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Seasonal and synoptic spatio-temporal variability on larval delivery mechanisms inferred from mussel settlement patterns in the Portuguese coast

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ABSTRACT

Demographic connectivity is the process by which population persistence and growth are affected by the dispersal of individuals. In sessile marine species that disperse by planktonic larvae and form metapopulations, the interaction between oceanographic forcing and larval biology drives the spatial extent and magnitude of larval delivery to suitable habitat patches. The present study investigates the supply of *Mytilus galloprovincialis* larvae to rocky intertidal habitats located within and around two marine protected areas (MPA) in central Portugal, one located on the exposed coast and the other one in a sheltered bay, using time series of settlement intensity and oceanographic variables. The results indicate that larval delivery at short time scales (days) is strongly dependent on the interaction of upwelling circulation with coastline topography. In the exposed MPA, located on a coastal island, the magnitude of mussel larval delivery is limited by the dynamics of an upwelling front and filament that intercepts the island as upwelling increases and decreases. In the sheltered bay, under an upwelling shadow, the upwelling front promotes recirculation of the water mass, intensifying larval retention and settlement. The results are also consistent with larval transport distances of tens of kilometres and ongoing connectivity between the two MPA. This study highlights the relevance of coastal topography and its interaction with mesoscale hydrodynamics in the modulation of larval delivery, crucial for the persistence of populations and communities and in systematic conservation planning.

1. Introduction

Connectivity is essential for ecosystem functioning and resilience, as well as for maintaining important ecological and evolutionary processes, such as the persistence, recovery and growth of species, populations and biodiversity (Balbar & Metaxas 2019; Maxwell et al., 2020; Beger et al., 2022). It promotes the exchange of organisms, genes, nutrients, energy and materials between distinct populations, communities, ecosystems and habitats (Cowen & Sponaugle, 2009).

In systematic conservation planning, connectivity is highlighted as an important factor in the design and planning of Marine Protected Areas (MPAs) and their networks (MPAn) (Watson et al., 2014; Balbar & Metaxas 2019; Maxwell et al., 2020). Connectivity is important not just to allow the persistence of metapopulations within protected networks but also to promote spill-over of individuals or larvae to adjacent areas, allowing for the extension of the benefits of protection outside the protected areas (Berkström et al., 2022).

At the species level, connectivity encompasses larval dispersal, migrations, intra- and inter-specific interactions and ontogenetic processes (Beger et al., 2022). Knowledge of marine population connectivity pathways enables understanding of marine systems dynamics, increasing our capacity to protect them (Bryan-Brown et al., 2017).

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Applying connectivity as an ecological criteria in MPAs and MPAn design improves its resilience to face climate and anthropogenic changes by supporting marine processes and persistence (also growth and recovery) of biodiversity, species, populations, community composition, habitats and ecosystems (Balbar & Metaxas 2019).

However, despite connectivity being considered a crucial factor in the design, management and evaluation of MPAs and MPAn, it is still not easily operationalized in spatial planning (Bryan-Brown et al., 2017; Beger et al., 2022; Berkström et al., 2022). This is partly because the concept of connectivity is complex, wide and dynamic (time and space) and tools for quantitative integration into conservation plans (*e.g.* definition of guidelines, quantifiable metrics, methods for decision-support tools) are still in development (Beger et al., 2022).

For MPAs to work as an effective fisheries management tool is necessary to know the patterns of settlement and recruitment of new individuals, which is highly dependent on the connectivity among neighbouring populations, acting as sources or sinks (Sale et al., 2005) in a larger metapopulation. For benthic demersal and sessile species with complex life cycles, connectivity mainly happens during the pelagic larval stage, from reproduction to settlement (Cowen and Sponaugle 2009). Settlement plays a strong role in many complex life-cycle species population dynamics, as the process linking larval and benthic stages (Connell, 1985), and it is not just dependent on larval supply but also on features of coastal ocean and nearshore hydrodynamics (Von der Meden, 2009), as well as on the characteristics of the available substrate (Pulfrich, 1996).

Upwelling systems have been widely studied in the scope of several national and international initiatives (*e.g.* WIOURI, 2016; EIOURI, 2017; CLIVAR, 2018; EVAR, 2019; CUSCO, 2019; REEBUS, 2019; PRIMUS, 2021) including the influence of wind stress on cross-shore and along-shore transport and the consequences for larval dispersal and connectivity (Shanks & Brink, 2005; Queiroga et al., 2007; Rivera et al., 2013; Oliveira et al., 2019). In eastern boundary upwelling systems, northerly winds drive surface waters offshore and equatorward, forcing deep water, colder, saltier and nutrient-enriched to the surface. The reverse happens when winds weaken or reverse, with surface water flowing poleward and onshore, resulting in downwelling at the coast (Relvas et al., 2007). Although upwelling systems are traditionally considered dispersive systems, the interaction between wind forcing and coastal geometry generates a large spatial heterogeneity in nearshore retentive capability (*e.g.* upwelling shadows, fronts, eddies, filaments) which, joint with different larval behaviour strategies, largely modulate dispersal patterns and connectivity. By controlling their vertical position in the water column, larvae can exploit vertical differences in current speed and direction to remain close to coastal areas and take advantage of convergent fronts to increase retention (Queiroga and Blanton, 2004; Shanks & Brink, 2005).

In this study, the focus was on the Portuguese coast, aiming to evaluate the spatial-temporal dispersal dynamics between two MPAs (Parque Natural da Arrábida, PNA, and Reserva Natural das Berlengas, RNB) and how those dynamics may condition their potential spill-over capacity to adjacent areas, using a model species, the mussel *Mytilus galloprovincialis*. Mussels are largely employed as model species, because of their ubiquitous distribution, but also because of their ecosystem services as bioengineers, bioremediators, food sources and the socio-economic impacts of their fishery and aquaculture (Jones et al., 1994; Borthagaray & Carranza, 2007; European Commission DG-RI and Group of Scientific Advisors, 2017; FAO, 2022). Previous studies have reported the presence of connectivity pathways in the region, which allow the interchange of mussel larvae between these two MPAs, at least during certain characteristic oceanographic conditions (Gomes et al., 2016; Nolasco et al., 2018). Nonetheless, studies evaluating seasonal and synoptic (days to weeks) dispersal mechanisms, which highly determine the variability in the amount of interchange between populations are lacking. These studies are particularly relevant in areas with highly seasonal oceanographic conditions, such as the Eastern Boundary Currents.

The Iberian Peninsula is affected by the Iberian−Canary current upwelling system, where upwelling-favourable winds are prevalent between March and September (Wooster et al., 1976; Fraga et al., 1988; Queiroga et al., 2007; Alvarez et al., 2008; Arístegui et al., 2009). The oceanography of the Western Iberian Peninsula is largely governed by the mesoscale activity, on scales of 10–100 Kms and 10s of days, such as fronts, buoyant plumes, eddies, stratification and coastal upwelling (Queiroga and Blanton, 2004; Relvas et al., 2007). The principal factor controlling the coastal circulation is wind stress, which presents more than 70 % of its variability along the coast explained in a temporal scale of a few tens of days (Álvarez-Salgado et al., 2003) and determines strongly the intensity and direction of the cross-shore and along-shore directions of the surface currents (Oliveira et al., 2019). Among these mesoscale physical processes, wind, tides and fronts are the most relevant structures for the transport of plankton community and the dispersion or retention of larval stages of invertebrates and fishes to nurseries or favourable areas (Queiroga et al., 2007; Santos et al., 2007) for settlement and recruitment.

The study of spatio-temporal settlement patterns is a classic indirect approach widely employed in understanding pre-settlement processes and population dynamics, particularly in coastal environments (Dudas et al., 2009). Despite some limitations, the combination of settlement time series with data on local oceanography allows for the detection of potential pathways for larval dispersal. Then, settlement time series from places with contrasting environmental conditions can shed light on the processes controlling connectivity.

In this study, we focus on two MPAs with contrasting oceanographical characteristics, a small coastal archipelago highly affected by upwelling (RNB) and a sheltered bay (PNA), located in an upwelling shadow. Seasonal (monthly) and synoptic (every other day) variation in the settlement of *M. galloprovincialis* was jointly characterised with oceanographic variables in these contrasting areas, in order to investigate their retentive capability and upwelling influence. This approach allows to elucidate the main larval dispersal mechanisms associated with mesoscale hydrodynamics and local geomorphology, which determine the retentive capability of each location and how that modulates the isolation or connectivity between two MPAs, as well as their spill-over capability.

