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resumo

Os estuários desempenham um papel crucial enquanto berçário para larvas de peixe sendo fundamentais durante as primeiras fases do ciclo de vida do desenvolvimento dos peixes. Os ecossistemas estuarinos são altamente afetados por impactos humanos e também por alterações climáticas. A variabilidade climática afeta as comunidades de ictioplâncton levando a alterações na cadeia trófica pelágica marinha e nos recursos pesqueiros (recrutamento). Este estudo tem como objetivo investigar a influência que a variabilidade ambiental tem nas alterações de abundância interanual de ictioplâncton no estuário do Mondego (Portugal). Para tal foi efetuado um programa de recolha de amostras ao longo de 13 anos (2003-2015) em seis locais de amostragem ao longo do estuário de modo a avaliar a distribuição espacial e sazonal das larvas de peixe relativamente a períodos de seca, chuvosos e regulares. A comunidade de larvas de peixe foi dominada por *Pomatoschistus* spp. e *Pomatoschistus microps* durante todas as estações do ano com abundância de larvas de peixe superior durante o verão e a primavera, independentemente das condições climáticas. As principais alterações à comunidade estão relacionadas com a sazonalidade e fenologia das espécies bem como uma redução na abundância total de larvas e um aumento de espécies marinhas durante eventos extremos. O caudal do rio, a precipitação e, consequentemente, a salinidade parecem ser os principais fatores a influenciar não só a abundância e o número de espécies, mas a sua distribuição dentro do estuário, com uma maior prevalência de espécies marinhas dentro do estuário durante anos secos.

keywords

Fish larvae, climate variability, environmental variability, Mondego estuary, extreme climatic events.

abstract

Estuaries play a key role as nurseries for fish larvae and are critical for the early life stages of fish development. However, these can be highly affected by direct human impacts as well as climate change. Climate variability distresses the ichthyoplankton assemblages with consequences in the marine pelagic food webs and fish populations biology (namely recruitment). This study aims to investigate the influence of environmental variability on interannual abundance of ichthyoplankton assemblages of the Mondego estuary (Portugal), on a long-term scale. For this, an ichthyoplankton sampling programme of 13 years (2003-2015) along six distinct sampling stations was analysed to evaluate spatial, seasonal and interannual changes of fish larvae distribution over periods of wet, regular and dry conditions.

The larval fish community was dominated by *Pomatoschistus* spp. and *Pomatoschistus microps* across all seasons and precipitation regimes, with higher abundances of larvae occurring during summer and spring. Main changes on the ichthyoplankton community were related with species seasonality and phenology as well as a reduction on total larval abundance and an increase of marine species during extreme events. River flow, precipitation and consequently salinity appeared as the main factors influencing not only the abundance and number of species but also their distribution in the estuarine area, with a major appearance of marine species inside the estuary during dry periods.

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1. Introduction

Coastal regions are known as diverse and complex, especially estuaries that are transition areas between freshwater and marine systems (Sousa et al., 2016).

Estuaries can include a great variety of habitats such as seagrass meadows, marshes, and mangrove forests, displaying an extremely high primary and secondary productivity which are responsible for their huge diversity and abundance of fish, invertebrates and birds (Beck et al., 2001). Estuaries are among the most biologically productive and valuable ecosystems in the world (Costanza et al.,1998), playing a key role also as nurseries for fish larvae. They provide optimal conditions for fish eggs and fish larvae development such as calm and shallow waters, refuges from predators, high primary productivity and food abundance, maximizing their survival (McLusky, 1989; Raz-Guzman et al., 2002).

The high value of estuaries as nursery areas is crucial, not only for typical estuarine species but also for marine spawning fish species which migrate into the estuary and use the estuarine habitats to complete their life cycle (Primo et al., 2013; Baptista et al., 2014). Also, their value as fishing ground areas for several commercial fishery resources is recognized worldwide and attracts large numbers of human population that establish near these coastal areas (Houde & Rutherford, 1993; Baptista et al., 2015).

Estuarine areas are highly affected by a severe human presence and activity, being subjected to powerful and growing pressures and impacts (Sousa et al., 2016). Anthropogenic factors such as dam construction, overfishing, and other human-controlled runoff activities, have been pointed out as responsible for a substantial decline in fishery resources and deepening decline in the future decades (Song et al., 2019). Additionally, data from Bindoff et al. (2019) shows that extreme weather events such as storms, floods, droughts, and heatwaves will increase in frequency and severity in the future, affecting the composition, function, biodiversity, and productivity of marine ecosystems (Grilo et al., 2011).

The early life stages (eggs and larvae) of fishes are referred as ichthyoplankton. Some species lay their eggs on the substrate or in nests (demersal eggs) but most of the marine species eggs are pelagic and drift in the water column. Due to their null or low swimming ability, the early life stages of fishes integrate the planktonic community as part of the meroplankton, organisms which occur in the plankton only during part of their life-cycle (Ré, 1999; Alemany & Garcia, 2017).

Fish larvae are particularly vulnerable to physical and biological processes (Primo et al., 2011), being affected by a variety of factors, such as predation, competition, parasitism, food abundance, and oceanographic conditions (Ré, 1999). Therefore, retention within the nursery areas, with optimal conditions, is crucial for their survival (Ré, 1999). As the abundance of fishery resources depends on the survival of fish eggs and larvae, a better knowledge of ichthyoplankton ecology is important to understand the fish spawning stock biomass and recruitment, as well as biology and ecology of the adult fish populations (Doyle et al., 2002; Hsieh et al., 2005).

As other lower trophic organisms, fish larvae are highly sensitive to climate change since small variations in hydrological conditions, salinity, temperature, zooplankton abundance, and wind variables will affect their survival (Primo et al., 2011; Voss et al., 2012; Song et al., 2019). Previous studies showed that environmental variability lead to changes not only in their spatial location and spawning timing (Walsh et al., 2015) but also in their abundance and number of species (Song et al., 2019).

Thus, a better understanding of ichthyoplankton assemblages and their relationship with environmental changes on a long-term scenario is an important tool to predict the impact of climate change on fish stocks and to better fisheries management. Besides, long-term studies are extremely important when addressing environmental variations, since the effects of those variations on the community can be delayed and not noticed on a shorter timing scale scenario (Franklin, 1989; Song et al., 2019).

The Mondego estuary (Portugal), the study site for this research, is a small, with shallow waters estuary, particularly important for species with high commercial interest such as the European sea bass *Dicentrarchus labrax*, flounder *Platichthys flesus* and sole *Solea solea*, (Martinho et al., 2007). The first studies carried out on larval fish dynamics of Mondego were conducted by Ribeiro (1991), focusing mainly on *Engraulis encrasicolus*, later Marques et al. (2006) continued the work, briefly addressing fish larval communities. In 2011, Primo and collaborators, fully characterized the dynamics of the larval fish species in the Mondego estuary, and how climate variability affected the ichthyoplankton community in a short period from January 2003 to December 2008, however, and due the recent climate change scenarios it is important to understand how this communities react to long term changes.

