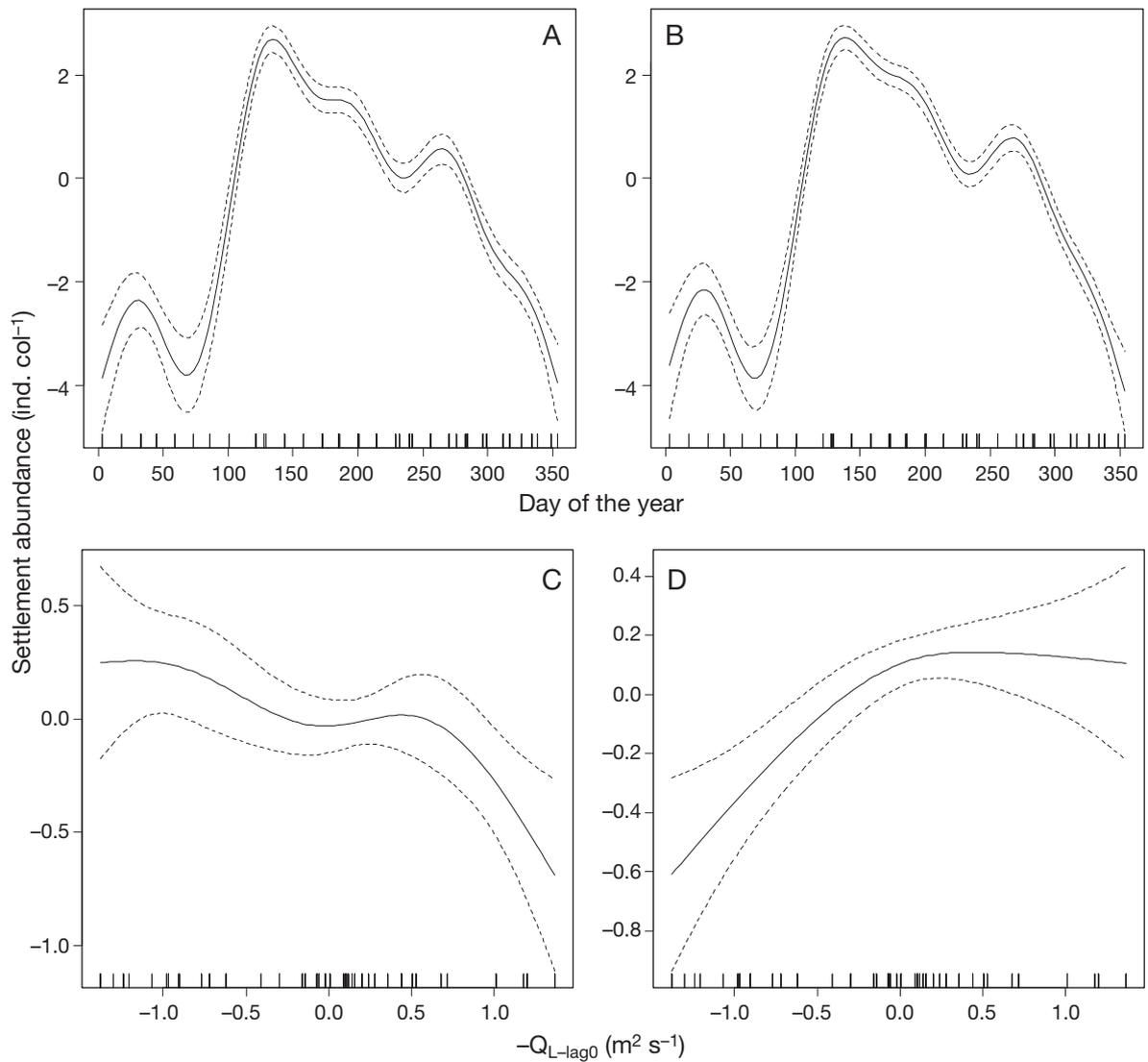
Fig. 6. Generalized additive models, showing the partial effects on settlement abundance of variables (A,B) 'day of the year' and (C,D) instantaneous longitudinal transport to the main axis of the ría $-Q_{L-lag0}$ ($m^2\,s^{-1}$) in (A,C) Arnela and (B,D) Miranda locations. Dashed lines show 95% CI, and tick marks along the *x*-axis below each curve represent the values of the effect where observations occurred

According to the percentage of the total variability explained and the BIC values, the models that best describe settlement patterns in both locations included the average $-Q_L$ during the 15 d previous to the deployment of the collectors ($-Q_{L-lag1}$; Table 5). These models explained 89.4% and 93.2% of the total variance at Arnela and Miranda, respectively (Tables 5 & 6). These models again showed a strong seasonal pattern which placed settlement during the upwelling-favourable season (Fig. 7A,B). In addition, maximum settlement abundances matched in both locations with values of $-Q_L$ around 0 $m^2\,s^{-1}$ during the fortnight previous to the deployment of the collectors (Fig. 7C,D).