2. Material and methods

2.1. Sampling design

The spatio-temporal settlement pattern of the Mediterranean mussel, *Mytilus galloprovincialis*, and its relationships with oceanographic variables (salinity, temperature, chlorophyll-*a* concentration and upwelling) were studied in three regions of the Portuguese coast: two MPAs (RNB and PNA) and one region without environmental protection (Peniche). RNB is an insular reserve with the same level of protection throughout the archipelago, where two sampling sites were selected (Buzinas and Forte; located on the main island of Berlenga; Fig. 1). The spill-over capability of this MPA was evaluated in the Peniche area (PEN), the adjacent unprotected continental zone around Cape Carvoeiro, where 5 sampling sites were selected (Foz do Arelho, Baleal, Porto de Areia Norte, Consolação and Porto Dinheiro), comprising locations to the north and south of the cape (Fig. 1). Finally, the PNA is an MPA which encompasses different degrees of protection but with forbidden mussel collection in all of them, where 2 sampling sites were selected: Galapos with partial marine protection and Sesimbra with complementary marine protection (Fig. 1). An additional unprotected site, Bicas, was selected in the PNA’s area of influence to evaluate the spill-over capability of this MPA (Fig. 1). The RNB and Peniche regions are located on the northwest coast, which is characterised by a meridional oriented coastline, with a wide coastal platform and gentle slope. On the other hand, the PNA is closer to the estuaries of the Tejo and Sado, southward

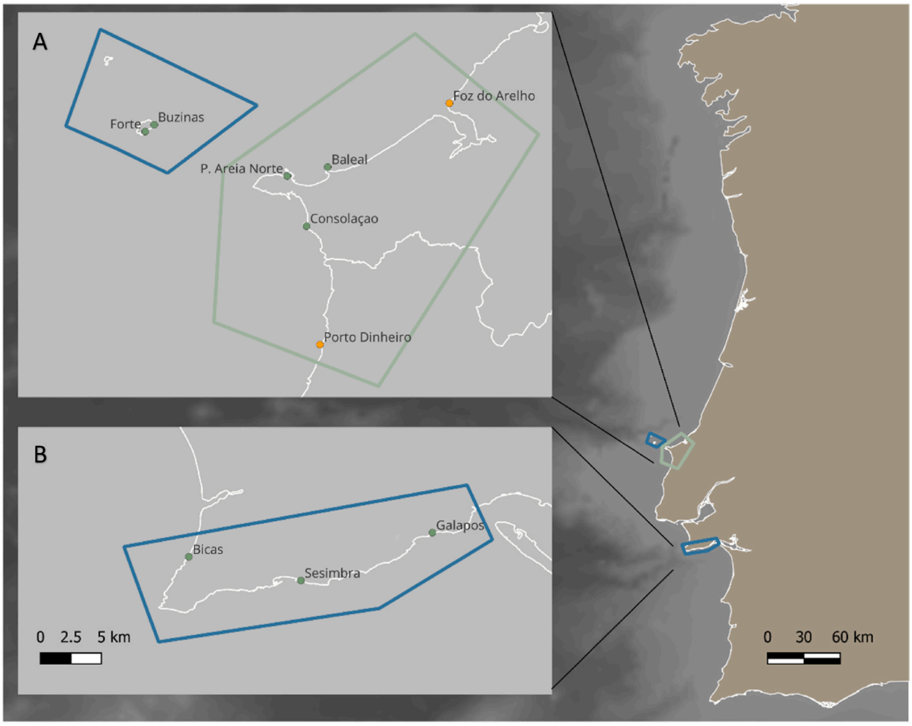

Fig. 1. Collection points location, low frequency time series (monthly, all points, green and orange) and high frequency time series (every other day in Spring, green points) in two Marine Protected Areas (MPA) on the Portuguese coast and adjacent areas. (A) Reserva Natural das Berlengas: Forte and Buzinas (inside MPA, blue polygon); Peniche: Foz do Arelho, Baleal, Porto de Areia Norte, Consolação and Porto Dinheiro (continental area, adjacent to MPA, green polygon), and (B) Parque Natural da Arrábida and adjacencies (blue polygon): Bicas (adjacent area to MPA), Sesimbra and Galapos (inside MPA). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

oriented and characterised by a narrower coastal platform with a greater slope (Fiuza, 1983). Mussels are broadly distributed along the rocky coast with no large differences between the northern and central regions of Portugal (Gomes et al., 2018).

Monthly mussel settlement time series were collected between February 2014 and January 2015 (with some gaps for reasons of logistic restrictions), to evaluate seasonal patterns. At each sampling point (Fig. 1), 3 replicated quadrats (6 × 6 cm) were randomly selected and scraped from the intertidal substrate during low tides. This low-frequency time series was complemented with high-frequency settlement samples collected every other day during the peak of reproduction of the mussels (May 2014) at selected locations (Fig. 1, green points), to evaluate high-frequency delivery mechanisms and synoptic environmental forcing variables. For the high-frequency time series, artificial settlement substrates (scouring pads: 6 × 6 cm), were placed and collected every other day, during low tides. Scouring pads are frequently employed as artificial substrates for mussel's settlement studies (Curiel-Ramírez and Cáceres-Martínez, 2010).

All samples were kept frozen until analysis. Subsequently, the samples were analysed under a stereoscopic microscope (SZ40, Olympus, Japan) to separate the juvenile mussels and calculate densities (individuals.cm^{-2}). From a representative subsample, the Individual length was then calculated as the maximum anteroposterior distance (mm) using ImageJ software (National Institutes of Health, USA) (Abràmoff et al., 2005), encompassing more than 50,000 individuals measured during the study.

2.2. Oceanographical conditions

The chlorophyll-*a* (Chl-*a*) concentration values were obtained from CMEMS Products (Global Ocean Satellite Observations, ACRI-ST based on Copernicus-GlobColour processor, U.S. Copernicus Marine Service Information, https://resources.marine.copernicus.eu/?option=com_csw&view=details&product_id=OCEANCOLOUR_GLO_CHL_L4_REP_OBSERVATIONS_009_082, accessed on May 11, 2017), consisting of multi-year time series of modelled daily data (daily averages), interpolated and reprocessed (forecast models with integration of observational data), from satellite observations (SeaWIFs, MODIS-Aqua, MERIS and VIIRSN), with a horizontal resolution of 1 km^2. Daily averages of sea surface salinity (SSS) and temperature (SST) were obtained from Mercator Ocean (GLORYS12V1, Global Ocean Physical Reanalysis, accessed on May 11, 2017), with resolution 1/12° (≈7 km for averages latitudes). The Upwelling Index (UI), defined as the volume of water transported in time and space, through a section parallel to the coastline, is calculated from the longitudinal component wind stress. For UI, the Ekman Transport sign is inverted to define positive values as offshore Ekman transport, consequence of upwelling favourable winds from the North, and negative values, as onshore Ekman transport, consequence of downwelling favourable winds from the south ($-Q_x$, m^3.s^{-1}.km^{-1}). UI time series were estimated according to the method of Bakun (1973), adapted from Álvarez-Salgado et al. (2003) and Gonzalez-Nuevo et al. (2014):

$$-Q_x = \frac{\tau_y}{f.\rho_w}\,.\,10^3 \qquad \tau_y = \rho_a\,.\,C_d\,.\,\sqrt{u^2+v^2}\,.\,v$$

Where $-Q_x$ is the volume transport from wind stress (τ_y), x and y subscripts are the zonal and meridional (east-west and north-south) components, respectively, f is the Coriolis parameter, defined as 2Ωsin (θ), at latitude θ, where Ω is the vertical component of the angular velocity of the Earth (7.29.10^{-5}), ρ_w is the density of seawater (≈1025 kg m^{-3}), ρ_a is the air density (1.22 kg.m^{-3} a 15 °C), C_d is the empirical dimensionless drag coefficient (1.4.10^{-3}, according to Hidy, 1972), and u and v are the zonal and meridional horizontal hourly averages of wind speed (m.s^{-1}), 10m above the sea level. The wind components (u and v), for each sampling point, were obtained from Copernicus Climate Change Service Information (Hersbach et al., 2018), accessed on July 27, 2020), through ERA5 climate reanalysis, which consists of multi-year time series of hourly modelled data, interpolated, with a horizontal resolution grid of 0.25° × 0.25° and disregarding ground points.

Generalized additive models (GAMs), as implemented in the mgcv library of R 3.6.2 (R Core Team, 2019), were used to investigate the seasonal patterns of the environmental variables measured (SST, SSS, Chl-*a* and UI), using Day of the Year as the continuous variable, as well as the effect of geographical variation, using Region as a factor.

Some differences observed in the SST, Chl-*a* concentrations and SSS between RNB and Peniche might be indicating the presence of an upwelling front between the island and the mainland. To verify its existence, a new variable was created, DifTemp, using the difference between RNB temperature and each mainland location at Peniche. Positive differences indicate that the temperature is warmer near the RNB, and negative values indicate warmer temperatures near the mainland coast. This variable can be considered a proxy of the presence of an upwelling front between the island and the mainland. Aiming to verify the occurrence of a delay between the upwelling favourable winds and the formation of the front, a cross-correlation analysis between DifTemp and UI by locations was employed. The relationship between DifTemp and UI was investigated regarding two different time-integrations of the upwelling index, in order to describe the different delays of the effect of wind stress on temperature. UI_0 represents the instantaneous effect of wind stress, while UI_10 is the integration of wind stress over the previous 10 days. GAMs were also used to test these relationships, as well as the interactions with the variable Location.

2.3. *Settlement analysis*

For the settlement analysis, mussels were grouped by size into 2 groups: (i) early plantigrades or newly settled individuals (<0.75 mm) which abundance is largely conditioned by larval delivery and primary settlement mechanisms and (ii) late plantigrades (0.75–2.5 mm) which include older settlers where secondary settlement (drifting) and post-settlement mortality can play a major role. To avoid interferences of post-settlement processes, only early plantigrades were used to understand the immediate effect of larval transport and dispersal processes on settlement. The seasonal synchrony of settlement between regions was evaluated using cross-correlations between the low-frequency settlement time series (monthly) of early plantigrades (<0.75 mm), after the elimination of seasonality by differentiation (x = x-x(lag), lag = 1), which was verified by applying autocorrelation analyses on settlement time series, in each location and region. Delays in settlement between stations would indicate different larval delivery mechanisms between them.

In order to infer larval delivery mechanisms, the relationships between environmental variability (SST, SSS, Chl-*a*, UI) and high-frequency settlement time series, as well as their interactions at the regional (Region) and local (Location) level, were also evaluated using GAMs (mgcv library of R). High-frequency settlement time series recorded every other day reflect hydrodynamic processes with event-scale variability as low as 4 days, allowing to infer the influence of typical cycles of upwelling/relaxation (6–20 days) on larval settlement at each location. The Akaike Information Criterion (AIC) was used to select the optimal set of variables for inclusion in the models. The validation of the models included the verification of homogeneity, normality and independence assumptions (Sokal and Rohlf, 1969; Zar, 1999; Zuur et al., 2009). The statistical analyses were performed using the software Statistica 12 (Stat Soft, USA) and R 3.6.2 (R Core Team, 2019).

