Spatial patterns of larval settlement and early post-settlement survivorship of *Mytilus galloprovincialis* in a Galician Ría (NW Spain). Effect on recruitment success.

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ABSTRACT

Larval settlement and recruitment play an important role on the population dynamics of marine benthic invertebrates, and are key factors in the management of aquaculture industries. In order to check the current strategies of mussel seed gathering from collector ropes in the Ria of Ares-Betanzos (NW Spain), this work analyses the seasonal and spatial variability of larval settlement and recruitment of the mussel Mytilus galloprovincialis, as well as the relationship between settlement and recruitment. Our results highlight the importance of the hydrographic characteristics of the Ría de Ares-Betanzos on the spatial distribution of larval settlement and on the early post-settlement mortality, which determines recruitment success. The spatial distribution of larval settlement, with higher abundances in the northern-shore but significant larval retention in the southern culture areas, is in agreement with the positive subtidal circulation of this embayment and the larger residence times in the southern shore. The positive subtidal circulation of the Ría favours larval transport from the culture areas located in the south to the northern shore, while the larger residence times allow larval retention in the southern shore. The strong linear relationship between settlement and recruitment suggest density-independent mortality and allowed estimating recruitment abundances and short-term survival rates. The highest and lowest post-settlement mortalities were registered at the most external and sheltered locations respectively, suggesting that the vulnerability to the hydrodynamic stress may be the main cause of early post-settlement mortality of mussel juveniles on suspended substrates. Our results confirm that the sheltered culture polygons located in the inner area of the Ría of Ares-Betanzos are favourable environments for the recruitment of *Mytilus galloprovincialis* spat, supporting the current strategies of seed gathering from collector ropes in the Ría of Ares-Betanzos.

Keywords: hydrographic regime, larval settlement, mussels, post-settlement mortality, recruitment.

1. INTRODUCTION

The life cycle of most benthic marine invertebrates, such as *Mytilus galloprovincialis*, involve a dispersive planktotrophic larval phase, which can last for several weeks, and a post-larval sedentary stage (Cáceres-Martínez and Figueras, 1998a; Grantham et al., 2003).. Larval settlement (the process by which individuals become associated with the substrate) and recruitment (the number of individual attached to the substrate an arbitrary time after settlement) play an important role in the population dynamics of marine benthic invertebrates (Arribas et al., 2015; Menge et al., 2009). Therefore, understanding all the processes that affect larval dispersal, settlement and recruitment would be of key importance for a proper management of exploited stocks (e.g. mussels and oysters), tracking invasions (e.g. *Xenostrobus securis* in the Galician Rías) or designating marine reserves (Levin, 2006; López-Duarte et al., 2012).

Settlement and recruitment of marine invertebrates are determined by many biotic and abiotic factors operating and interacting on multiple time and spatial scales in numerous environments (Levin, 2006; Pineda et al., 2008). The timing and magnitude of larval supplies (Cáceres-Martínez and Figueras, 1998a; Porri et al., 2006), the presence of conspecifics (Tumanda et al., 1997), algal and microbial coverage (Hunt and Scheibling, 1997; O'Connor et al., 2006) among others, are biotic factors that determine larval settlement. On the other hand, larval survivorship and development during the planktonic stage are affected by abiotic factors such as physic-chemical characteristics of water (e.g. temperature, salinity and oxygen concentration) and food availability (Alfaro, 2005; O'Connor et al., 2007; Phillips, 2004, 2002; Widdows, 1991). In particular, larval settlement in heavily affected by hydrodynamic conditions controlling larval dispersal and nutrients availability (Peteiro et al., 2011; Smith et al., 2009; Xavier et al., 2007), along with the type of settlement substrate. Recruitment of marine benthic invertebrates is determined by the interaction between settlement abundance and post-settlement processes, such as migration and mortality. Post-settlement mortality has been mainly attributed to the physiological stress associated with metamorphosis, a greater vulnerability to physical stress in smaller individuals, predation and intra and/or interspecific competition for food and/or space (Bownes and McQuaid, 2009; Capelle et al., 2014; Dolmer and Stenalt, 2010; Gosselin and Qian, 1997; Peteiro et al., 2010; Peteiro et al., 2007a).