The purpose of this research is to investigate the influence of the environmental variability on ichthyoplankton assemblages of the Mondego estuary through the course of 13 years (2003-2015), therefore, being the first attempt to address how the ichthyoplanktonic community responds to climate change on a long-term scenario.

2. State of the Art

Changes in climate are imminent, and the impact on the oceans are severe. Since the 1970s, observations clearly show a globally spread warming pattern of the water column. Progressive warming of the oceans will result in acidification and oxygen loss of the ecosystem (Bindoff et al., 2019). Furthermore, an increase stratification will lead to a reduction of nutrients and dissolved gases affecting the functions of the ecosystem interactions and primary and secondary production (Rijnsdorp et al., 2009; Bindoff et al., 2019). Also, sea level rise, due to melting of the polar caps will result in increased salinization of the estuaries and wet land (Bindoff et al., 2019; Ducrotoy et al., 2019). These are already aggravated by extreme weather events like severe drought periods, which tend to increase in the near future, resulting in longer dry periods with low river flow (Miranda et al., 2006; Baptista et al., 2010).

Long-term studies regarding changes on ichthyoplankton assemblages have been carried out around the world, showing how climate change can impact the larval fish community, either in oceanic (e.g.: Voss et al., 2012; Walsh et al., 2015; Alvarez-Fernandez et al., 2015; Maynou et al., 2020), and estuarine habitats (e.g.: Costa & Muelbert, 2017; Guan et al., 2017; Song et al., 2019). Generally, temperature, salinity, chlorophyll-*a*, atmospheric-ocean variables, upwelling, and freshwater discharge as well as the presence of eddies and meanders directly influence the abundance, diversity, and distribution of ichthyoplankton (Boeing et al., 2008; Song et al., 2019). Furthermore, these physical, chemical, and oceanographic drivers, affects the pelagic food web, through alterations in the zooplanktonic community, thus affecting the ichthyoplankton feeding ecology (Voss et al., 2012).

Warming water temperatures has been related with latitudinal changes of fish larvae distribution (e.g.: Friedland et al. 2007; Walsh et al. 2015). Increased temperatures can affect the entire pelagic food web by bottom-up control. Walsh et al. (2015) reported a northward shift between the periods 1977–1987 and 1999–2008 in the Northeast US shelf ecosystem, which mirror the species prey distribution. Similarly, Beaugrand et al. (2002) found that temperature changes and the North Atlantic Oscillation (NAO) lead to strong biogeographical shifts in copepod populations which can latter affect higher trophic levels. In the Mediterranean Sea, surveys carried out on the last three decades (1980-2010) related a reduction in the abundance of eggs and larvae of anchovy *Engraulis encrasicolus*, in impairment to round sardinella, *Sardinella aurita*, due to an increase in water temperature and salinity and a decrease in chlorophyll *a* (Maynou et al., 2020). In the Baltic Sea, increased temperatures triggered the abundance of the copepod species *Acartia* spp*.,* the main prey for sprat larvae and a decrease in copepod *Pseudocalanus* spp., the most important prey for cod larvae (Voss et al. 2003; Voss al., 2012). Consequently, it was observed an increase in sprat eggs from 1973-2010 and a decrease in cod eggs (Voss al., 2012). Also, according to Song et al. (2019), in the Yellow River estuary, China, the larval fish community structure has become recently more unstable compared to studies conducted in the 1980s.

Previously dominant species with high commercial value such as *Platycephalus indicus*, was replaced by lower trophic and small size species such as *Harengula zunasi* and *Clupanodon punctatus*. In all cases, a high commercially valuable species and/or top predator is being replaced by a less valuable and lower trophic species.

Increased temperature can also affect indirectly the survival of the fish larvae which is strongly species-and-stage specific (Pitois et al., 2012). A long term study in the North Sea conducted by Alvarez-Fernandez et al. (2015) reports that, since 2002, even though the numbers on the spawning-stock biomass were high, post yolk larvae numbers decreased due to lack of food. Zooplankton abundance, particularly *Pseudocalanus* spp. was the key factor explaining this decrease showing a positive correlation with the decrease in post yolk *Clupea harengus* larvae (Alvarez-Fernandez et. al., 2015). Similarly, other plankton communities in the North sea have already been pointed out as responsible to alter the dynamics of local fish communities, as cod and horse mackerel (Reid et al., 2001; Beaugrand et al., 2003).

Climate variability is also responsible to influence the timing of annual events across multiple trophic levels. These phenological changes are a key topic on the research of the impacts of climate change (Edwards & Richardson, 2004; Genner et al., 2010) occurring on both terrestrial and marine environments (Hughes, 2000). In particular, phenological changes on marine/estuarine environment may be responsible for reduced survival success of the larval fish community (Beaugrand et al., 2003; Alvarez-Fernandez et al., 2015). Once the vitelli reserves on the yolk sack of the fish larvae run off, the larvae needs to find food in the environment, namely, zooplankton (Ré, 1999). Environmental variables, such as warming water temperatures, may be responsible to alter the timing of appearance and spatial distribution of zooplankton. In this way, reducing the quality and quantity of food available in the environment for fish larvae to consume, subsequently, reducing survival success and failed recruitment (Reid et al., 2001; Beaugrand et al., 2003; Pitois et al., 2012; Lynam et al., 2017; Capuzzo et al., 2018). The scarce of food coupled with increase metabolic rates and higher energetic demands induced by warming temperatures, seems likely to negatively affect fish species growth and survival (Beaugrand et al., 2003; Friedland & Hare, 2007).

Large scale ocean-atmosphere events, such as NAO in the North Atlantic, or El Niño in the tropical Pacific may induce several changes at different trophic levels both in terrestrial and marine ecosystems (Ottersen et al., 2001; Ottersen et al., 2010; Schroeder & Castello, 2010) . In the Patos Lagoon estuary (Southern Brazil), a 13 years study reported that spatial patterns of fish eggs and larvae were highly related with temperature, estuarine circulation and salinity. The years of 2003 and 2010, described as years of moderate El Niño events, resulted in a very low recruitment of eggs into the estuary when compared to other years of the study (Costa & Muelbert, 2017). In the Strait of Georgia, temperature shifts associated with a strong La Niña event in 2007 led to changes in the community from a strong dominance by *Merluccius productus* in 2007, to

dominance by *Clupea pallasi* and *Gadus chalcogrammus* in 2009, and a dominance by benthic species including *Sebastes* spp. and several flatfishes in 2010 (Guan et al., 2017).