The models that included the longitudinal transport with a 30 d lag ($-Q_{L-lag2}$) explained 81.8% and 86.2% of the total variance at Arnela and Miranda, respectively (Tables 5 & 6). Again the seasonal effect led to settlement within the upwelling-favourable season (Fig. 8A,B). Settlement abundance increased linearly (estimated df ~ 1; Table 6) with $-Q_{L-lag2}$ values in both locations (Fig. 8C,D), but p-values again showed a larger influence of $-Q_{L-lag2}$ at Miranda (Table 6).

Fig. 9 illustrates the differences between settlement time series observed and predicted at Arnela and Miranda using instantaneous or lagged response models.

Fig. 7. General additive models showing the partial effects on settlement abundance of variables (A,B) 'day of the year' and (C,D) 15 d lagged longitudinal transport to the main axis of the ría $-Q_{L-lag1}$ ($m^2\,s^{-1}$) in (A,C) Arnela and (B,D) Miranda locations. Dashed lines show 95% CI, and tick marks along the *x*-axis below each curve represent the values of the effect where observations occurred

DISCUSSION

The time series of *Mytilus galloprovincialis* settlement in the Ría de Ares-Betanzos showed a strong seasonal pattern in both study years (Figs. 4 & 5). Settlement was concentrated during the upwelling-favourable season (late spring to early autumn), which was characterized by the prevalence of north-easterly winds and a low river inflow (Figs. 2 & 3). Seasonality alone can explain most of the variability recorded, not just in the presence of settlement (Table 1) but also in mussel abundance (Table 5).

Settlement abundance is characterized by an initial major peak followed by several peaks of decreasing magnitude (Figs. 6 to 8).

Temporal patterns characterized by several settlement peaks are usually related to either the synchronized spawning of gametes and subsequent simultaneous development, the occurrence of common transport episodes that cause a massive arrival of larvae to settlement locations, or a combination of both processes (Pineda 2000).