Mussels are dominant organisms on many rocky shores worldwide, where they serve as ecosystem engineers because they attenuate storm surge, stabilize the shoreline, sequester carbon and provide food and habitat for many species, and are a central component of community structure (Commito et al., 2014; Lawrie and McQuaid, 2001; Menge and Branch, 2001; Navarrete and Menge, 1996; Petraitis, 1998; Rilov et al., 2008) In addition, mussels have important commercial value worldwide, which has motivated the continuous increase of aquaculture industry along the last decades. Filter-feeders (e.g. mussels, oysters) grown in suspended culture also have an important influence in the ecosystem, mainly in areas dominated by aquaculture (Ferreira et al., 2007; Pérez-Camacho et al., 2014) .These effects may include a top-down control of eutrophication symptoms (Bricker et al., 2003) and changes in the water column biogeochemistry (Souchu et al., 2001). The important ecological role of mussels and the need of mussel seed for the aquaculture industry have motivated an increasing interest on understanding the pre and post-settlement processes that determine their abundance and dynamics.

Eastern boundary coastal upwelling systems (EBUS) represent less than 1% of the total volume of the oceans but they provide to humankind more than 20% of the proteins of marine origin (Fréon et al., 2009). The Galician Rías (NW Spain), located in the in the northern boundary of the Iberian–Canary Current upwelling system, are characterized by a high mussel productivity. The importance of larval dispersal and recruitment for the management of mussel culture in this area has motivated an important body of research (e.g. Cáceres-Martínez and Figueras, 1998a; Fuentes and Molares, 1994; Peteiro et al., 2011 and references therein). Cáceres-Martinez et al. (1993) and Peteiro et al. (2011) found that larval settlement is concentrated during spring-summer, i.e. the upwelling favourable season (Alvarez et al., 2008; Figueiras et al., 2002). Filgueira et al. (2007) confirmed that *Mytilus galloprovincialis* has clear settlement preferences for textured and complex substrates because they offer increased surface area, acting as refuges against predators thus reducing post-settlement mortality. Peteiro et al. (2007a) and Peteiro et al. (2010) identified self-thinning, which regulates population density to allow individual growth, and predation, which can eliminate the settled population, as the main causes of post-settlement mortality. Peteiro et al. (2011) developed a model to determine the effects of intermittent-upwelling events on the settlement patterns of *Mytilus galloprovincialis* in two distinct locations of the Ría of Ares-Betanzos. Peteiro, (2010) analysed the effect of the physico-chemical characteristics of the water on larval settlement.

This work focusses on the settlement and recruitment patterns of *Mytilus galloprovincialis* grown in suspended culture in the Ría of Ares-Betanzos. Our main goals were to evaluate if the current seed collector strategies are optimal or can be improved, and to test whether the recruitment of mussel juveniles is more affected by settlement abundances or by post-.settlement processes. To this purpose, larval settlement and recruitment abundances of mussel juveniles were measured fortnightly during a year on artificial suspended substrates, which were deployed at four locations subjected to different oceanographic regimes and with different adult abundances. The analysis conducted in this work can be summarized in two points: (i) characterize the spatial and temporal variability of settlement and recruitment abundances of mussels in this embayment, and (ii) study the relationship between larval settlement and recruitment and estimate post-settlement mortalities. The results of this study allowed us the characterize the spatial variability in the seasonal patterns of larval settlement and recruitment of Mytilus galloprovincialis along the Ría of Ares Betanzos, showed that in this embayment the recruitment of mussel juveniles is more determined by settlement abundances than by post-settlement processes, and confirmed the suitability of the current strategies of mussel seed gathering on collector ropes in the Ría of Ares-Betanzos.

2. MATERIALS AND METHODS

2.1. *Study area*

The Ría of Ares-Betanzos is the largest of the six embayments located in the northern Galician coast, between Cape Fisterra and Cape Prior (NW Iberian Peninsula; Figure 1), with a surface area of 72 km^2, a volume of 0.75 km^3 and a maximum length of 19 km. This ría has two main branches: Ares, the estuary of river Eume, and Betanzos, the estuary of river Mandeo. In the outer part, the two branches converge into a confluence zone that is freely connected to the adjacent shelf through a mouth that is 40 m deep and 4 km wide. This embayment is characterized by its positive circulation pattern, with a bottom inflow and a surface outflow, and by the existence of a cyclonic gyre in the confluence zone (Duarte et al., 2014).

Mussel aquaculture is the main economic activity in the Ría the Ares Betanzos, which supports 147 rafts distributed in four culture polygons (Figure 1). Most of the rafts are concentrated in Arnela and Lorbé, located in the southern inner (SI) and outer sides of the Ría, respectively. Industrial seed gathering has been mainly conducted in Miranda and Redes, located in the northern outer (NO) and inner (NI) sides of the ría, respectively, and in the inner polygon of the southern shore (Arnela), while Lorbé has been dedicated exclusively to the culture of adult mussels.