In Portugal, several studies had addressed estuarine ichthyoplankton assemblages and their associated environmental forcing (e.g.: Chícharo et al., 1991; Ribeiro, 1991; Faria et al., 2006; Ramos et al., 2006; Primo et al., 2011). Estuarine ichthyoplankton communities are generally dominated by Gobiidae species, mainly *Pomatoschistus* spp.*,* followed with seasonal increases of other species as *Ammodytes tobianus*, *Sardina pilchardus*, *Engraulis encrasicolus*, *Solea senegalensis, Symphodus melops* and *Parablennius gattorugine*. Higher abundances of ichthyoplankton occur during the warm months of spring and summer due to optimal conditions to a rapid growth, mainly high availability of food in the environment (Whitfield, 1990; Faria et al., 2006). Also, spring and summer periods coincide with the reproductive timing of most of the taxa (Faria et al., 2006). Besides temperature, responsible for seasonal differences in the abundance of larval fish species, salinity and river flow were the main factors contributing to alterations on fish larval densities and their distribution within the estuarine ground (Chícharo et al., 1991; Ribeiro, 1991; Faria et al., 2006; Ramos et al., 2006; Primo et al., 2011). The first work characterizing the ecology of ichthyoplankton in the Mondego estuary was carried out by Ribeiro (1991). He conducted a crucial pioneer work about the larval fish dynamics and the anchovy reproduction in the Mondego estuary. Ribeiro (1991) suggested that the abundance and distribution of anchovy early life stages appears to be closely related to temperature and salinity. Later, Marques et al. (2006) studied ichthyoplankton assemblages from January 2003 to June 2004 reporting a strong positive correlation with temperature. Since then, several studies conducted on the Mondego estuary focused on the zooplanktonic assemblages showed strong association with local, regional and large-scale environmental forcing (e.g.: Marques et al., 2007, 2014, 2018; Primo et al., 2009, 2012, 2015) which certainly impact the larval fish community. Ichthyoplankton studies on the Mondego estuary were proceeded by Primo et al., (2011) which reported climate variability effects in the period from January 2003 to December 2008. Main results reported drought-induced effects on larval fish assemblages related to an increase in marine species. Moreover, temperature, chlorophyll *a* and river flow were the principal features affecting the ichthyoplankton community and their distribution inside the estuarine area (Primo et al., 2011). Other studies of the same author analysed the dynamics of the fish larvae within the estuary reported vertical migration according tidal and diel changes (Primo et al. (2012a, 2012b), and the importance of the estuary as nursery for flatfish species (Primo et al., 2013). Larval fish community of the Mondego estuary presented few changes across the analysed studies (Ribeiro, 1991; Marques et al., 2006; Primo et al., 2011). *Pomatoschistus* spp. represent over 80% of the total larval catch with an increased seasonal presence of other species: *Atherina presbyter*, *Solea solea, Syngnathus abaster*, *Crystallogobius linearis* and *Platichthys flesus*, during spring/summer and *Ammodytes tobianus*, *Callionymus* spp., *Echiichthys vipera* and *Liza ramada*, during autumn/winter (Primo et al., 2011). Significant differences were found mainly regarding *Engraulis*

encrasicolus which numbers has progressively decreased to 2% of the total larval catch compared to 44% in 1991 (Ribeiro, 1991; Primo et al., 2011).

In the future, precipitation levels are estimated to be 40% lower in the Portuguese territory and severe drought conditions tend to increase (Miranda et al., 2006; Baptista et al., 2010). Hence, the present study aims to understand how climate variability, mainly extreme weather events like severe drought, will affect the ichtyoplanktonic community of the Mondego estuary by analysing a long-term database of 13 years.

3. Methodology

3.1 Study site

The sampling location for this study is located in the Iberian Peninsula on the western coast of Portugal, the Mondego estuary, a small warm-temperate mesotidal system (40º 08'N, 8º 50'W) (Fig. 1). With an area of 8.6 km^2, the hydrological basin of the Mondego, provides an average freshwater flow rate of 79 m^3 s^{-1} (Dolbeth et al., 2010).

The estuary is formed by two arms (north and south) with particular hydrological characteristics, separated by the Murraceira Island, converging again near the mouth, where the influence of both the river flow and neritic waters is strong, and the depth is around 6-13 m. The north arm is deeper (4-8m during high tide) and presents a low residence time (<1 day) and since it constitutes the main navigation channel, suffer from regular dredging activity. The south arm is shallower (2–4 m deep, during high tide) and has higher residence time (2–8 days) (Baptista et al., 2015). For a fully detailed description of this system consult (Marques et al., 2006).
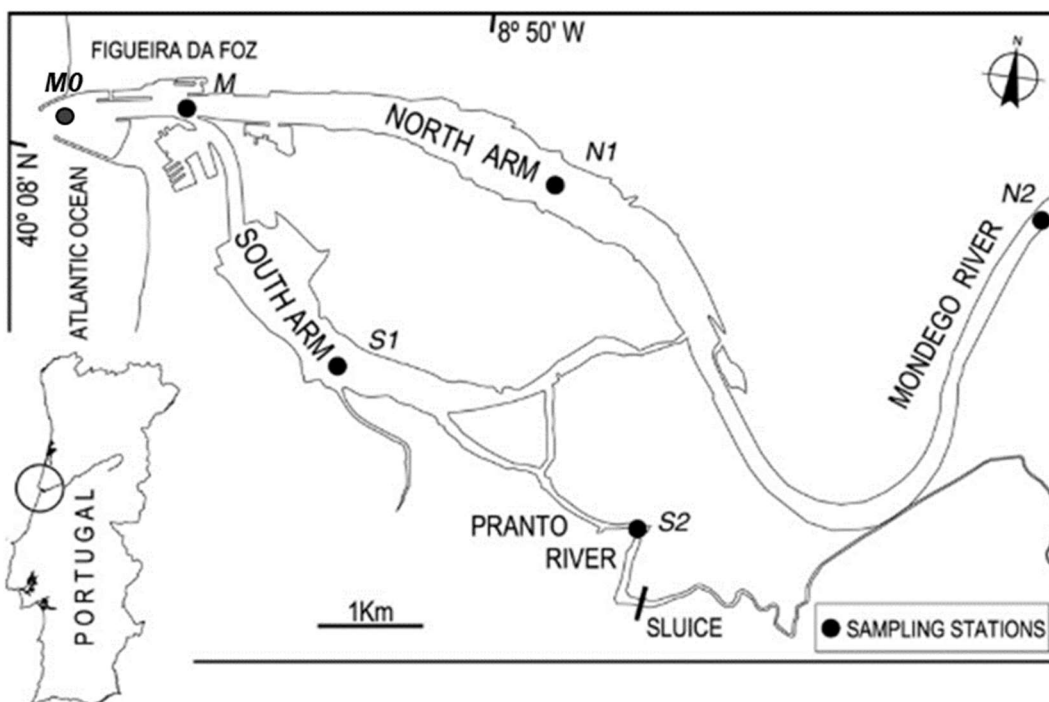

Figure 1- Map of the Mondego estuary, located on the western coast of Portugal. Sampling stations surveyed in this study are indicated (M0 and M, mouth stations; S1 and S2, southern arm stations; N1 and N2, northern arm stations)

3.2 Sampling methodology

Sampling was carried out monthly at high tide, from January 2003 to December 2015 at six stations, two at the mouth of the estuary M0 and M, (sampling program at station M0 only started on January 2011), and two in each one of the arms, S1 and S2 in the south arm, and N1 and N2 in the north arm covering the salinity gradient (Fig. 1).