Mytilus galloprovincialis can release and fertilize gametes during the whole year at intermediate
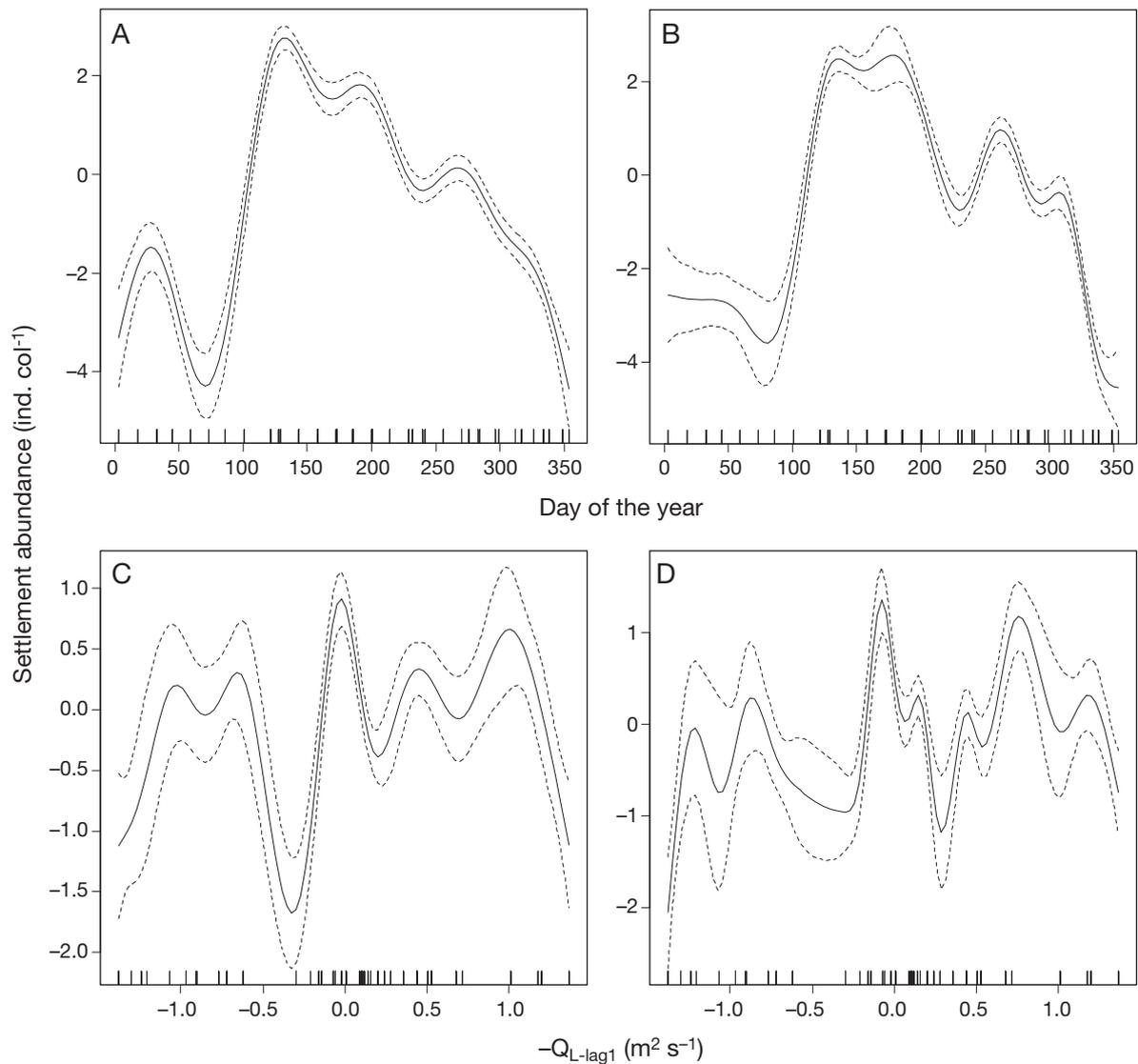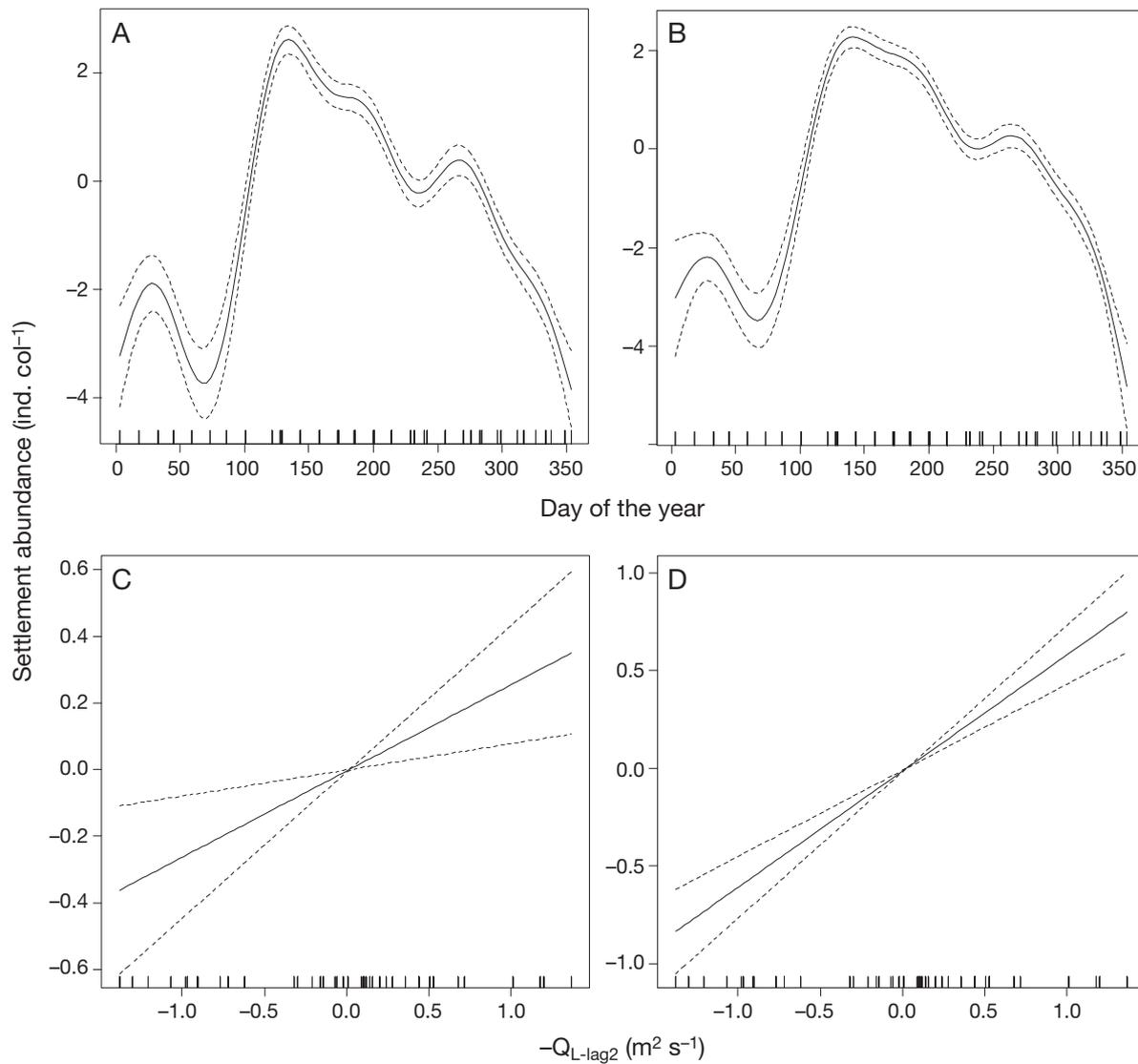
Fig. 8. General additive models showing the partial effects on settlement abundance of variables (A,B) 'day of the year' and (C,D) 30 d lagged longitudinal transport to the main axis of the ría $-Q_{L\text{-lag2}}$ ($m^2\,s^{-1}$) in (A,C) Arnela and (B,D) Miranda locations. Dotted lines show 95% CI, and tick marks along the x-axis below each curve represent the values of the effect where observations occurred