Settlement and recruitment of Mytilus galloprovincialis spat were monitored fortnightly during 2007 at each culture polygon using three collector ropes covered with jute. Prior to their deployment in the field, collecting ropes were kept for 30 days in seawater filtered through a 100 µm mesh, renewing the water every 2 days to allow the development of an adequate biofilm but preventing the attachment of epifauna (Peteiro et al., 2007b; Porri et al., 2006). Three conditioned ropes were suspended on long-lines/rafts fortnightly at each location and sampled 45 days after deployment. Sampling consisted on the collection of three sub-samples of known area (6 cm x 2 cm) from the jute covering each rope at two depths (1 and 6 m/ 1 and 4 m in Redes). Samples were collected at these depths to test for differences in the settlement and recruitment patterns between the surface and the bottom. 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 a 5-minutes ultrasound bath. Detached individuals were then sorted using a sieve kit with mesh sizes ranging from 125 to 2360 µm, to ease their counting under a binocular microscope. The average size of individuals retained was calculated measuring the length (L, mm) of the ante-posterior axis of the larvae (subsample of 100-150 individuals for large samples) for each replicate and sieve size. Taking into account the taxonomic classification of post-larvae settlement (Dare, 1976; Dare et al., 1983), individuals were divided into settlers ($L < .5$mm) and recruits ($L \geq 0.5$mm). Settlement and recruitment abundances (N) were calculated as the number of individuals per meter of rope (ind/m).

2.2. Statistical analysis

Our first aim was to characterize the spatial variability of the seasonal patterns of larval settlement and recruitment in the Ría of Ares-Betanzos. To this purpose, we need to fit settlement and recruitment abundances as a function of time and then test for differences between locations and depths. We also tested for differences between the temporal patterns of larval settlement and recruitment. The nonlinear relationship between the response (N, ind/m) and explanatory (date) variables, clearly discourages the use of classical regression models and cuvariance analysis. Thus, we used non-parametric regression techniques.

For each group, defined by location, depth and taxa (settlers/recruits), the seasonal pattern of mussel abundance can be defined as

$$y_{ij} = g_j\left(t_i\right) + e_{ij}$$

where t_j is the date of the i-est sampling for group j. y_{ij} is the square-root transformed settlement/recruitment abundance, this transformation was conducted to reduce overdispersion, and the errors, e_{ij} are assumed to be independent and normal. In this work, independence and normality of errors were checked by the Box-Jenkins and the Shapiro tests, respectively The unknown curves that define the relationship between the covariate and the response variable, g_i, were estimated by kernel regression (Nadaraya, 1965)

$$g_j(t_i) = \frac{\sum_{i=1}^{n} y_{ij} K_h\left(t - t_i\right)}{\sum_{i=1}^{n} K_h\left(t - t_i\right)} \quad (1)$$

where K_h is a symmetric, unimodal density function with mean 0 and standard deviation h, these parameter is known as bandwidth and is key to obtain a proper estimation. In this work the bandwidth was selected by cross-validation.

The null hypothesis assumes equality between groups of smooth curves, e.g. the seasonal patterns of settlement abundances at a given depth is the same at the four locations:

$$\begin{aligned} H_0 &: y_{ij} = g\left(t_{ij}\right) + e_{ij} \\ H_1 &: y_{ij} = g_j\left(t_{ij}\right) + e_{ij} \end{aligned} \tag{2}$$

By analogy with one-way analysis of variance, to test whether H_0 is true the individual estimators of each group are compared with the common estimator using the following statistic:

$$TS = \frac{\sum_{J=1}^{p}\sum_{I=1}^{n_j}\left(\hat{g}\left(t_{ij}\right) - \hat{g}_j\left(t_{ij}\right)\right)^2}{\hat{\sigma}^2} \tag{3}$$

where p is the number of groups (e.g. p=4 when the effect of location is tested), and n_j the number of observations in group j. The estimator of the error variance was included in the denominator to reduce the effect of scale (see details in Young and Bowman (1995))

The dependence between settlement and recruitment was checked by Pearson´s cross-correlation analysis. In agreement with the results obtained in the cross-correlation analysis, which detected a strong linear dependence between settlement and recruitment at lag 1, i.e. with a delay of two weeks, a generalized linear model was fitted to estimate recruitment abundance according to the settlement registered two weeks earlier. Model selection was conducted by F-tests to search for effects of location and depth on both the intercept and slope. A Box-Jenkins test (p-value = 0.1938) confirmed the independence of residuals. Once the model was fitted, Wald tests (Harrell, 2013) were conducted to check for differences in comparison post-settlement fortnightly survival rates (slopes) between locations.