Samples were collected by horizontal subsurface tows (Bongo net: mesh size 335 µm, mouth diameter: 0.5 m, tow speed: 2 knots), equipped with a Hydro-Bios flowmeter (volume filtered average 45 m^3) and preserved in a 4% buffered formaldehyde seawater solution. Additionally, at each site, salinity, water temperature (°C), dissolved oxygen (mg l^{-1}), pH and turbidity (Secchi disc depth, m) were also recorded.

In the laboratory, plankton samples was transferred from 4% buffered formaldehyde to 80% ethanol and ichthyoplankton was separate from the rest of the sample, counted (number of invidious per 100m³), and identified to the lowest taxonomic level through stereo microscope (Primo et al., 2011).

3.3 Data Analysis

Sampling months were grouped into four conventional seasons: winter (December, January, and February), spring (March, April, and May), summer (June, July, and August) and autumn (September, October, and November). Species were characterized in three main ecological guilds (adapted from Elliott et al. 2007): marine stragglers (MS, species that spawn at sea and typically enter estuaries in low numbers occurring frequently in the lower reaches), marine migrants (MM, species that spawn at sea and often enter estuaries in large numbers) and estuarine species (ES, species capable of completing their entire life cycle within the estuarine environment and those with stages of their life cycle completed outside the estuary). Finally, different years from 2003 to 2015 were classified as dry, regular and wet based on the 25 years mean river runoff (1991-2016) of the winter months (December, January, and February). Mean winter anomalies were calculated by subtracting the winter runoff from the long-term average for each of the sampled years. River runoff values were obtained from the Portuguese Water Institute (http://snirh.pt/; station 12G/01AE, accessed on February 24th of 2020). Years with negative anomalies values were considered dry, with positive were considered wet and with anomalies values near zero were considered regular.

PERMANOVA+ (PRIMERv6 & PERMANOVA+v1, PRIMER-E Ltd.) was used to perform a non-parametric permutation univariate analysis of variance to test for differences between climate and seasons for the total number of larvae, abundance by guild, salinity, river flow and precipitation. The analysis was based on Euclidian distance similarities between samples, considering all the factors (climate, season) as fixed and unrestricted permutations of raw data.

Community structure was investigated by multivariate PERMANOVA and Principal Coordinate Analysis (PCO). Larval abundances were ln(X+1) transformed and analysis were based on Euclidian distance similarities between samples, considering all the factors (climate, season) as fixed and permutation of residuals under a reduced model. Subsequently, a SIMPER (percentage similarity procedure) was carried out to identify species that contribute most to the differences observed between climate conditions.

Environmental data for the Mondego estuary were used to test links with the ichthyoplankton community. Local hydrological variables included river runoff, water salinity and temperature measured *in situ*. Regional environmental data included precipitation (http://snirh.pt/, station 13F/01G and https://www.ipma.pt/, Cernache, accessed on February 24th of 2020), air temperature, Sea Surface Temperature (SST) and Sea Level Pressure (SLP) acquired from International Comprehensive Ocean Atmosphere Data Set (ICOADS) online database (http://dss.ucar.edu/pub/coads, accessed on February 24th of 2020). Finally, North Atlantic Oscillation (NAO, http://dss.ucar.edu/pub/coads, accessed on February 24th of 2020) was used and large-scale environmental forcing. Environmental variables were normalized and a principal component analysis (PCA) was applied to hydrological and regional variables and on fish larvae community data. Dominant patterns of local hydrological and regional climate variability, as well as dominant patterns observed on community structure were identified by extracting the PC1 of each analysis. Spearman correlation analysis was performed between signals extracted from community structure and NAO variability, local hydrological and regional patterns observed.

Heatmaps and correlation tests were performed through the Software Sigma plot 12.0. Uni and multivariate analyses were performed using PRIMER v6 + PERMANOVA package (Anderson et al., 2008; Clarke & Gorley, 2015). The significance level for all statistical tests used was p = 0.05.

4. Results

4.1 Environmental conditions

The Mondego estuary showed a typical seasonal pattern, for temperate regions, of precipitation and freshwater discharge throughout the 13-years sampling period, with higher precipitation and runoff values during winter and lower during summer (Fig. 2). According to winter anomaly values of river runoff, the years of 2005, 2006, 2008, 2012 and 2015 presented negative values, thus were considered as dry condition years (Fig. 2A). On the other hand, 2003, 2010 and 2014 were considered wet years due to positive anomaly values. Finally, the years with winter anomaly values near zero were considered as regular (2004, 2007, 2009, 2011, and 2013) (Fig. 2A).

Univariate PERMANOVA analysis presented significant interactions between the factors "climate conditions" and "season" for runoff (Pseudo-F = 8.48; p = 0.001), precipitation (Pseudo-F = 5.33; p = 0.001) and salinity (Pseudo-F = 3.41; p = 0.002).

Runoff seasonal variation showed that summer and autumn were similar within each climate condition, presenting lower values (pairwise p(perm) > 0.05) (Fig. 2A). During dry conditions winter and spring also showed similar runoff than autumn (pairwise p(perm) > 0.05) (Fig. 2A). Furthermore, wet winter runoff was higher than in dry and regular conditions (pairwise p(perm) < 0.05) while spring and summer dry periods showed lower runoff than wet (pairwise p(perm) < 0.05) (Fig. 2A).

Seasonal variation of precipitation showed lower values during summer in all climate conditions (pairwise p(perm) > 0.05). Winter precipitation was also lower than spring in wet conditions and then autumn in dry periods (pairwise p (perm) > 0.05) (Fig. 2B). Furthermore, during wet years, winter precipitation levels were higher than in regular and dry years (pairwise p (perm) < 0.05) (Fig. 2B).