latitudes, although massive spawnings are concentrated between early spring and summer (Snodden & Roberts 1997, Cáceres-Martínez & Figueras 1998b, Suárez et al. 2005). Although previous studies in the Ría de Ares-Betanzos described a single spawning event in mid-summer (Villalba 1995), our results showed the largest settlement densities in the spring. This pattern agrees best with the reproductive cycle described in the Southern Galician rías (Villalba 1995) and harmonizes larval development with the upwelling season.

Spawning in many invertebrate and fish species occurs primarily during the upwelling-favourable season suggesting some kind of advantage for larval development (Guisande et al. 2001, Shanks & Eckert 2005, Otero et al. 2008, Morgan et al. 2009b, Otero et al. 2009). Although upwelling systems have been traditionally considered as dispersive environments (Roughgarden et al. 1988, Broitman et al. 2008), several studies have reported simple behaviours in different species of invertebrate larvae, for example the maintenance of a preferential depth, which allows for high larval retention close to parental habitats

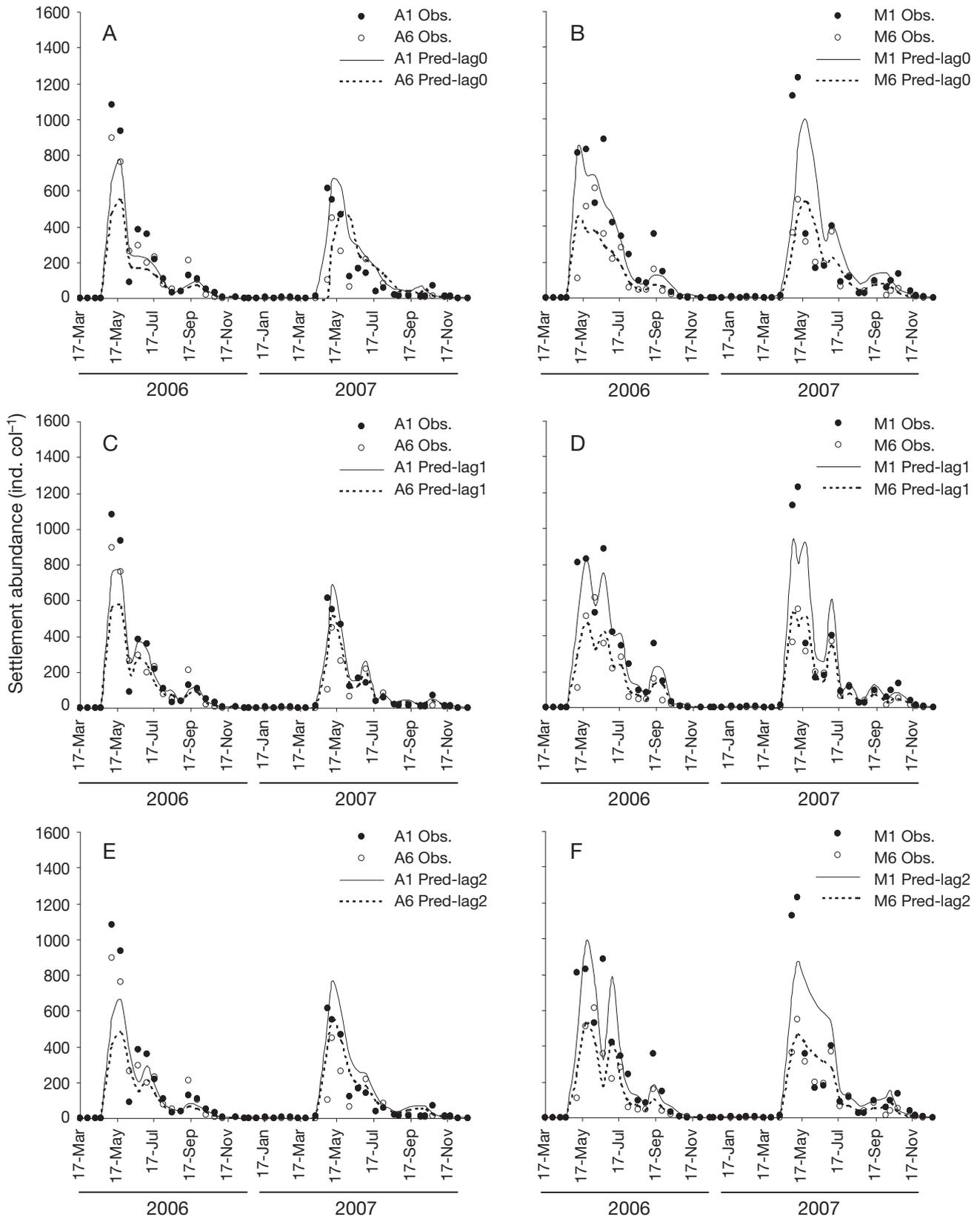Fig. 9. Settlement time series observed and predicted at (A,C,E) Arnela and (B,D,F) Miranda using optimal models selected for (A,B) $-Q_{L\text{-}lag0}$, (C,D) $-Q_{L\text{-}lag1}$ and (E,F) $-Q_{L\text{-}lag2}$. ind. col.$^{-1}$ = individuals per collector

(Sponaugle et al. 2002, Shanks & Brink 2005, Morgan et al. 2009b). In the present study, preferential settlement of *Mytilus galloprovincialis* at 1 m depth was observed (Tables 1, 3, 4 & 6), which suggests a higher concentration of competent larvae at the surface. Several studies have shown a highly variable vertical distribution for bivalves, which is species-specific (Shanks & Brink 2005) and dependent on the larval developmental stage (Dobretsov & Miron 2001, Morgan & Fisher 2010). The differences among studies regarding the vertical distribution of mussel larvae in the water column (Dobretsov & Miron 2001, Alfaro & Jeffs 2002, McQuaid & Phillips 2000, Morgan et al. 2009a) might be related to the dependence between vertical position and physical or biological discontinuities in the water column (Metaxas 2001, Shanks et al. 2003), as well as to the local topographic and hydrodynamic characteristics of each study area. Although in the present study settlement at 1 m was more probable and abundant at both locations, we also observed a greater difference in settlement magnitude between depths at Miranda (Tables 3, 4 & 6). The topography and shallowness of Arnela (Fig. 1) may favour the action of local wind-stress from the surface to the bottom, allowing for a more homogeneous larval distribution in the water column in spite of significantly higher concentrations at the surface.