Data analysis was conducted with the statistical package R.3.1.3 (R Development Core Team, 2015). The *sm* package of R (Bowman and Azzalini, 2014) was used to fit the seasonal patterns of mussel abundances and perform the non-parametric covariance analysis.

3. RESULTS

Table 1 reports higher settlement abundances of *Mytilus galloprovincialis* in the northern than in the southern shore of the ría, with Miranda, the outermost sampling location in the Northern shore (see Figure 1) having the highest mean values. Larval settlement was higher in the surface (1m) in all locations but Redes (NI), which is the shallowest position. Our results alos reflect the overdispersion (see standard deviations in Table 1) of both settlement and recruitment abundances, Figure 2 shows a clear seasonal pattern for both settlement (solid line) and recruitment (dashed line) of mussel spat. Larval settlement (N > 500ind/m) was concentrated from mid-April to mid-November, which comprises the upwelling- favourable season, while the rest of the year only residual larval retentions were registered (N < 500ind/m). Settlement was characterized by a high peak in late April and successive episodes during summer and early autumn. This peak was higher at 1m than at 6m, and was particularly important in Miranda (NO, up to 150.000ind/m) and Arnela (SI, up to 58.000ind/m). Figure 2 also shows higher spat abundances in Miranda during the settlement episode registered in July. In Lorbé (SO), where the first peak was barely significant, larval settlement registered lower seasonal variability than in the other locations.

Comparison between the seasonal patterns of larval settlement and recruitment abundances (Table 2) detected significant differences between taxa except in Arnela at 6m. Figure 2 shows that recruitment was lower than settlement abundance at all locations, which indicates post-settlement mortality. Recruitment of mussel juveniles was registered from early-May to December, and its seasonal pattern is characterized by a first peak in May and successive episodes up to December, i.e. settlement and recruitment abundances exhibited similar seasonal patterns with a delay of 2 weeks in the later. As observed for larval settlement, the northern shore registered higher recruitment of mussel juveniles than the southern shore of the ria. However, differences between locations in recruitment abundances were lower than those observed for larval settlement, particularly in the spring peak,

Despite the differences observed in Figure 2, the non-parametric analysis of covariance (Table 2) only detected a significant effect of depth on the recruitment of mussel juveniles in

Lorbé (SO). The non-parametric analysis of covariance (Table 3) confirmed a differential recruitment pattern in Miranda (NO), which registered the highest recruitment abundances. Significant differences in recruitment were found between Lorbé (SO) and the northern locations, as well as between Redes (NI) and the southern locations in the deepest position (Table 3).

Table 4 shows that the correlations between settlement and recruitment were positive and relatively strong up to lag 2 (4 weeks) at most locations. The strongest dependence was observed for a lag of 2 weeks. This linear relationship between larval settlement and recruitment abundances indicates that early post-settlement mortality is density independent and suggests the use of generalized linear models to predict the recruitment abundances at a given week according to the settlement abundances registered two weeks earlier. The model selection tests (Table 5) indicated that the the interaction between location and settlement abundance provided the best estimator of recruitment abundances of mussel juveniles, while the effect of depth was not significant. The fitted model (Table 6) shows that recruitment and settlement were proportional (no significant intercept at any location), thus the slopes can be seen as survival rates. These rates ranged between the 27.2% registered in Miranda (NO), and the 46.4% in Arnela (SI). Comparison between slopes revealed higher post-settlement survivorships in the inner locations (Arnela and Redes) than in the outer (Miranda and Lorbé). Particularly, the Wald test (Table 7) found significant differences between Arnela (SI) and the outer locations, as well as between Miranda (NO) and the inner locations. Comparison between observed and fitted values (Figure 3) confirmed the goodness of fit of the model.

4. DISCUSSION

Larval settlement in the Ría of Ares-Betanzos exhibited a clear seasonal pattern with a major peak in mid-spring and subsequent episodes during the upwelling favourable season (up to mid-autumn). This season is characterized by intermittent short-term upwelling episodes followed by periods of stratification or weak downwelling, and low continental runoffs (Peteiro et al., 2011). The larval pelagic stage of *Mytilus galloprovincialis* ranges between 10 and 30 days (Cáceres-Martínez and Figueras, 1998a; Grantham et al., 2003), thus the seasonal pattern of larval settlement should mainly reflect temporal fluctuation in larval production. Analysis conducted by Toupoint et al. (2012) on eastern Canada shows the coupling between the seasonal patterns of settlement and occurrence of larvae in the water column.