Seasonal variation of salinity showed lower values in winter and higher in summer during wet conditions (pairwise p(perm) < 0.05) (Fig. 2C). In regular conditions only winter showed lower salinity values than the other seasons while in dry periods winter and spring salinity was lower than summer and autumn (pairwise p(perm) < 0.05) (Fig. 2C). Furthermore, in wet spring and autumn periods, salinity was lower than in dry and regular, while dry winter salinity observed in the estuary was higher than in wet and regular climate conditions (pairwise p(perm) < 0.05) (Fig. 2C).
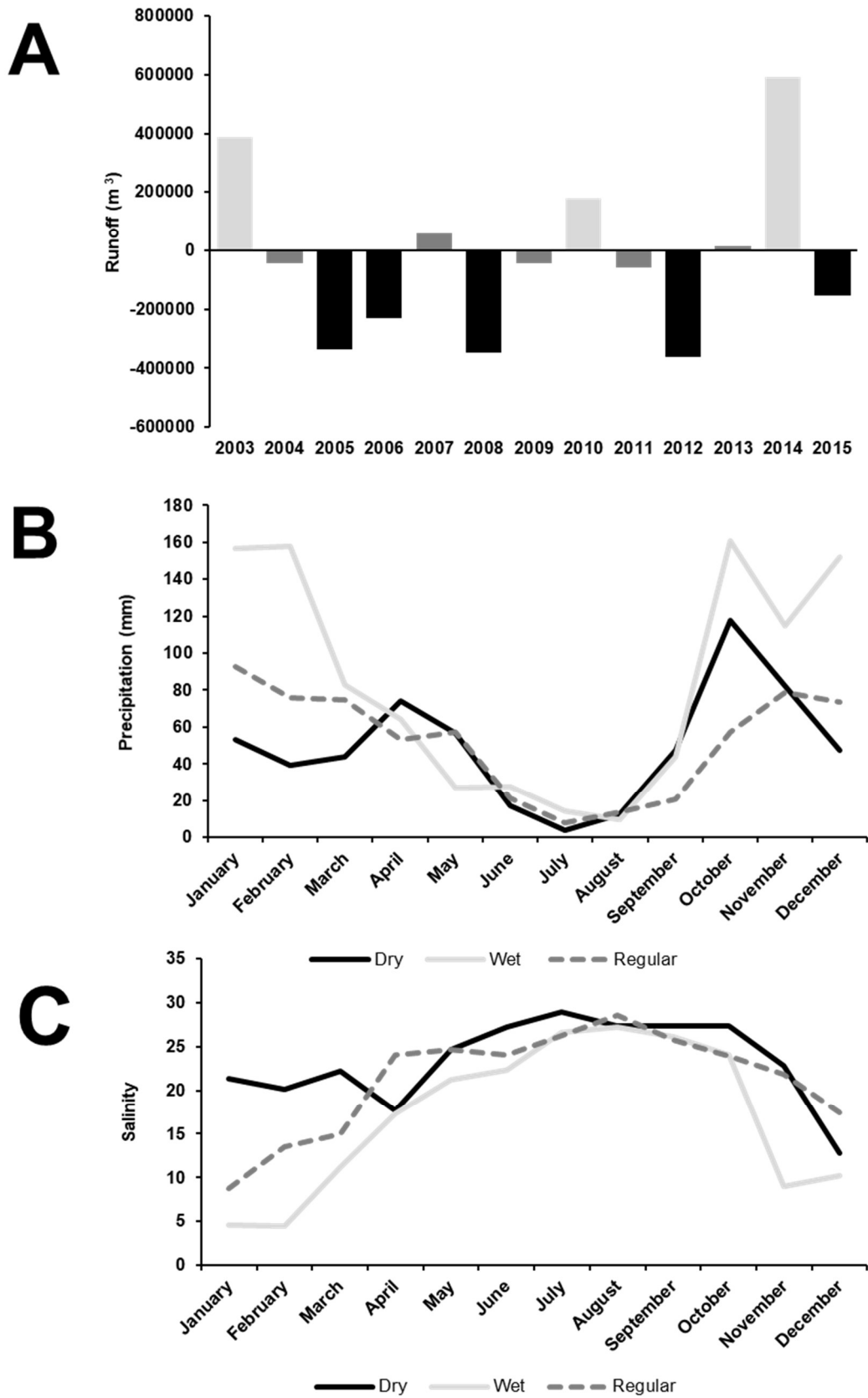
Figure 2-Environmental condition in the Mondego estuary during the sampling period. Mean annual winter anomaly (A), Mean precipitation (mm) (B) and monthly average salinity values (C).

4.2 Larval fish assemblage: Taxonomic composition and abundance

A total of 28119 larvae were collected and identified into 47 different taxa. The most abundant family was the Gobidae, and the most abundant species was *Pomatoschistus microps* (36.6%) followed by *Pomatoschistus* spp. (36.0%). *Gobius niger* was also very abundant (4.6%) followed by *Pomatoschistus minutus* (4.2%). *Engraulis encrasicolus* (2.3%) was more abundant than *Sardina pilchardus* (2.05%), with wet years showing higher abundances of *E. encrasicolus*, and dry years, higher abundances of *S. pilchardus*. Other important species were *Parablennius pilicornis* (1.21%), *Ammodytes tobianus* (1.19%), *Liza ramada* (1.04%) and *Solea senegalensis* (1.01%). Non-identified larvae accounted for 2.90% of the total catch and generally, these larvae corresponded to very small, in the yolk-sac stage, or highly damaged larvae (Table 1).

Fish larvae density clearly showed a seasonality pattern, with higher densities during spring and summer (Pseudo F = 11.2; $p < 0.05$; pairwise t-test < 0.05). Generally, average larval density was higher during wet years (pairwise t-test < 0.05) and lower during regular ones. For dry and wet years, there are two seasonal peaks of larvae abundance, a smaller one during spring and a greater one during summer. However, during wet years, the smaller peak during spring occures sooner, starting during late winter and early spring, and the greater peak during summer also occures later in summer than the peak during dry years (Fig.3).
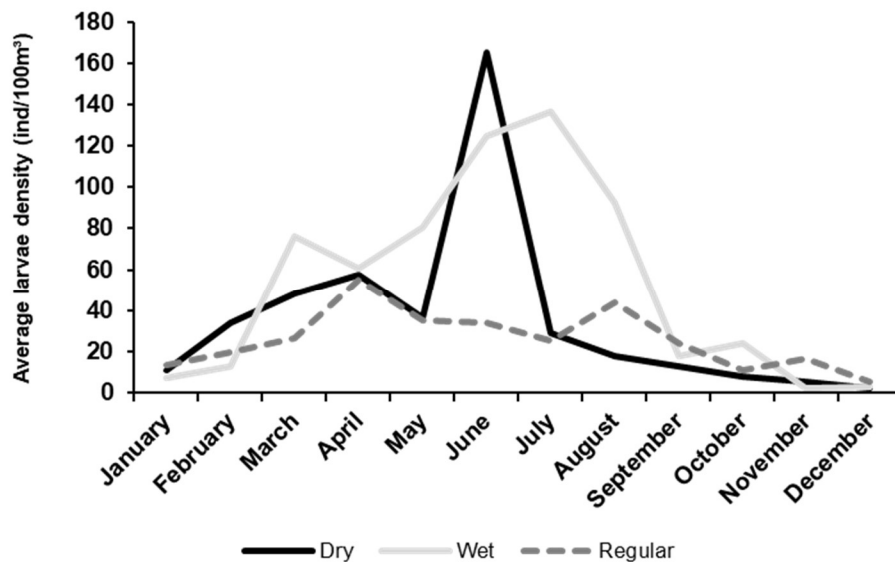
Figure 3-Mean monthly fish larvae density (ind/100m³) for dry, wet and regular years

According to the ecological guilds, marine stragglers' densities showed significant interaction between the factors "climate conditions" and "season" (Pseudo-F = 3.40; p = 0.003). During winter, dry periods showed higher densities than regular ones (pairwise p(perm) > 0.05) Spring and autumn presented higher MS densities in wet periods than in regular, while in wet summer and autumn showed higher MS densities than during dry periods (pairwise p(perm) < 0.05) (Table 2). Furthermore, MS were higher in spring wet conditions than in winter (pairwise

p(perm) < 0.05). Regular climate conditions showed increased MS densities during summer while in dry conditions MS peak occurred during autumn ((pairwise p(perm) < 0.05) (Table 2).