From a dispersive point of view, preferential depth at the surface may facilitate the onshore transport by different transport mechanisms like onshore coastal winds, sea breeze or internal waves (Shanks 1995). Larval concentration at the surface would also favour larval displacement to the shelf during active upwelling events and return to the coast during the subsequent upwelling relaxation or downwelling episodes (Roughgarden et al. 1988). Villegas-Ríos et al. (2011) suggested that the subtidal circulation in the inner part of the Ría de Ares-Betanzos is positive independently of the coastal winds, but they reported an increase in average flushing time during downwelling events with regard to upwelling episodes. A reversal of the circulation might occur in the outer part of the Ría de Ares-Betanzos in response to southwesterly coastal winds, as has been suggested for other Galician rías (Álvarez-Salgado et al. 2000, Piedracoba et al. 2005). Settlement delays detected in Miranda at 6 m depth might support the presence of reversed circulation events only in the outer ría. Although continental runoff may be a factor modulating flushing times and subtidal circulation in the Ría de Ares-Betanzos (Álvarez-Salgado et al. 2011, Villegas-Ríos et al. 2011), no significant effect of this variable on settlement was detected in the present study. Nevertheless, the regression models obtained showed that $-Q_L$ had a significant instantaneous and also delayed effect on the settlement magnitude of *Mytilus galloprovincialis* (Tables 5 & 6). The parallel time course of the longitudinal and transversal components of the coastal winds does not allow us to isolate the effect of the longitudinal Ekman transport (caused by transversal shelf winds) from the effect of the longitudinal wind stress (caused by longitudinal shelf winds). Therefore, $-Q_L$ should be interpreted as a proxy for regional scale circulation conditions.

Upwelling at our latitudes consists of a succession of moderate to intense wind stress and relaxation cycles occurring every 10 to 20 d (Álvarez-Salgado et al. 1993). This high frequency of upwelling episodes might constrain our capacity to relate a specific event with a settlement pulse because of the fortnightly sampling frequency of settlement densities.

With regard to the instantaneous effect of $-Q_L$ ($-Q_{L\text{-lag0}}$) an inverse result on settlement magnitude was observed at the inner (Arnela) and outer (Miranda) locations (Fig. 6C,D). Intense offshore transport during the sampling interval, due to both longitudinal wind stress and Ekman transport, showed a detrimental effect on settlement magnitude at Arnela (Fig. 6C). On the contrary, settlement abundance decreased at Miranda when onshore transport prevailed (Fig. 6D). Prevalence of onshore transport enhanced the settlement at the inner part of the ría (Arnela) and reduced it at the outer part (Miranda), suggesting that larvae are mainly delivered from the inside of the ría. This pattern is consistent with the spatial distribution of reproductive adults, which are concentrated on the southern shore of the Ría de Ares-Betanzos (107 mussel rafts in Lorbé and 40 in Arnela; Fig. 1). Differences in the relevance of $-Q_{L\text{-lag0}}$ on settlement between locations (p-values; Table 6) would support the hypothesis that differential larval supply is determined by differential wind forcing between the outer (Miranda) and inner (Arnela) ría. Since Miranda is located in the outer ría, its hydrodynamics might be more influenced by shelf wind stress and the coastal upwelling–downwelling regime, as reported in other Galician rías (Álvarez-Salgado et al. 2000, Piedracoba et al. 2005).

Although the regression model that includes $-Q_{L\text{-lag0}}$ helps to understand differences in settlement patterns between locations, the model that best describes settlement abundances in the ría included the average $-Q_L$ during the 15 d previous to the deployment of the collectors ($-Q_{L\text{-lag1}}$). Settlement magnitude at both locations showed an optimum for $-Q_{L\text{-lag1}}$ values around 0 m^2 s^{-1} (Fig. 7C,D) and pointed out the importance of the intermittency of