Villalba (1995) stated that the reproductive cycle of *Mytilus galloprovincialis* in the Ría of Ares-Betanzos in characterized by a single spawning event in mid-summer. However, the seasonal pattern found in this work agrees more with the reproductive cycle of mussels in the southern Galician Rías (Cáceres-Martinez et al., 1993; Cáceres-Martínez and Figueras, 1998b; Suárez et al., 2005; Villalba, 1995). Studies conducted at intermediate latitudes on both rocky shores (Broitman et al., 2008; Johnson and Geller, 2006; Menge et al., 2011; Navarrete et al., 2008) and collector ropes (Toupoint et al., 2012) found significant settlement abundances of Mytilus spp. from mid-spring to early-fall, although the main settlement peak varied between late summer and early winter depending on the latitude (Broitman et al., 2008). Recruitment of Mytilus spp. in Central Chile was found to be less seasonal (Navarrete et al., 2008).

Our results report higher settlement abundances in the northern shore of the ría (Miranda and Redes), although the musel adult population is concentrated in the southern shore (Arnela and Lorbé). The positive subtidal circulation of this embayment and the upwelling episodes, which reduce flushing times, have been identified as the main causes of larval transport from the southern culture areas to the northern-outer side (Duarte et al., 2014; Peteiro et al., 2011; Piedracoba et al., 2014; Villegas-Ríos et al., 2011). Prior studies in the Galician Rías have also reported the highest settlement abundances in the most seaward location (Cáceres-Martínez and Figueras, 1998c; Fuentes and Molares, 1994). Larval retention in the southern shore may be attributed to the lower current velocities registered in the culture areas, and to the sheltered position of Arnela, which prevents water displacement to the East and North and the lost by advection of larvae and nutrients supplied by the adjacent shelf

(Piedracoba et al., 2014). Indeed, according to the hydrodynamic model developed by Duarte et al. (2014), residence times during the upwelling season can reach 10 and 5 days in Arnela (SI) and Lorbé (SO), while in Redes (NI) are less than three days.

During the last years several studies have highlighted the important role of hydrographic dynamics and wind regimes on larval dispersal and settlement of *Mytilus spp.* and other marine benthic invertebrates (Menge et al., 2014, 2011; Newell et al., 2010; Pineda et al., 2010; Rilov et al., 2008; Smith et al., 2009; Zhang et al., 2015)**. T**he model developed by Peteiro et al., (2011) was able to describe the effect of wind regime on larval transport, survivorship and settlement in the Ría of Ares-Betanzos. Coastal water fertilization during the upwelling events favour larval survival during the planktonic stage, while the intermittent offshore transport enhance larval dispersal from the southern culture areas to the northern-outer shore of the ría. Peteiro (2010) found that, in addition to the intermittent upwelling regime, water stratification and pH also affect larval settlement. Water stratification in the Ría of Ares-Betanzos occurs when the temperature of the surface is above 14ºC (Peteiro, 2010), i,e, under optimal conditions for larval development (Bayne, 1965; O'Connor et al., 2007). Water stratification may also favour active larval transport to the surface (Rawlinson et al., 2004 and references therein), which results in higher settlement and recruitment abundances of Mytilus galloprovincialis in the surface than in the bottom, as observed in this work. The positive effect of pH, which is a stable indicator of primary production, on larval settlement confirms the important role of food availability on pre-settlement larval survivorship and development. Food availability is a limiting factor on the development and growth of bivalve larvae, which determines the length of the planktonic stage and larvae physiological conditions at metamorphosis (Phillips, 2004, 2002). Given the high mortality rates during the planktonic stages, fast larval development may favor larval survivorship and increase settlement abundance (Widdows, 1991).

As stated in the previous paragraph, Peteiro et al., (2011) detected a significant effect of the wind regime on larval transport and settlement in southern-inner (Arnela) and northern-outer (Miranda) culture polygons, which exhibited similar seasonal patterns, but this effect has not been tested in the other locations (Lorbé (SO) and Redes (NI)). Given that the subtidal current in Redes does not depend on wind regime (Piedracoba et al., 2014), a lower effect of wind regime on the settlement patterns is also expected in this site. Although Peteiro et al., (2011) did not find any significant effect of the continental runoff on larval settlement in Arnela and Miranda, large continental runoffs during upwelling periods enhance off-shore transport (Aguiar et al., 2015) and may lead to lower mussel larval retention in the northern-inner location (Redes) and higher abundances in northern-outer polygon (Miranda), as indicated by peak recorder in spring.

The cross-correlation analysis allows checking whether recruits affect settlement patterns, and understanding the relative effects of settlement abundance and short-term post-settlement processes on recruitment. The positive correlation observed at lag 0, i.e. between individuals attached to the same rope, suggests that the presence of settled spat may increase settlement. The disposition of individuals on the ropes after settlement may increase the complexity of the substrate, providing refuge against mortality risks such as predation and hydrodynamic forces (Capelle et al., 2014; Carl et al., 2012; Filgueira et al., 2007; Peteiro et al., 2010).