Estuarine species' density showed differences according to climate conditions (Pseudo-F = 3.00; p = 0.041) and season (Pseudo-F = 11.04; p = 0.001). Wet periods showed higher ES densities than regular (pairwise p(perm) < 0.05) (Table 2). During summer and spring, estuarine species density was higher than during winter and autumn (pairwise p(perm) < 0.05) (Table 2).

Finnaly, marine migrants density showed no significant differences between seasons or climate conditions (p > 0.05) (Table 2).

Table 1- Mean larval density (ind./100m³) of species collected during the sampling period in wet, regular and dry years. MS, Marine Straggler; MM, Marine Migrant; ES, Estuarine Species; CA, Catadromous; na, non identified.

Family	Species	Guild	Wet	Regular	Dry	MD%
Ammodytidae	*Ammodytes tobianus*	MS	0.20	0.13	1.09	1.19%
Ammodytidae	*Ammodytidae* n. id	na	0.00	0.00	0.01	0.01%
Anguillidae	*Anguilla anguilla*	CA	0.00	0.01	0.01	0.02%
Gobiidae	*Aphia minuta*	MS	0.02	0.01	0.06	0.07%
Bothidae	*Arnoglossus thori*	MS	0.00	0.00	0.01	0.01%
Atherinidae	*Atherina presbyter*	ES	0.92	0.03	0.04	0.83%
Atherinidae	*Atherina* spp.	ES	0.00	0.02	0.04	0.04%
Blenniidae	*Blenniidae* n. id	na	0.00	0.01	0.01	0.02%
Blenniidae	*Blennius ocellaris*	MS	0.04	0.00	0.01	0.04%
Sparidae	*Boops boops*	MS	0.00	0.00	0.02	0.01%
Soleidae	*Buglossidum luteum*	MM	0.27	0.05	0.08	0.34%
Callionymidae	*Callionymus* spp.	ES	0.00	0.00	0.02	0.02%
Clupeidae/Engraulidae	*Clupeidae/Engraulidae* n.id	na	0.00	0.01	0.04	0.04%
Blenniidae	*Coryphoblennius galerita*	MS	0.01	0.09	0.13	0.20%
Gobiidae	*Crystallogobius linearis*	MS	0.04	0.02	0.00	0.04%
Moronidae	*Dicentrarchus labrax*	MM	0.00	0.00	0.02	0.02%
Sparidae	*Diplodus* spp.	MS	0.00	0.02	0.14	0.14%
Trachinidae	*Echiichthys vipera*	MS	0.05	0.00	0.05	0.08%
Engraulidae	*Engraulis encrasicolus*	MS	1.28	0.93	0.51	2.30%
Gobiidae	*Gobiidae* n. id	ES	1.17	0.30	0.23	1.43%
Gobiidae	*Gobius niger*	ES	2.07	1.24	2.13	4.58%
Gobiidae	*Gobius* spp.	ES	0.30	0.55	0.19	0.87%
Gobiidae	*Gobius xanthocephalus*	ES	0.02	0.00	0.00	0.02%
Gobiidae	*Gobiusculus flavescens*	ES	0.00	0.00	0.01	0.01%
Ammodytidae	*Hyperoplus lanceolatus*	MS	0.00	0.00	0.01	0.01%
Labridae	*Labridae* n. id	na	0.00	0.00	0.02	0.02%
Labridae	*Labrus bergylta*	MS	0.00	0.00	0.01	0.01%
	Larva n. id.	na	1.11	1.41	0.93	2.90%
Blenniidae	*Lipophrys pholis*	MS	0.13	0.10	0.16	0.33%
Blenniidae	*Lipophrys* spp.	MS	0.00	0.00	0.01	0.00%
Mugilidae	*Liza ramada*	CA	0.00	0.02	0.01	0.03%
Mugilidae	*Liza* spp.	CA	0.00	1.19	0.04	1.04%
Blenniidae	*Parablennius gattorugine*	MS	0.00	0.02	0.01	0.03%
Blenniidae	*Parablennius pilicornis*	MS	0.28	0.27	0.88	1.21%
Pleuronectidae	*Platichthys flesus*	MM	0.31	0.10	0.13	0.45%
Pleuronectidae	*Pleuronectidae* n.id	MM	0.00	0.02	0.01	0.03%
Gadidae	*Pollachius pollachius*	MS	0.07	0.00	0.00	0.06%
Gobiidae	*Pomatoschistus microps*	ES	22.32	4.73	16.45	36.63%
Gobiidae	*Pomatoschistus minutus*	ES	3.10	1.40	0.54	4.24%
Gobiidae	*Pomatoschistus pictus*	ES	0.06	0.24	0.27	0.48%
Gobiidae	*Pomatoschistus* spp.	ES	20.19	11.53	11.00	35.96%
Scophthalmidae	*Psetta maxima*	MM	0.00	0.00	0.02	0.01%
Clupeidae	*Sardina pilchardus*	MM	0.30	0.73	1.40	2.05%
Soleidae	*Solea senegalensis*	MM	0.64	0.28	0.28	1.01%
Soleidae	*Solea solea*	MM	0.33	0.10	0.11	0.45%
Soleidae	*Soleidae* n. id.	na	0.16	0.04	0.01	0.18%
Sparidae	*Sparidae* n. id.	na	0.12	0.07	0.02	0.18%
Sparidae	*Spondyliosoma cantharus*	MS	0.00	0.01	0.00	0.01%
Labridae	*Symphodus melops*	MS	0.00	0.03	0.02	0.04%
Syngnathidae	*Syngnathus abaster*	ES	0.02	0.02	0.03	0.05%
Syngnathidae	*Syngnathus acus*	ES	0.01	0.13	0.09	0.20%
Syngnathidae	*Syngnathus* spp.	ES	0.00	0.00	0.03	0.03%
Syngnathidae	*Syngnathus typhle*	ES	0.00	0.03	0.01	0.03%
Gadidae	*Trisopterus luscus*	MS	0.01	0.00	0.00	0.01%
Gadidae	*Trisopterus minutus*	MS	0.02	0.00	0.00	0.02%

Table 2 – Fish larvae density (ind./100m³) for each guild in different climate conditions and seasons. MS, Marine Stragglers; ES, Estuarine Species; MM, Marine Migrants.

Season	Year	MS	ES	MM
winter	wet	0.78	6.44	0.39
spring	wet	3.65	62.73	2.21
summer	wet	1.64	113.25	3.10
autumn	wet	2.47	9.44	1.49
winter	regular	0.91	6.04	0.39
spring	regular	1.27	32.58	1.81
summer	regular	3.86	27.16	1.10
autumn	regular	0.52	14.40	1.81
winter	dry	5.27	6.47	4.27
spring	dry	2.02	41.99	1.05
summer	dry	4.82	66.33	1.77
autumn	dry	0.53	6.00	1.36

Spatial distribution for each guild in the estuary showed that in winter dry conditions MS species presented higher concentrations near the mouth (M0, M) reaching station N1 in lower numbers. Similarly, during summer dry conditions, higher concentrations occured near the mouth (M0 and M) and in the south arm sampling stations (S1, S2) (Fig. 4). During regular conditions MS species peak occurred near the mouth during winter, and on station S2 during summer. During wet years, higher abundances occurred during spring on station M0, M and S2 (Fig. 4).