longitudinal transport on settlement abundance of *Mytilus galloprovincialis.* The succession of active upwelling (offshore transport) and relaxation (onshore transport) periods allows for an optimal balance between the supply of nutrients for phytoplankton, growth of plankton in general and coastal retention of primary production (Figueiras et al. 2002, Otero et al. 2008, Villegas-Ríos et al. 2011). The intermittence of these episodes might affect settlement patterns, both indirectly through feeding patterns determining larval development and survival, and directly by limiting larval dispersal through the modulation of residence times and bottom shelf inflow in the ría. In this way, the decrease observed in settlement magnitude in 2007 compared with 2006 (Tables 3 & 4) might be related to the lower variability of $-Q_L$ during 2007 (Fig. 2A). Recent works pointed out the relevance of frequency and variability of upwelling episodes in recruitment dynamics of diverse invertebrate species (Guisande et al. 2001, Otero et al. 2008, 2009, Pfaff et al. 2011). In addition, several studies have shown lower recruitment rates in areas with persistent downwelling (Menge et al. 2003) or upwelling conditions (Navarrete et al. 2005, Broitman et al. 2008, Dudas et al. 2009b, Smith et al. 2009) compared to geographical areas characterized by intermittent upwelling.

In relation to the 30 d delayed effect of $-Q_L$ ($-Q_{L-lag2}$) on settlement abundance, a direct relationship between both variables was observed (Fig. 8C,D). Increases in larval settlement associated with positive values of $-Q_L$ during early larval stages (30 to 45 d before settlement) suggest that offshore transport associated with upwelling events is not limiting the larval supply to the ría. Several studies have reported similar results (Morgan et al. 2009a, Shanks & Shearman 2009, Morgan & Fisher 2010) and also a positive relationship between settlement and upwelling intensity (Pfaff et al. 2011). Different strategies have been suggested to avoid advection during upwelling events (Queiroga & Blanton 2004, Shanks & Brink 2005, Morgan et al. 2009b, Shanks & Shearman 2009). In addition several mechanisms other than downwelling episodes (i.e. local winds, sea breeze, internal waves) have been described as effective for returning larvae to the coast (Shanks 1995). Although, the relationship between $-Q_{L-lag2}$ intensity and settlement is more relevant at Miranda (p-values; Table 6), the same pattern was observed at the inner location (Arnela), less influenced by shelf winds. This suggests an indirect relationship between $-Q_{L-lag2}$ and settlement abundance. The prevalence of upwelling favourable winds could develop a front across the mouth of the bay which might contribute to larval retention into the estuary, as has been previously observed in different estuaries (McCulloch & Shanks 2003). The positive relationship at both locations would also suggest that the preponderance of upwelling episodes during the early larval stages (30 to 45 d before settlement) enhances their survival because of food availability. Almost 100% of the limiting nutrients are provided to the Ría de Ares-Betanzos by shelf bottom waters during upwelling events, enhancing the net ecosystem production between 5 and 7 times in comparison to downwelling episodes (Villegas-Ríos et al. 2011). The increase in larval survival/settlement might be related to the fertilization of coastal waters during the upwelling season, which enhances primary and secondary production in the system (Guisande et al. 2001, Otero et al. 2008).

Changes detected in the coastal wind regime off the NW Iberian Peninsula during the last 40 yr indicate a reduction of 30% in the duration of the upwelling-favourable period and a 45% reduction in its intensity (Álvarez-Salgado et al. 2008). Based on the results of the present study, these changes in the wind regime could have a direct influence on the settlement of *Mytilus galloprovincialis*, as has been suggested for other commercial species with life cycles adapted to the seasonality of coastal upwelling in the NW Iberian Peninsula (*Sardina pilchardus*: Guisande et al. 2001; *Octopus vulgaris*: Otero et al. 2008, 2009).

In summary, the results of the present work illustrate the link between mussel settlement and the northeasterly winds prevalent during the upwelling favourable season. The positive effect of coastal upwelling events during the early planktonic life ($-Q_{L-lag2}$) suggests a relevant role of coastal water fertilization for larval survival. The relevance of intermittent offshore transport/upwelling episodes during larval development ($-Q_{L-lag1}$) seems to be related to the equilibrium provided between food supply and larval retention in the ría. At the end of larval development, longitudinal transport ($-Q_{L-lag0}$) showed certain effects on the regulation of transport and meta-population connectivity, modulated by local hydrography and larval behaviour. The increasing evidence of many invertebrate species with life cycles highly adapted to coastal upwelling (Cury & Roy 1989, Guisande et al. 2001, Shanks & Eckert 2005, Otero et al. 2008, Morgan et al. 2009b, Shanks & Shearman 2009, Pfaff et al. 2011) highlights the need for understanding ecosystem responses to changing environmental conditions and developing effective management and conservation strategies.

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