The strong correlation between recruitment and settlement abundances registered two weeks earlier suggests that the seasonal pattern of recruitment is mainly determined by larval settlement. Post-settlement mortality has been mainly attributed to the physiological stress associated with metamorphosis, the vulnerability to physical stress in smaller individuals, predation and intra and/or interspecific competition for food and/or space (Bownes and McQuaid, 2009; Capelle et al., 2014; Dolmer and Stenalt, 2010; Gosselin and Qian, 1997; Peteiro et al., 2007a; Peteiro et al., 2010). The linear relationship found between settlement and recruitment indicates a lack of density-dependent effect on post-settlement mortality. Studies conducted in the west coast of US: found a positive correlation between settlement and recruitment for mussels and barnacles on rocky shores, which suggest that post-settlement mortality was density-independent (Broitman et al., 2008; Menge et al., 2010). Thus, in contrast with the findings of Peteiro et al. (2007a) for a longer period, short-term mortality cannot be attributed to self-thinning caused by competition for food and space. The spatial variability in the survival rates recorded during this study, with higher values in the inner side of the Ría, indicate that the vulnerability to hydrodynamic forces may be the major cause of early post-settlement mortality and/or dislodgement from the collector ropes.

This study confirms that larval settlement of *Mytilus galloprovincialis* in the Ría of Ares-Betanzos follows the typical seasonal pattern of this species in temperate latitudes, with a major peak after the first spawning event and subsequent episodes along the upwelling favourable season. The spatial distribution of larval settlement, with higher abundances in the northern shore, but significant larval retention in the southern culture areas is in agreement with the hydrographic characteristics of this embayment. The analysis of the relationships between larval settlement and recruitment, which detected higher mortality rates in the most exposed areas, suggests that hydrodynamic pressures may be the main cause of early post-settlement mortality. Thus, although the northern-outer location registered the highest larval settlement, it can be stated that the inner area of the embayment, which registered significant larval retention and lower mortality risks, constitutes a favourable environments for the recruitment of Mytilus galloprovincialis spat on collector ropes. Therefore, these results support the current strategies of mussel seed gathering on collector ropes in the Ria of Ares-Betanzos, which develop this activity in the culture polygon with the highest settlement abundance (Miranda, NO), and in the sheltered polygons located in the inner side of the ría, which provide refugee against early post-settlement mortality risks (Arnela and Redes).

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Table 1: Descriptive summary of larval settlement and recruitment during 2007 for each culture polygon and depth

		Settlement		Recruitment	
		mean	sd	mean	sd
Arnela	1m	6993	14251.14	3311	7576.19
	6m	3958	6680.16	1814	3353.12
Lorbé	1m	6291	8682.93	2833	4056.73
	6m	5171	7015.15	1360	2233.48
Miranda	1m	18615	38015.97	6928	10867.56
	6m	10489	15838.56	4004	6225.50
Redes	1m	7124	13236.71	3681	6826.79
	4m	9044	13866.42	4132	5927.11

Table 2: P-values of the non- parametric covariance analysis conducted to compare the seasonal patterns of mussel (*Mytilus galloprovincialis*) abundances. Top: comparison between taxa (settlers vs recruits) for each location and depth. Bottom: comparison between depths for each location and taxa. to test for effects of type (settlement vs. recruitment), and depth on the seasonal patterns of . Mussel abundances were square-root transformed prior to conduct the tests.

	Arnela		Lorbé		Miranda		Redes	
	1m	6m	1m	6m	1m	6m	1m	4m
Taxa	0.0646	0.1005	0.0158	0.0068	0.0196	0.0128	0.0302	0.0171
	Settlers	Recruits	Settlers	Recruits	Settlers	Recruits	Settlers	Recruits
Depth	0.2690	0.5847	0.9997	0.0215	0.5734	0.5360	0.8542	0.2232

Table 3: P-values of the non- parametric covariance analysis conducted to test for the effect of location on the seasonal patterns of mussel (*Mytilus galloprovincialis*) abundances (square-root transformation).

		All locations	**Pairwise**					
			A-L	A-M	A-R	L-M	L-R	M-R
Settlers	1m	0.0104	0.3780	0.0766	0.9989	0.0826	0.2989	0.0245
	6m	0.0831	0.9788	0.0201	0.2826	0.0254	0.2577	0.9845
Recruit	1m	0.3044	0.8910	0.3540	0.9713	0.0133	0.0780	0.5214
	6m	0.0184	0.7971	0.1074	0.0566	0.0318	0.0245	0.9376

Table 4: Cross correlations between larval settlement and recruitment of *Mytilus galloprovincialis* up to lag 4 (8 weeks).