3. Results

3.1. *Oceanographical conditions*

The environmental variables (SST, SSS, Chl-*a* and UI) showed small variations between sampling locations within each region, therefore average values for each region were used to evaluate seasonal patterns and variability between regions (Fig. 2).

The GAM employed to verify the seasonality and variability of the environmental parameters (Table 1), confirmed a large seasonal effect in the SSS and SST time series, with 61.5%–88.5% of the deviation explained. However, the Day of the Year showed a smaller influence on chlorophyll-*a* content or upwelling index, explaining 22.9% and 10.9% of the variability of those environmental variables, respectively (Table 1).

SST and SSS showed a gradient from North to South, with colder and less salty waters in Peniche than in the PNA (Table 1). Nonetheless, differences between mainland (Peniche) and the island (RNB) at the same latitude, were also significant, with RNB showing similar average sea surface temperatures than PNA and intermediate sea surface salinity values (Table 1).

Concerning Chl-*a* content, Peniche and PNA showed similar values but significantly higher than those recorded for RNB (Table 1). No significant differences in UI were observed between regions, although the northern locations (RNB and Peniche) showed a larger influence of upwelling than PNA (Table 1).

Differences in sea surface temperature between the island (RNB) and the mainland (Peniche) can be explained by an upwelling process in which cold waters rise to the surface close to the mainland's shore creating an upwelling front between both regions with a delay of no longer than 1 day, as illustrated by the maximum correlations detected at lag 0 and lag 1 ($r = 0.105$ and $r = 0.108$, respectively) in the cross-correlation analysis between DifTemp and UI time series.

Regarding the differences of sea surface temperatures at each of the mainland sampling locations (Peniche) in comparison to Berlengas (DifTemp), which are presumed to reflect the intensity and position of the upwelling front and how it is influenced by topographic features (Fig. 3; Table 2), the GAM analysis indicated that significant effects were only observed at Foz de Arelho and Baleal, the two most Northern locations. Both locations showed a linear increment of temperature differences as UI_0 increased. UI_10 indicates the persistence of upwelling events considering it represents the average UI value for the previous 10 days. UI_10 showed a significant influence on the differences of sea surface temperatures between RNB and all the mainland sampling locations evaluated (Table 2; Fig. 3). Once again, Foz de Arelho and Baleal showed a different pattern than the rest of locations, maintaining a linear relationship between UI and the increment of differences in sea surface temperature concerning the island. For the rest of the locations, differences in sea surface temperature tend to increase when UI reached positive values, but then decrease indicating that water got warmer in those locations of the mainland than in the island when UI surpassed intermediate positive values.

Fig. 4 shows the detail of the environmental variables during Spring 2014, when the high-frequency settlement samples were collected (May 2014). Regarding temperature and salinity (Fig. 4A and B), the pattern observed agrees with those recorded throughout the year (Fig. 2), where the PNA kept warmer and saltier waters than the RNB or Peniche. The RNB also showed warmer and saltier waters than Peniche during the first half of the month, but during the second half the island and Peniche recorded similar values for both variables (Fig. 4A and B).

Chlorophyll-*a* concentrations (Fig. 4C) showed the highest values in Peniche, followed by PNA and RNB, with the three regions having 2 peaks of Chl-*a*, at the beginning and in the middle of the month, however with a certain time lag between regions.

Considering the upwelling index (Fig. 4D), upwelling predominated throughout the month, with lower intensity in the PNA than in the rest of the northern regions and only one downwelling episode was recorded in the middle of the month with similar intensity in all regions.

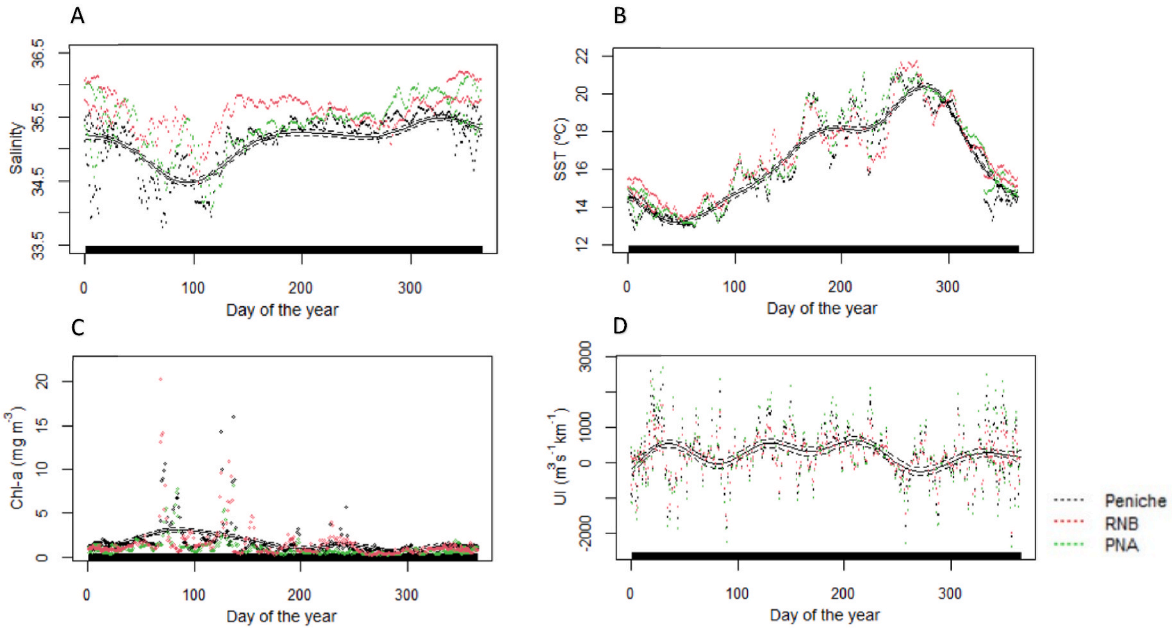

Fig. 2. (A) Salinity (SSS), (B) Sea surface temperature (SST, °C), (C) chlorophyll-*a* concentration (Chl-*a*, mg.m^{-3}) and (D) upwelling index (UI, m^{3}.s^{-1}.Km^{-1}), expressed as daily averages at the sampling regions: Reserva Natural das Berlengas (RNB), Peniche and Parque Natural da Arrábida (PNA), and the estimated smoothing curves of Day of the year for each variable, from December 2013 to January 2015. Dashed lines show a 95% confidence interval and tick marks along the x-axis represent where the environmental values (points) occurred.

Table 1

Structure of the General Additive Model describing sea surface temperature (SST, °C), sea surface salinity (SSS), chlorophyll-*a* concentration (Chl-*a*, mg.m^{-3}) and upwelling index (UI, m^{3}.s^{-1}.Km^{-1}) variability along the study regions: Reserva Natural das Berlengas (RNB), Peniche coastline (Peniche) and Parque Natural da Arrábida (PNA), from December 2013 to January 2015. S.E.: standard error; e.d.f.: estimated degrees of freedom.

Region	SST (°C)				SSS			
	Parametric Coefficients				Parametric Coefficients			
	Estimate	S.E.	*t*	*p*	Estimate	S.E.	*t*	*p*
Peniche (Intercept)	16.226	0.039	417.79	**< 2 x 10^{-16}**	35.123	0.013	2664.70	**< 2 x 10^{-16}**
RNB	0.324	0.055	5.90	**4.7 x 10^{-9}**	0.261	0.019	25.26	**< 2 x 10^{-16}**
PNA	0.336	0.055	6.12	**1.2 x 10^{-9}**	0.471	0.019	14.01	**< 2 x 10^{-16}**
	Smooth terms (non parametric)				Smooth terms (non parametric)			
	e.d.f	F	*p*		e.d.f	F	*p*	
Day of the Year	8.95	1076	**< 2 x 10^{-16}**		8.64	154.4	**< 2 x 10^{-16}**	
	R^2 adjusted: 0.884		% Deviance explained: 88.5%		R^2 adjusted: 0.612		% Deviance explained: 61.5%	
Region	Chl-*a* (mg.m^{-3})				UI (m^{3}.s^{-1}.Km^{-1})			
	Parametric coefficients				Parametric coefficients			
	Estimate	S.E.	t	*p*	Estimate	S.E.	t	*p*
Peniche (Intercept)	1.590	0.042	39.387	**< 2 x 10^{-16}**	249.60	33.27	7.503	**1.17 x 10^{-13}**
RNB	−0.604	0.094	−6.406	**2 x 10^{-10}**	65.73	47.05	1.397	0.163
PNA	−0.123	0.094	−1.305	0.192	−47.08	47.05	−1.001	0.317
	Smooth terms (non parametric)				Smooth terms (non parametric)			
	e.d.f	F	*p*		e.d.f	F	*p*	
Day of the Year	8.71	36.65	**< 2 x 10^{-16}**		8.87	15.99	**< 2 x 10^{-16}**	
	R^2 adjusted: 0.222		% Deviance explained: 22.9%		R^2 adjusted: 0.102		% Deviance explained: 10.9%	

3.2. Settlement analysis

3.2.1. Low-frequency settlement time series

Fig. 5 shows the densities of *Mytilus galloprovincialis* along the low-frequency time series (monthly sampling), which took place between February 2014 and January 2015. The settled mussels were grouped by size: early plantigrades, smaller than 0.75 mm (*ca.* age: max. 15 days) and late plantigrades, with size between 0.75 mm and 2.5 mm (*ca.* age: between 15 days and max. 2 months).

Although both size classes show similar patterns at each region, indicating similar delivery processes for early and late plantigrades (Fig. 5), we only used the early plantigrades data to investigate larval transport and dispersal processes due to the scale (days) of the environmental process in analysis.