Marine migrants, showed higher abundances near the mouth (M0, M) in both dry winter conditions and regular spring conditions (Fig. 4). However, during wet years, marine migrants appear only in station S1 in reduced numbers (Fig. 4).

Estuarine species, in spring and summer dry conditions were higher in sampling stations S1/S2 and N1/N2, respectively (Fig. 4). During regular years, ES were mainly present in the south arm, while during wet years, higher peaks abundances ocurred during spring on station S2 and during summer on station S1 and N2 (Fig. 4).

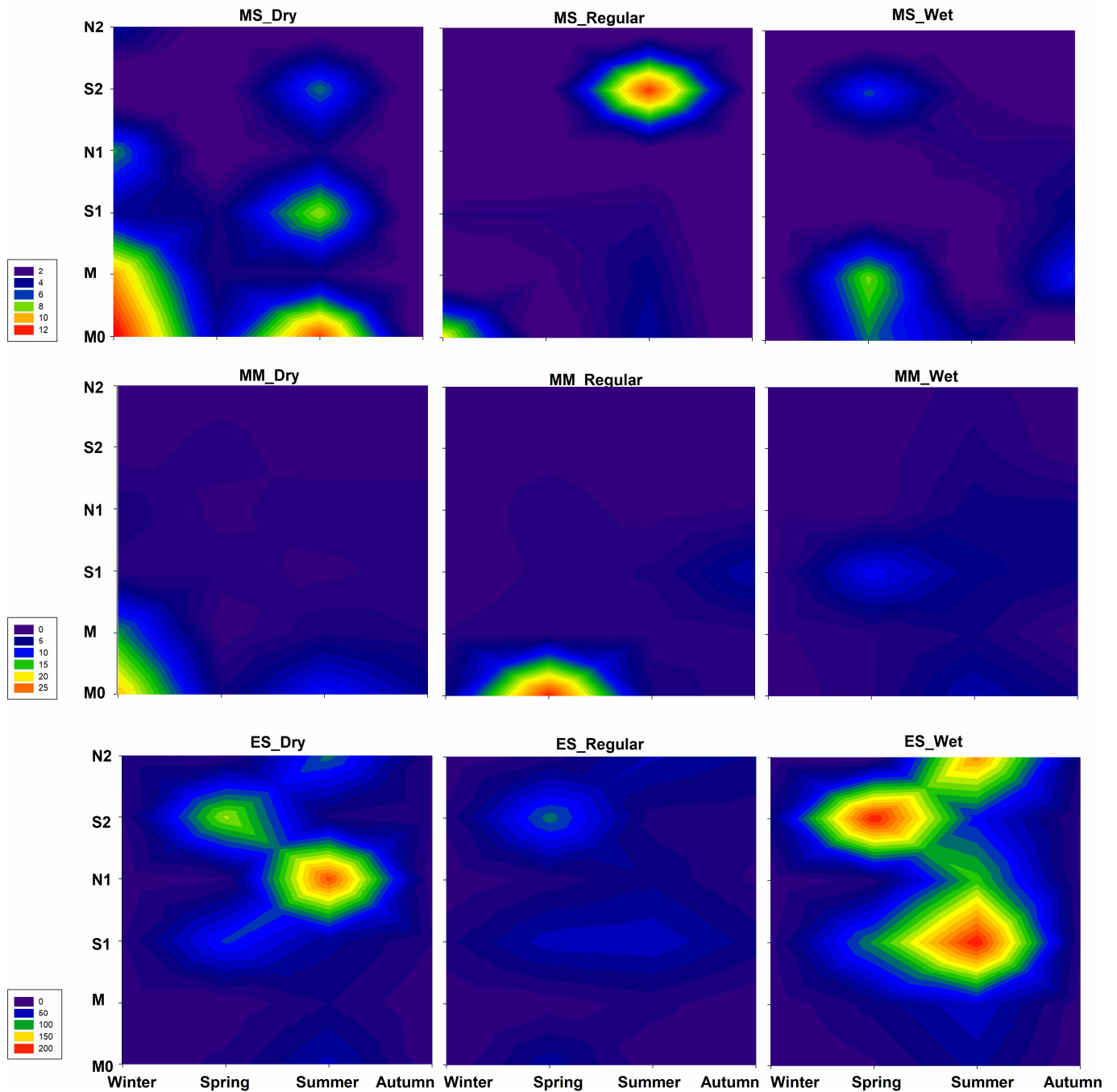**Figure 4**-Spatial and seasonal density (ind./100 m³) distribution of the three main fish larvae guilds during the sampling period for each climate condition. MS, Marine Straggler; MM, Marine Migrant; ES, Estuarine Species.

4.3 Community structure and relation with environmental variables

Community structure analysis revealed a strong interaction between climate conditions and season (Pseudo-F = 2.20; p = 0.001). Wet and dry periods presented similar seasonal variation with no distinction between summer and spring (pairwise p(perm) > 0.05) while in regular conditons community structure were distinct in all seasons (pairwise p(perm) > 0.05) (Fig. 5). Furthermore, wet summer larval assemblages were distinct from regular and dry (pairwise p(perm) < 0.05) and regular autumn community structure was also different from wet and dry autumn (pairwise p(perm) < 0.05) (Fig. 5) resulting in six different assemblages. Despite climate conditions, *Pomatoschistus* spp., *A. tobianus*, *P. microps* and *S. pilchardus* were the most important species in the assemblage during winter, and *Pomatoschistus* spp., *P. microps*, and *G. niger* during spring. During regular and dry summers, the assemblages was mostly constituted by Gobiidae species, *E. encrasicolus* and *P. pilicornis* while the latter two species decrease considerable during wet summers. During wet and dry autumns, the assemblage was mainly constituted by Gobidae species as well as *S. senegalensis* and *B. luteum*. In regular autumns, there is a decrease in the abundance of both flatfish species.
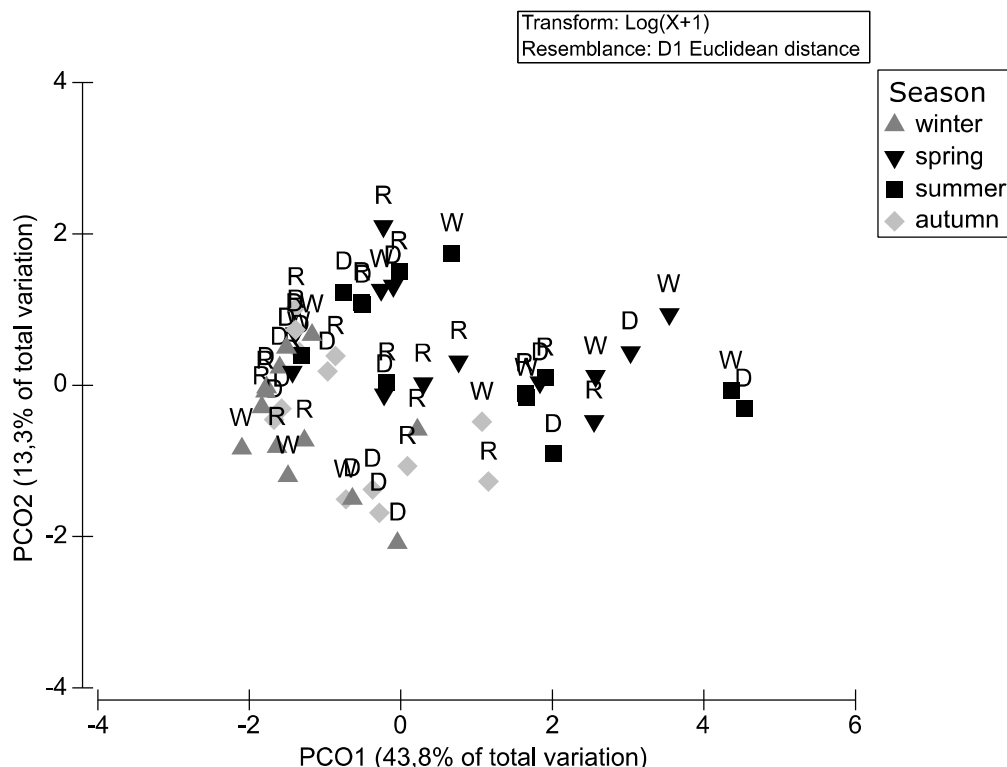
Figure 5-Principal coordinates ordination (PCO) plot of larval fish assemblages during the studied period in the Mondego estuary. W, Wet; D, Dry; R, Regular years.