		0		**1**		**2**		**3**		**4**
Arnela	1m	0.533	*	0.929	***	0.253		0.047		0.025
	6m	0.878	***	0.591	*	0.429	.	0.174		0.029
Lorbé	1m	0.561	*	0.831	***	0.849	***	0.555	*	0.225
	6m	0.657	**	0.785	***	0.828	***	0.541	*	0.404
Miranda	1m	0.373	**	0.896	***	0.675	***	0.186		0.106
	6m	0.524	*	0.835	***	0.758	**	0.452		0.365
Redes	1m	0.466	*	0.781	***	0.886	***	0.463	*	0.052
	4m	0.473	.	0.828	***	0.804	***	0.572	*	0.399

(***) p-value < 0.001, (**) p-value < 0.01, (*) p-value < 0.05, (.) p-value < 0.1.

Table 5: F-tests for comparison of nested generalized linear model conducted to select the model used to predict recruitment of *Mytilus galloprovincialis* spat.

	Res.Df	RSS	Df	Sum of Sq	F	Pr(>F)	
Recruit ~ settle	178	2171864803					
Recruit ~ loc +settle	175	2131315041	3	40549762	1.2577	0.2908	
Recruit ~ loc*settle	172	1900658177	3	230656863	7.154	0.0002	***
Recruit ~ depth +loc*settle	171	1880017636	1	20640541	1.9205	0.1677	
Recruit ~ loc*depth*settle	164	1762544870	7	117472766	1.5615	0.1503	

(***) p-value < 0.001, (**) p-value < 0.01, (*) p-value < 0.05, (.) p-value < 0.1.

Table 6: General linear model to estimate recruitment of *Mytilus galloprovincialis* spat according to location and larval settlement, with a lag of 2 weeks.

	Estimate	Std. Error	t value	Pr(>|t|)		Adj. R2
(Intercept)	21.4	563.1	0.038	0.9697		0.7433
Lorbé	282.9	835.4	0.339	0.7352		
Miranda	1555.2	797.6	1.95	0.0528	.	
Redes	830.1	807.0	1.029	0.3051		
settle	0.464	0.045	10.353	<2e-16	***	
Lorbé:settle	-0.177	0.073	-2.442	0.0156	*	
Miranda:settle	-0.192	0.048	-4.006	9.19e-05	***	
Redes:settle	-0.082	0.058	-1.42	0.1574		

(***) p-value < 0.001, (**) p-value < 0.01, (*) p-value < 0.05, (.) p-value < 0.1.

Table 7: Post-settlement fortnightly survival rates of *Mytilus galloprovincialis* spat, and p-values of the Wald test for comparison between slopes of the GLM summarized in Table 6.

	Survival rate	**Wald test**		
		Arnela	**Lorbé**	**Miranda**
Arnela	0.464			
Lorbé	0.287	0.0156		
Miranda	0.272	9.19e-05	0.8026	
Redes	0.382	0.1574	0.1607	0.0067

FIGURES:

Figure 1: Ría of Ares-Betanzos. Samplings were conducted at the four culture polygons: Miranda (M) and Lorbé (L) in the outer part (north and south, respectively) and Redes and Arnela at the inner part (north and south, respectively). Isoclines of the bathymetry of the Ría are also provided.

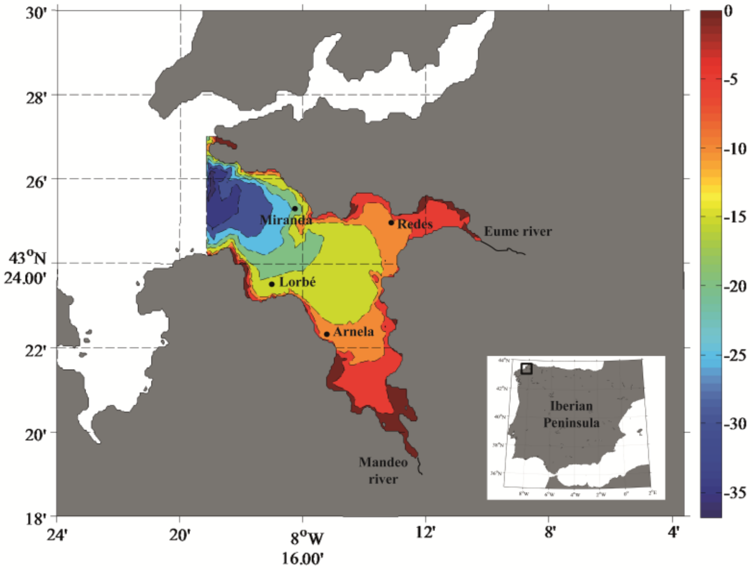

Figure 2: Settlement (solid lines) and recruitment (dashed lines) abundance of *Mytilus galloprovincialis* during 2007 for each location and depth.