Settlement peaked at different times of the year in each region. While settlement in the archipelago of RNB showed its maximum values in late-winter/early-spring, the maximum values at Peniche were recorded ≈1 month later, during late-spring/early-summer (RNB vs Peniche r = −0.70 at lag-1); while the southern locations showed the period of maximum settlement 4–5 months later, in late-summer/early-autumn

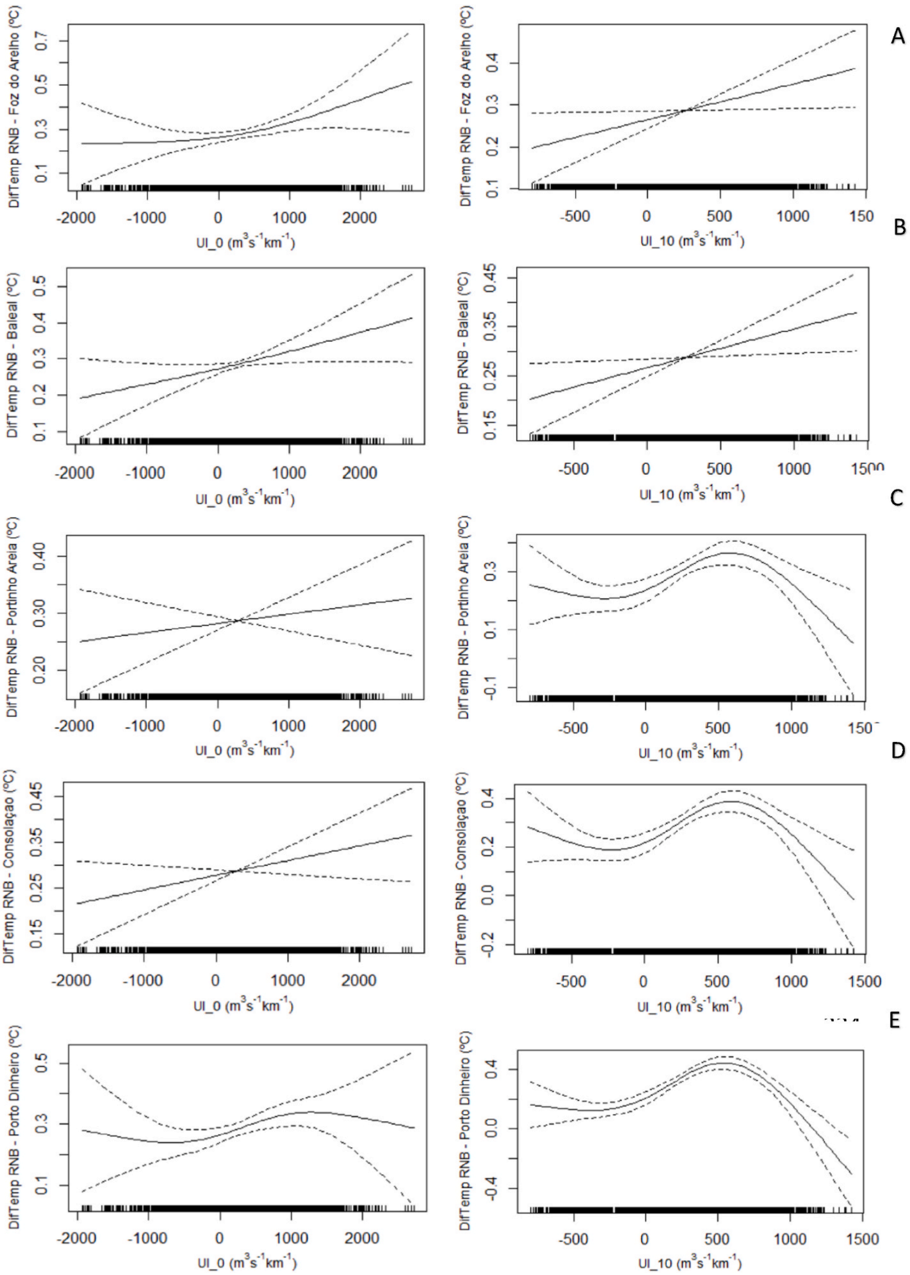

Fig. 3. Result of the Generalized Additive Models (GAM), showing the partial effect of Instantaneous Upwelling Index (UI_0, $m^3.s^{-1}.Km^{-1}$, left column) and the UI averaged during the last 10 days (UI_10, $m^3.s^{-1}.Km^{-1}$, right column) in the difference of temperature between each of the mainland sampling locations (from North to South: A) Foz do Arelho, B) Baleal, C) Porto de Areia Norte, D) Consolação, E) Porto-Dinheiro). Dotted lines indicate 95% confidence intervals, and tick marks along the X-axis below each curve represent effect values where observations occurred.

(RNB vs PNA r = −0.86 at lag-5; Peniche vs PNA r = 0.76 at lag −4; Fig. 5). Cross-correlations between regional settlement time series, also showed an inverse relationship between settlement in RNB and the other two locations (RNB vs Peniche r = −0.70 (lag-1); RNB vs PNA r = −0.86 (lag-5)), suggesting the opposite larval delivery mechanisms between the archipelago and mainland.

Large differences were also observed in settlement magnitude between regions, with maximums at PNA, followed by Peniche and RNB (RNB: 10, Peniche: 10^2 and PNA: 10^3; Fig. 5).

With regard to the particular patterns of settlement within each region, at the RNB settlement seems to have been delayed at the most sheltered locations (Forte) with regard to the most exposed one (Figs. 1 and 5). At the Peniche region, the largest settlement occurred at the locations farther from the influence of the Carvoeiro Cape (Foz do Arelho and Porto Dinheiro), being much larger at the northern location (Foz do Arelho). With regard to the other three sampling stations in Peniche, located around the cape, the northern one (Baleal), again receiving a larger number of settlers than the locations at the tip (Porto de Areia Norte) or south of the promontory (Consolação) (Figs. 1 and 5). When looking at the settlement time series recorded at the PNA, the arrival of early and late-plantigrades seemed to be decoupled both in space and time (Fig. 5). The largest arrivals of early-plantigrades occurred in September at Sesimbra, located in the middle of the bay, while the largest density of late-plantigrades was recorded one month earlier at Bicas, north to the Espichel Cape and outside of the bay influence, suggesting also different delivery mechanisms between locations within the PNA region.

Table 2
Results of the Generalized Additive Models (GAM), showing the partial effect of instantaneous UI (UI_0, $m^3.s^{-1}.Km^{-1}$) and prevalent UI (averaged during the previous 10 days; UI_10, $m^3.s^{-1}.Km^{-1}$) on the differences of temperature (DifTemp) observed between the mainland sampling locations (Peniche) and the island (RNB).

	UI_0 ($m^3.s^{-1}.Km^{-1}$)				UI_10 ($m^3.s^{-1}.Km^{-1}$)			
	Parametric Coefficients				Parametric Coefficients			
	Estimate	S.E.	*t*	*p*	Estimate	S.E.	*t*	*p*
(Intercept)	0.287	0.007	41.85	$<2 \times 10^{-16}$	0.287	0.007	42.84	$<2 \times 10^{-16}$
	Smooth terms (non parametric)				Smooth terms (non parametric)			
Location	e.d.f	F	*p*		e.d.f	F	*p*	
Foz do Arelho	1.64	3.122	**0.0437**		1	4.601	**0.03207**	
Baleal	1.14	4.291	**0.0414**		1	5.453	**0.01963**	
Porto de Areia Norte	1	0.626	0.4288		2.87	5.577	**0.00155**	
Consolaçao	1	2.347	0.1257		2.92	7.332	**5.3×10^{-5}**	
Porto Dinheiro	2.43	1.874	0.1448		2.95	20.759	**$< 2 \times 10^{-16}$**	
R^2 adjusted: 0.007			% Deviance explained: 1.07%		R^2 adjusted: 0.051		% Deviance explained: 5.56%	

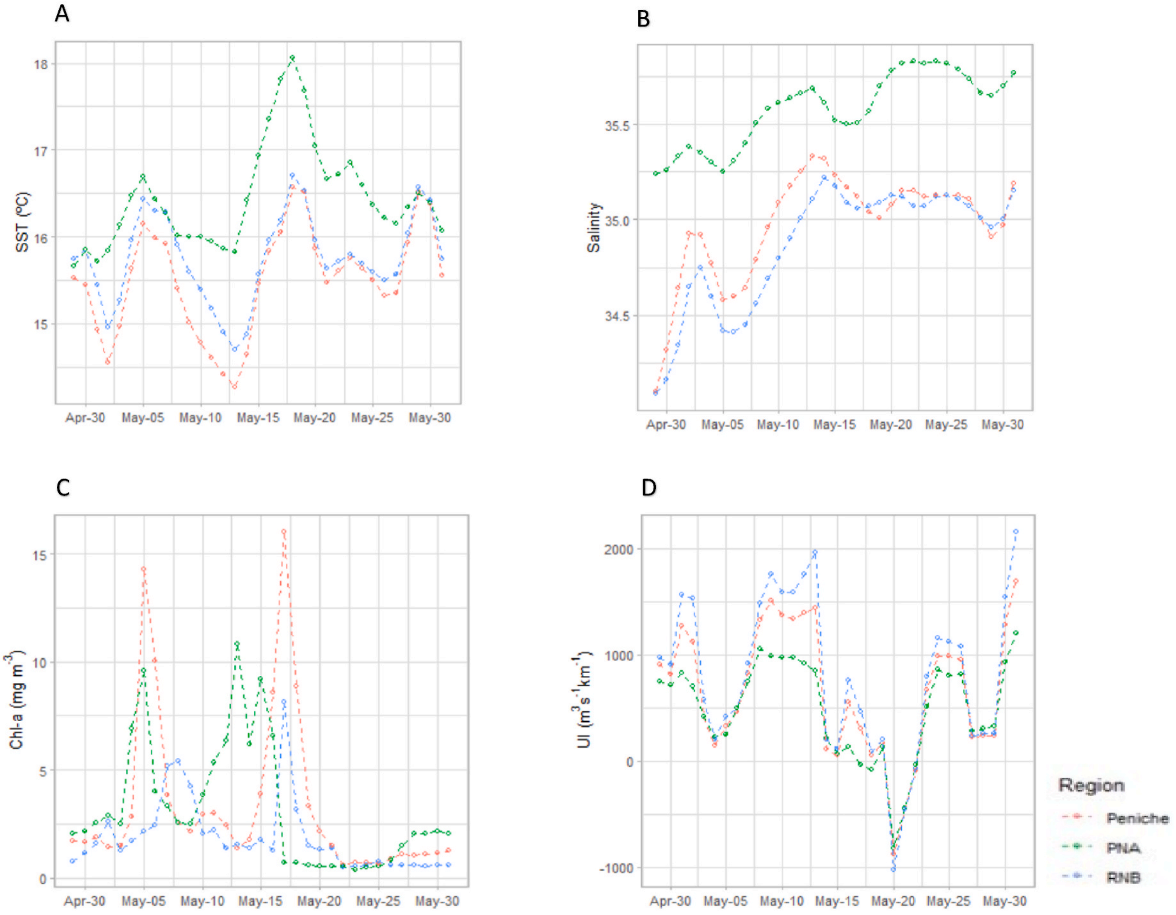

Fig. 4. (A) Sea surface temperature (SST, °C), (B) salinity (SSS), (C) chlorophyll-*a* concentration (Chl-*a*, $mg.m^{-3}$) and (D) upwelling index (UI, $m^3.s^{-1}.Km^{-1}$), during Spring 2014 (May), expressed as daily mean between locations for each region: Peniche (red), Parque Natural da Arrábida, PNA (green) and Reserva Natural das Berlengas, RNB (blue). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

3.2.2. *High-frequency settlement time series*

The high-frequency settlement time series, recorded every other day during May 2014, showed some of the patterns observed in the low-frequency sampling, such as a much larger magnitude of settlement at PNA (Fig. 6) and the inverse relationship between settlement time series in the archipelago (RNB) and the other two mainland regions (RNB vs Peniche $r = -0.59$ at lag -2; RNB vs PNA $r = -0.69$ at lag -2) (Fig. 6). Also, the locations within each region which maintained the largest settlement magnitudes were the same ones detected through the monthly time-series: Forte in RNB, Baleal in Peniche and Sesimbra in PNA (Fig. 6). Additionally, the abundance of early- and late-plantigrades was decoupled in time and space only at PNA (Fig. 6).

GAMs were employed to attempt to identify the relationship between the environmental variables and the differential settlement pattern observed between regions. According to the AIC (Table 3), the best model, explaining 43.1% of the variance observed on settlement between regions, included the environmental variables SSS, SST and Chl-*a* and their interaction with the factor Region (Table 4).

When trying to explain differences in settlement patterns between the three regions, most of the variability was dominated by the PNA

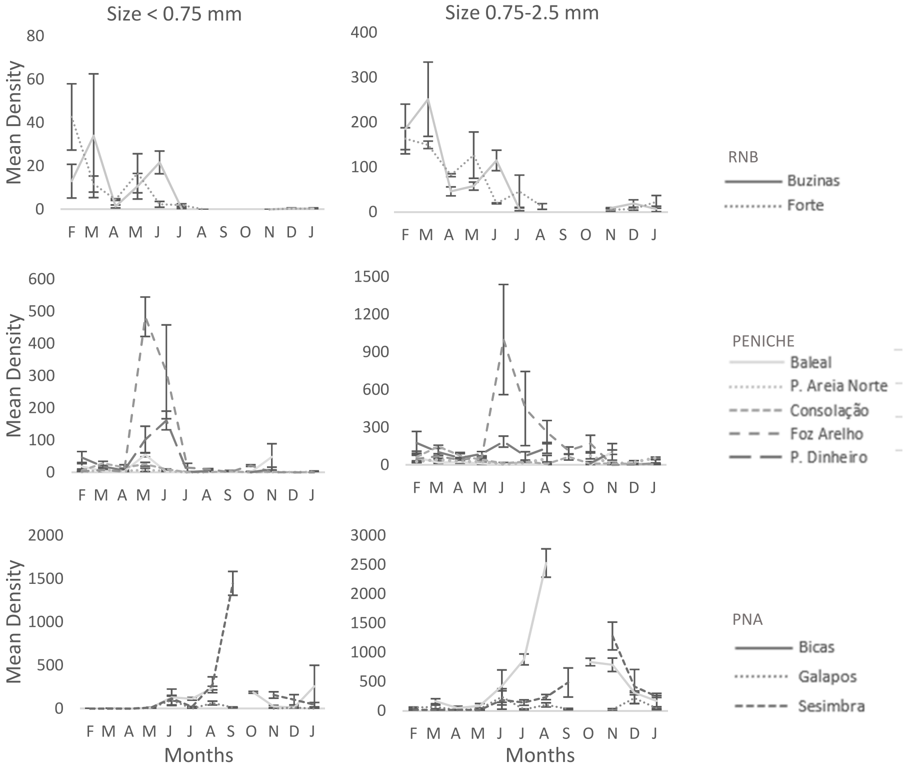

Fig. 5. Monthly settlement time series. Average densities of *Mytilus galloprovincialis* settlers (triplicated collectors of 36 cm^2), by sampled locations at each region: Reserva Natural das Berlengas (RNB), Peniche and Parque Natural da Arrábida (PNA), grouped by size (column on the left: <0.75 mm, right: between 0.75 mm and 2.50 mm). Samples were collected between February 2014 and January 2015. Bars represent standard error.

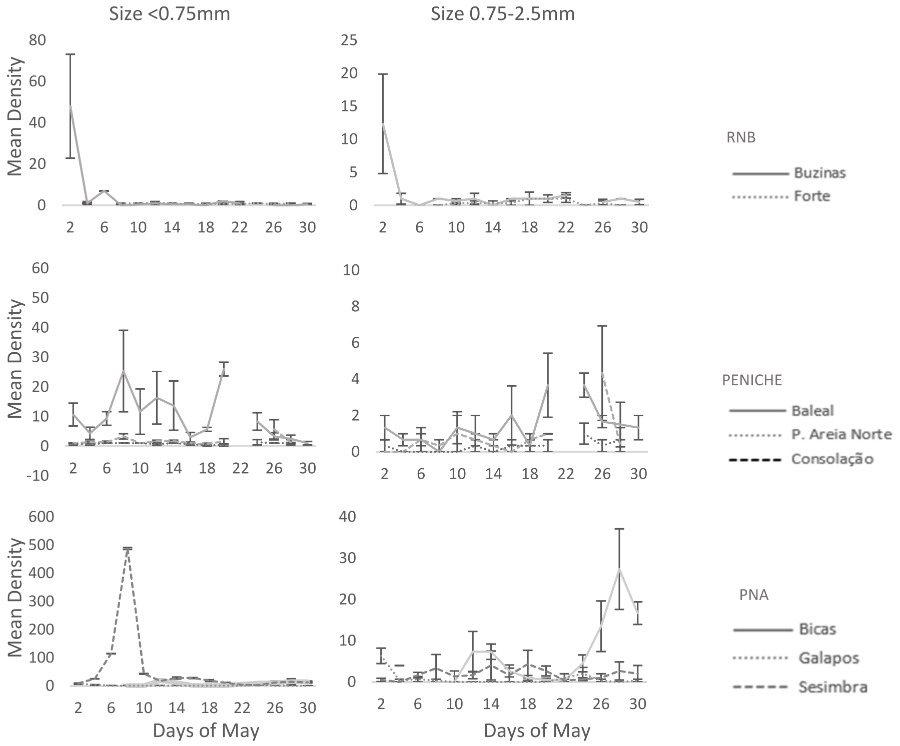

Fig. 6. High-frequency settlement time series. Average densities of *Mytilus galloprovincialis* mussels (triplicate, number of individuals per sampled area, 36 cm^2), by sampled locations at each region (RNB: Reserva Natural das Berlengas, Peniche and PNA: Parque Natural da Arrábida), grouped by size (column on the left: <0.75 mm, right: between 0.75 mm and 2.50 mm. Samples were collected every other day during the Spring 2014 (May). Bars represent standard error.

Table 3

Summary of Akaike Information Criteria (AIC) for the selection of the optimal set of variables for inclusion in the models to explain every other day early plantigrades settlement (<0.75 mm) between the study areas and inside them: Reserva Natural das Berlengas (RNB), Peniche and Parque Natural da Arrábida (PNA) during May 2014. Oceanographic variables: average of sea surface salinity (Av. SSS), chlorophyll-*a* concentration (Av. Chl-*a*, mg.m^{-3}), sea surface temperature (Av. SST, °C) and upwelling index (UI, m^{3}.s^{-1}.Km^{-1}), expressed as averages of two days (day sample and day before). Variables values used for the analysis were averaged for each location (d.f.: estimated degrees of freedom).