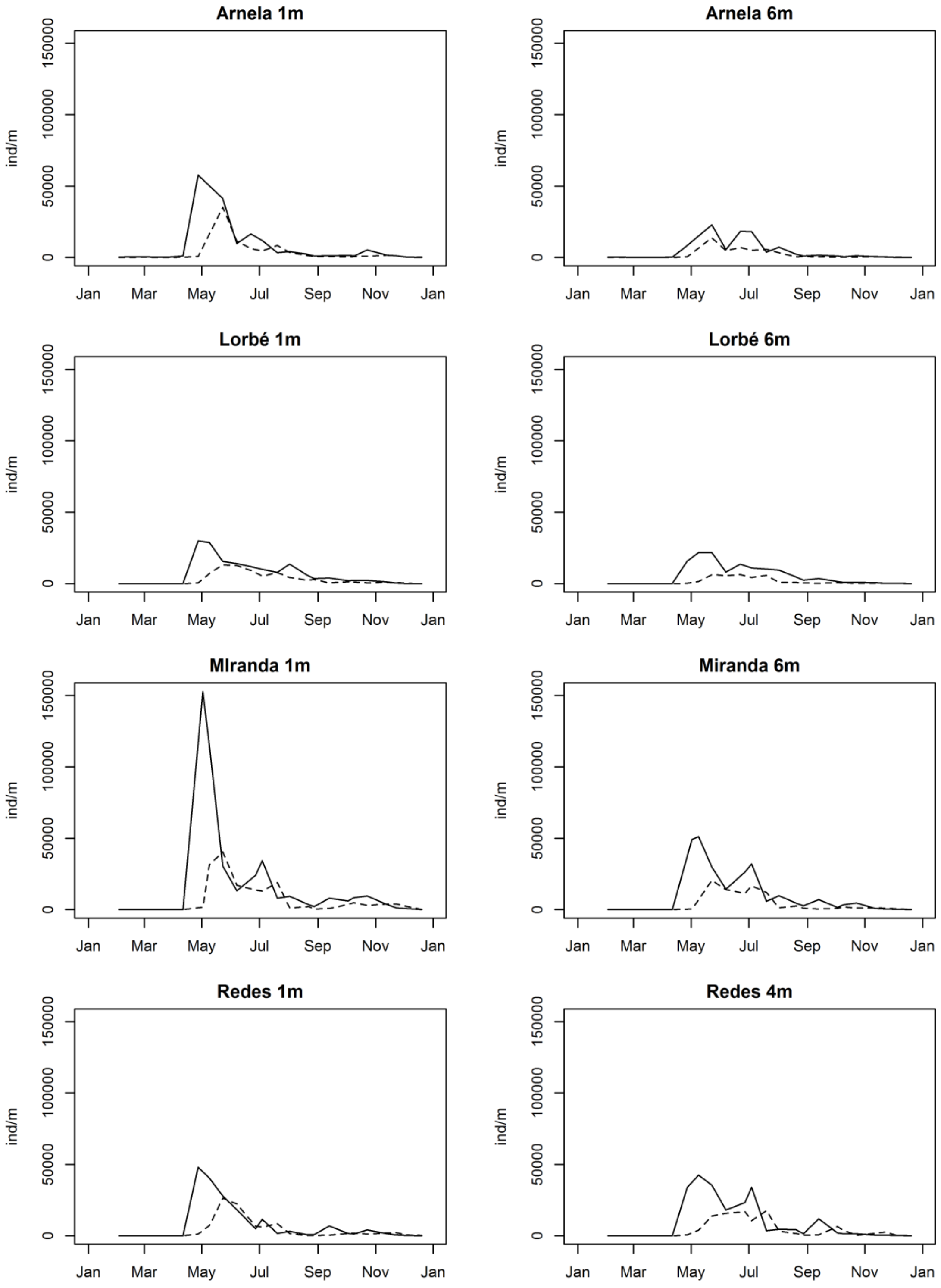

Figure 3: Observed (points) and fitted (lines) recruitment abundances of *Mytilus galloprovincialis* provided by the generalized linear model (Adj $R^2 = 0.7433$) outlined in Table 6. Dashed lines indicate 95% confidence intervals for the fitted values.