Model	Regional			PNA			RNB + Peniche		
	edf	AIC	% var.	edf	AIC	% var.	edf	AIC	% var.
Chl-*a* * Region	13.46	388.83	26.50	7.69	150.70	43.10	4.76	95.61	47.50
SSS * Region	13.06	345.51	35.70	7.46	115.72	57.20	6.83	135.14	13.80
SST * Region	10.37	399.97	22.40	6.97	173.71	30.50	4.76	143.27	4.71
UI * Region	16.01	399.60	25.20	7.35	185.69	23.80	5.80	141.62	8.70
Chl-*a* * Region + SSS * Region	18.69	349.65	37.10	10.42	119.27	58.00	10.42	76.57	61.10
Chl-*a* * Region + SST * Region	15.32	379.53	29.50	15.14	132.12	56.80	9.85	95.46	51.10
Chl-*a* * Region + UI * Region	17.04	385.14	29.00	12.08	151.72	46.70	8.93	90.69	52.70
SSS * Region + SST * Region	16.95	340.59	38.20	**13.30**	**107.55**	**63.60**	8.24	131.75	22.90
SSS * Region + UI * Region	20.85	336.60	40.40	11.22	117.66	59.10	8.96	133.62	22.60
Chl-*a* * Region + SSS * Region + SST * Region	**25.96**	**332.06**	**43.10**	16.29	108.50	65.10	12.82	76.37	65.60
Chl-*a* * Region + SSS * Region + UI * Region	26.58	336.57	42.50	14.55	120.92	60.20	**12.55**	**70.20**	**63.30**

Table 4

Results of the Generalized Additive Models (GAM), showing the partial effect of SSS, SST and Chl-*a* and their interactions with the factor Region, on differences observed in the settlement patterns (early plantigrades, <0.75 mm, May) between regions.

	Parametric Coefficients			
	Estimate	S.E.	*t*	*p*
(Intercept)	0.4673	0.2044	2.286	0.0229
	Smooth terms (non parametric)			
Region	e.d.f	F	*P*	
SSS:RNB	3.214	6.235	**0.0046**	
SSS:Peniche	3.236	2.722	**0.02191**	
SSS:PNA	4.433	6.939	**5.78×10^{-6}**	
SST:RNB	1	0.061	0.80552	
SST:Peniche	1.793	1.458	0.25022	
SST:PNA	1.997	1.997	**0.0389**	
Chl-*a*:RNB	2.865	0.64	0.65294	
Chl-*a*:Peniche	1	0.093	0.76006	
Chl-*a*:PNA	4.421	3.104	**0.00689**	
	R^2 adjusted: 0.385		% Deviance explained: 43.1%	

(Table 4; Fig. 7), since it was the region with larger settlement observed by one and two orders of magnitude with regard to RNB or Peniche, respectively (Fig. 6). Therefore, the model selected explains better the variability observed in settlement at PNA, which seems to be reduced during periods of lower temperature and high concentration of Chl-*a* (Fig. 7), commonly related to upwelling episodes, suggesting better conditions for settlement at PNA during downwelling events. Nonetheless, low salinity values, which are commonly associated with downwelling episodes, showed a detrimental effect over settlement in the PNA until they reached values over 35 (Fig. 7).

The relationship between environmental variables and settlement patterns at PNA are better illustrated when analysed separately by sampling location within the region (Fig. 8; Table 5). The interaction between Location and SST and SSS explained the largest variability (63.6%; Table 3), unveiling opposite relationships between the locations protected by the Setúbal Peninsula (Sesimbra and Galapos) and the location exposed to the open coast (Bicas). Settlement at Bicas showed a linear and positive relationship with salinity and an inverse relationship with temperature (Fig. 8), suggesting a positive effect of upwelled waters (cold and saltier) on larval delivery to this location. On the other hand, settlement in Sesimbra and Galapos decreased as salinity increased, with a more marked effect at the innermost location, Galapos (Fig. 8). Concerning temperature, it was also detected an increase of settlement as temperature rose in Sesimbra until it reached a plateau around 16 °C (Fig. 8). Although the same relationship with temperature was not detected in Galapos, it seems that settlement in locations protected by the Peninsula was enhanced by downwelling favourable conditions which brings warmer water with lower salinity.

To better understand the environmental influence over settlement in the northern regions, a separate GAM without PNA was performed, using only two locations which concentrated most of the settlement observed at RNB (Buzinas) and Peniche (Baleal). According to the AIC, the model which better explains the variability observed in the settlement between these two locations were UI, Chl-*a* and SSS (Table 3; 63.30%).

GAM results illustrate the different influence of upwelling on mussel settlement at the archipelago (Buzinas) in comparison to the mainland (Baleal, Peniche) (Table 6; Fig. 9). While Peniche shows a linear increase in settlement as UI increases, no significant relationship between settlement and UI was detected at the RNB. Nonetheless, at RNB mussel settlement decreases as salinity increases until it reached a plateau, suggesting some sort of larval delivery associated with upwelling relaxation or downwelling events (Fig. 9). Differences were also patent concerning the effect of Chl-*a*. In Peniche settlement showed an optimum at intermediate-high values of Chl-*a*, while in RNB, Chl-*a* only influences settlement when it reached very high values (Fig. 9).

4. Discussion

This study highlights the relevance of coastal topography and its interaction with upwelling in the modulation of larval delivery, to explain the large spatio-temporal variability usually recorded on settlement processes. Winds, tides, freshwater inputs and ocean currents are important processes (Cowen, 2002) interacting with the geomorphology of the coast (Fiuza, 1983; Alvarez et al., 2008; Bird, 2008; Largier, 2020), largely determining larval dispersal processes (Shanks et al., 2000; Shanks and McCulloch, 2003; Satterthwaite et al., 2020; Killeen et al., 2023). Topography modulates the oceanography and consequently influences the larval transport, dispersal, retention, survival and connectivity between populations In large, meso and small scales (Wolanski and Hamner, 1988; Cowen, 2002; Killeen et al., 2023). Moreover, the interaction of topography with physical and biological factors increases the complexity of the larval delivery mechanisms, resulting in what might seems to be a stochastic larval supply process, with large spatio-temporal variability and cascading effects on recruitment and maintenance of marine populations (Cowen, 2002; Siegel et al., 2008). The results of the present study suggest that, along the Portuguese coast, the interactions between upwelling regimes and topography are the most relevant processes governing mussel larval delivery to intertidal habitats, both when looking at seasonal or synoptic settlement patterns.

With regard to the seasonal settlement patterns, a strong temporal

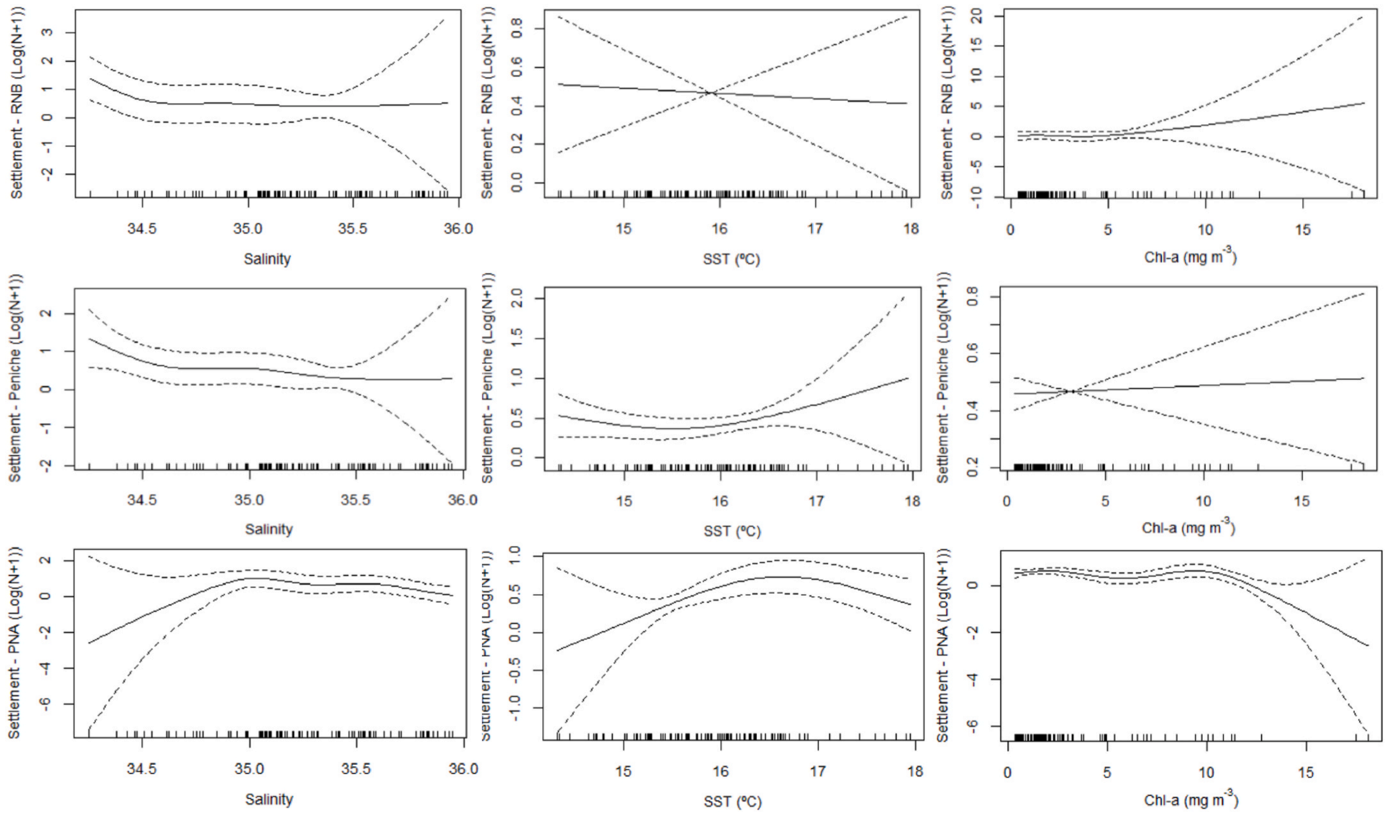

Fig. 7. Results of the Generalized Additive Models (GAM), showing the partial effect of SSS, SST and Chl-*a* and their interactions with the factor Region in the settlement patterns (early plantigrades, <0.75 mm, May). Dotted lines indicate 95% confidence intervals, and tick marks along the X-axis below each curve represent effect values where observations occurred.

decoupling between the northern regions (RBN and Peniche) highly influenced by upwelling, and the southern wide open bay (PNA), located in an upwelling shadow, was detected. Peaks of settlement in the north are synchronized with the upwelling favourable season, while at PNA maximum settlement occurs during the fall, when downwelling favourable winds become predominant (Fig. 5). One reason for the decoupling observed between regions might be related to the interactions between upwelling and local topography on larval delivery mechanisms.

Bays located in upwelling regions (upwelling bays) are one of the most productive nearshore waters, since they provide sheltered habitats and enlarged retention times for upwelled waters, sometimes larger than the synoptic variability timescale, which favour the concentration of organisms and primary production (Graham and Largiert, 1997; Ryan et al., 2017; Satterthwaite et al., 2020; Largier, 2020). Upwelling bays can present an upwind boundary formed by a step, where the wind is distanced from the coast, originating an upwelling shadow zone where winds weaken and water warms, favouring the formation of a thermal front between the cold alongshore water current (upwelling jet/filament) and the bay. This interaction between topography and winds generates a cyclonic circulation inside the bay, which increases water residence time inside the bays and accumulation of food and organisms (Largier, 2020), as observed at the Lisbon-Setúbal embayment (Oliveira et al., 2009; Moita et al., 2003) where the PNA is located. At the Setúbal Bay, the Espichel Cape represents that boundary (Fig. 1) distancing the wind from the bay and promoting the formation of an upwelling shadow, which favours the much larger magnitude of settlement in this region (1 and 2 orders of magnitude larger than at RNB and Peniche, respectively). The differences observed between locations within the PNA region also suggest how this upwelling shadow forms and interacts with winds and other environmental factors (Fig. 8). While settlement at Bicas, located to the north of Espichel Cape and outside of the Setúbal Bay, showed a positive relationship with cold and salty water (Fig. 8A) characteristic of upwelled water, settlement inside of the bay (Sesimbra and Galapos; Fig. 1), showed an inverse relationship with those variables (Fig. 8B–C). These observations agree with other studies reporting hydrodynamic patterns in this area, which highlight that during the intensification of northerly winds, SST decreases northward of Cabo Espichel, while in Setúbal Bay water temperatures remain warm during the intensification and relaxation of upwelling (Oliveira et al., 2009). Warm water enhance settlement in the middle of the bay (Sesimbra), almost linearly until a plateau was reached, which might indicate the formation of a thermal front associated to the upwelling shadow. Something similar was observed with salinity, where a linear detrimental effect on settlement was observed only after salinity rose above certain values, also supporting the relationship with a front around the bay (Fig. 8B). In the innermost location of the bay, the detrimental effect of salinity started at lower salinity values, and was more pronounced (Fig. 8C), which might indicate that the preferential position of the front is closer to the middle of the bay and less stable at the inner station. These observations also agree with the fact that settlement of early-plantigrades is much larger at the middle of the bay (Sesimbra) than in the inner station (Galapos) or at the station located outside of the bay (Bicas). Therefore, our results suggest that settlement inside of the bay is intensified by the formation of a front associated to upwelling and modulated by the morphology of the bay. The relaxation of the front can then deliver accumulated larvae to the open coast. On the other hand, outside of the bay (Bicas), larval delivery was mostly associated to upwelled waters, although interchange of larvae and postlarvae with the bay might also be relevant when the front dissolves, as can be inferred from the decoupling observed between early and late-plantigrades at PNA (Figs. 5 and 6).

For species that present high fecundity and mortality rates, such as the bivalves, increasing the water retention time may be favourable not

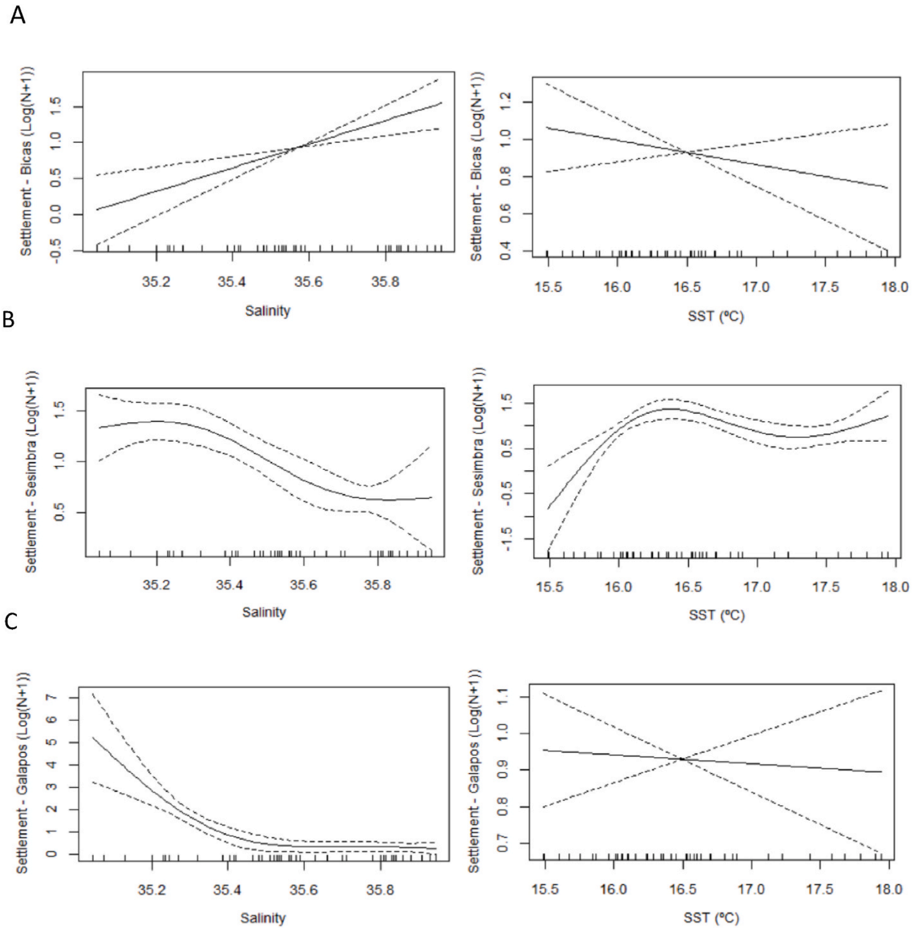

Fig. 8. Results of the Generalized Additive Models (GAM), showing the partial effect of SSS (left panel) and SST (right panel) in settlement patterns (early plantigrades, <0.75 mm, May), at each Location (A) Bicas, (B) Sesimbra and (C) Galapos, in the PNA region. Dotted lines indicate 95% confidence intervals, and tick marks along the X-axis below each curve represent effect values where observations occurred.

Table 5
Results of the Generalized Additive Models (GAM), showing the partial effect of SSS and SST and their interactions with the factor Location, on differences observed in the settlement patterns (early plantigrades, <0.75 mm, May) between Locations in the PNA region (Bicas, Sesimbra and Galapagos).

	Parametric Coefficients			
	Estimate	S.E.	*t*	*p*
(Intercept)	0.92982	0.06465	14.38	**$< 2 \times 10^{-16}$**
	Smooth terms (non parametric)			
Location	e.d.f	F	*P*	
SSS:Bicas	1	12.733	**0.000534**	
SSS:Sesimbra	2.652	10.133	**6.33×10^{-5}**	
SSS:Galapos	2.762	16.318	**$< 2 \times 10^{-16}$**	
SST:Bicas	1	1.249	0.26618	
SST:Sesimbra	2.884	5.645	**0.001458**	
SST:Galapos	1	0.1	0.752586	
	R^2 adjusted: 0.598		% Deviance explained: 63.6%	

Table 6
Results of the Generalized Additive Models (GAM) showing the partial effect of SSS, UI and Chl-*a* and their interactions with the factor Region, on differences observed in the settlement patterns (early plantigrades, <0.75 mm, May) between the regions of RNB (Buzinas) and Peniche (Baleal).

	Parametric Coefficients			
	Estimate	S.E.	*t*	*P*
(Intercept)	0.78756	0.05383	14.63	$<2 \times 10^{-16}$
	Smooth terms (non parametric)			
Region	e.d.f	F	*P*	
SSS:RNB	2.594	8.126	**57.73×10^{-5}**	
SSS:Peniche	1	0.009	0.92379	
Chl-*a*:RNB	2.871	24.585	**$< 2 \times 10^{-6}$**	
Chl-*a*:Peniche	2.089	7.391	**0.000705**	
UI:RNB	1	0.077	0.7815	
UI:Peniche	1	8.788	**0.004064**	
	R^2 adjusted: 0.608		% Deviance explained: 65.6%	

just to diminish larval wastage offshore, but also indirectly by increasing primary production and therefore food availability and larval survival (Graham and Largiert, 1997; Largier, 2020). Although the increase in water residence time within upwelling bays is shorter than the common pelagic larval duration to settlement of bivalves (2–4 weeks or more), this time is relevant for the population persistence (Gosling, 1992; Shanks, 2009; Largier, 2020). On average, residence times in upwelling bays has been estimated to be around 6–8 days (Monterey Bay, Graham and Largiert, 1997). However, planktonic organisms can present vertical migration and interact with fronts and other features increasing their retention time, sometimes more than 20 days (Queiroga and Blanton, 2004; Marta-Almeida et al., 2006; Yannicelli et al., 2006; Morgan et al., 2018; Largier, 2020; Bandara et al., 2021). Although our results suggest a large influence of the interaction between upwelling and topography on larval retention and delivery around this region, specific studies on larval abundance across fronts and other topographic features should be performed to confirm our hypothesis.

The productive and sheltered characteristics of upwelling bays

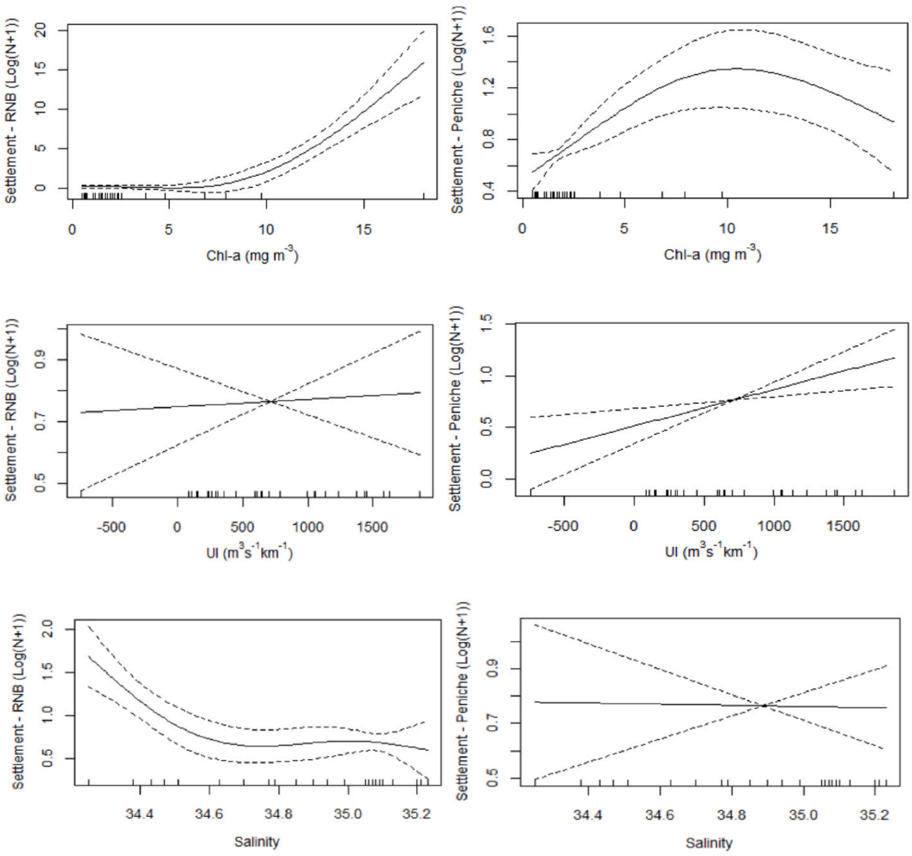

Fig. 9. Results of the Generalized Additive Models (GAM), showing the partial effect of SSS, UI and Chl-*a* in settlement patterns (early plantigrades, <0.75 mm, May), at each Region (RNB, left column and Peniche, right column). Dotted lines indicate 95% confidence intervals, and tick marks along the X-axis below each curve represent effect values where observations occurred.

favour the development of trophic webs and the recruitment of local species with complex life cycles (self-recruitment) and might perform a crucial role acting as sink and source of new individuals for the maintenance of large metapopulations (Largier, 2003; Hastings and Botsford, 2006; White et al., 2010; Largier, 2020). Enhanced self-recruitment and potential corridor for connectivity are essential factors for the persistence of populations and communities, and from that perspective, setting MPAs in upwelling bays might be a good strategy for conservation.

Our results corroborate the relevance of the PNA for mussel settlement, which was 1–2 orders of magnitude larger than at the other studied regions, and deepen the understanding of the mechanisms controlling the role of this region as a source for other populations or as a sink. In this sense, previous studies on the connectivity between the PNA and the RNB, as a factor to estimate the coherence between this MPA network, reported high levels of self-recruitment at PNA during downwelling events, but also an important delivery of larvae to the north when southerly winds predominate (Gomes et al., 2016). The large dispersal distances reported, greater than 100 km to the North, confirmed the ability of connection between PNA and RNB or the Peniche regions under those particular conditions of downwelling (Gomes et al., 2016), and agree with observations and bio-physical modelling predictions (Oliveira et al., 2009; Gomes et al., 2016; Nolasco et al., 2018).

With regard to the settlement patterns at the northern locations (RNB and Peniche), upwelling and its interaction with topography also seem to have played a major role controlling larval delivery between these two regions, and between locations within regions. Peniche is likely to be highly influenced by the upwelling jet from the north and the typical filament associated to pronounced capes, in this case Carvoeiro Cape (Fig. 1). The cape separates the upwelling jet from the coast to overpass the cape, and later this filament moves eastward to follow the coast again (Relvas et al., 2007; Oliveira et al., 2009). This jet forms a front at the junction between the upwelled and the displaced coastal waters because of their difference in salinity and temperature (Oliveira et al., 2009), which might be commonly located in between the RNB archipelago and mainland Peniche, as could be inferred from the higher temperatures and low Chl-*a* concentrations registered in the RNB with regard to mainland (Table 1; Fig. 3). The behaviour of this filament with regard to the intensification of upwelling can be inferred from the associated differences in temperature between the RNB archipelago and Peniche observed in this study (Fig. 3). Upwelling intensified the differences in temperature between the island and mainland along the study area (UI_0; Fig. 3), but as the persistence of upwelling favourable winds intensify, locations at the Carvoeiro Cape and south of the promontory loose the upwelling influence and reach higher temperatures than the island, suggesting that the cold filament has been displaced by the cape and reached the island (UI_10; Fig. 3). Those observations agree with the patterns previously described for the area, where the cold water filament associated to upwelling becomes wider with the intensification of upwelling until a certain point when it can reach the island (Oliveira et al., 2009) and a recirculation area is formed south of the Carvoeiro Cape and the archipelago, embracing Consolação and Porto Dinheiro areas. The interaction between upwelling and the Carvoeiro Cape could explain the differences observed between locations within the Peniche region (Figs. 5 and 6). The largest magnitudes of settlement were recorded in the locations to the north of the cape (Foz de Arelho and Baleal), where the water mass advected from the north is not yet deflected by the cape (Fig. 5) and also at the southernmost location (Porto Dinheiro) where recirculation processes might intensify larval delivery. On the other hand, the sampling stations located closer to the Carvoeiro Cape received much lower settlement, which might be caused by the offshore displacement of the filament to overpass the cape and limiting the larval delivery to those stations (Figs. 5 and 6).

The observations also suggest that the upwelling front associated to that filament modulates the intensity of settlement at Peniche, but also at the RNB archipelago. Fronts are natural boundaries between two masses of water with different physical characteristics, which can act as actual barriers for larvae, accumulating them and also influencing their cross-shore transport (reviewed by Queiroga et al., 2007). Larvae accumulated at the upwelling front move offshore during upwelling favourable conditions until wind relax or reverse, then, the less dense oceanic surface layer moves back to the coast and in certain conditions the upwelling front might stay intact and move onshore transporting the accumulated material (Farrell et al., 1991; Shanks et al., 2000; Pineda et al., 2007; Morgan and Fisher, 2010).

In this sense, the upwelling front might act as a barrier for larval delivery to the RNB archipelago and at the same time might favour settlement in Peniche by limiting the offshore transport of larvae. The settlement peaks observed in the RNB occurred after more intense upwelling events (*ca*. UI $= 3800$ and 6700 $m^3\ s^{-1}.Km^{-1}$, February and March, respectively), which may have moved the resurgence front beyond the archipelago, thus connecting island and continent, and promoting the delivery of mussels to the archipelago throughout seasonal corridors of connectivity generated by the front. Larvae might be only reaching the RNB under particular conditions when downwelling dissipates the front or when very intense upwelling events let the front reach the island.

This interpretation might also explain the opposite patterns observed between the RNB archipelago and Peniche with regard to the effects of UI, Chl-*a* and salinity on settlement. While in Peniche settlement increases linearly with upwelling intensity, no significant effect was detected in RNB, since larval delivery might be associated to both downwelling and very intense upwelling episodes (Fig. 9). Chl-a show a positive effect on settlement at both regions, but in Peniche the optimum effect is detected at intermediate values while at the RNB, the Chl-*a* have an exponential effect on settlement but only when it reaches very high values, associated to very intense upwelling events. The inverse relationship between salinity and settlement at RNB might reflect the relevance of downwelling events to deliver larvae at the archipelago. Although no completely isolated, the limited circumstances which allow connectivity between the RNB and the mainland might explain the much lower settlement values recorded at the archipelago in comparison with the mainland locations. Nonetheless specific studies on larval abundance between the archipelago and mainland along with different upwelling conditions should be performed to confirm this mechanism.

In summary, the results of our study suggest the presence in the region of different larval delivery mechanisms highly modulated by topography and the wind driven currents regime, like the formation and movement of upwelling fronts and upwelling shadows, which have been previously reported as very relevant mechanisms (Shanks et al., 2000; Pineda et al., 2007; Morgan and Fisher, 2010). According to the mechanism suggested, the seasonality, intensity and frequency of predominant winds by modulating surface currents direction and intensity, might also determine the degree of connection between different areas in the Portuguese coast, switching their role as source or sink, and increasing the complexity of the relationships between the populations. Specific studies on larval abundance across different topographic features along different upwelling scenarios will help to confirm the role of the mechanisms suggested on larval delivery and population connectivity. Understanding what determines larval dispersal and interchange of individuals between populations is crucial in planning for marine community persistence and ecosystem functioning, in achieving both MPA ecological persistence objectives and enhancing fisheries objectives.

CRediT authorship contribution statement

G.F. Oliveira: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **J. Pimentel-Santos:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **I. Gomes:** Writing – review & editing, Methodology, Investigation, Funding acquisition, Formal analysis. **R. Albuquerque:** Writing – review & editing, Methodology, Investigation. **H. Queiroga:** Writing – review & editing, Writing – original draft, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **L.G. Peteiro:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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