PC1 extracted from community structure, regional atmospheric environment and local hydrological changes explained 39.8%, 53.6%, 73.0% of the total variances observed,

respectively. In this way, each one of this PC1 axes encompasses the main signal relative to community and the environment observed over the studied period (Fig. 6).

Spearman correlation analysis showed that the extracted variability of the larval fish assemblages during the studied period was strongly related with regional environment (Spearman $R^2 = -0.29$; $p < 0.001$) (Fig. 6A, 6D) and local hydrological variability (Spearman $R^2 = -0.47$; $p < 0.001$) (Fig. 6B, 6D). However, no relationship was found with the NAO index (Fig 6C, 6D).

Figure 6-Interannual variability of environmental forcing on the Mondego Estuary over the period 2003–2015. (A) Regional climate, (B) Local hydrology, (C) NAO - North Atlantic Oscillation Index, and (D) Ichthyoplankton.

5. Discussion

Previous research on the Mondego nursery area has been carried out to portray how the larval fish community behaves facing environmental variability, however, this is the first study investigating how contrasting hydrological years affects the community on a large-scale term of 13 yea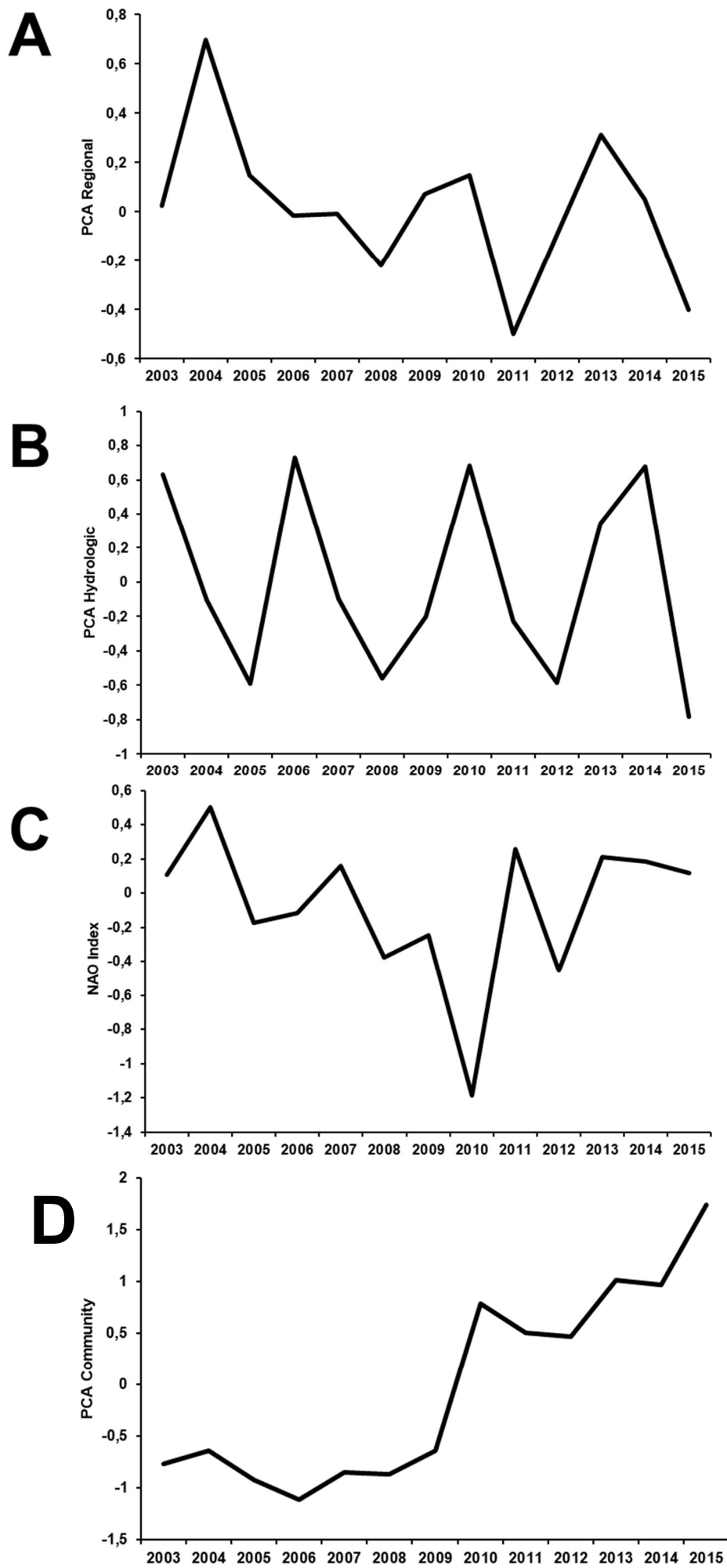rs duration. Studies around the world point out alterations on the community structure of ichthyoplanktonic species in coastal and estuarine grounds, due to climate variability, evidencing increased abundances of lower commercial species replacing higher valuable ones (Voss et al., 2012; Guan et al., 2017; Song et al., 2019; Maynou et al., 2020). This seems not to be the case in the Mondego estuary, however fish larvae community showed strong relationship with climatic variability.

In this study, a total of 47 different taxa were identified and the community was dominated by the Gobidae familly: *Pomatoschistus microps* (36.6%) *Pomatoschistus* spp. (36.0%) were highly abundant across all year, particularly during wet years, followed by *Gobius niger* (4.6%) and *Pomatoschistus minutus* (4.2%). *Engraulis encrasicolus* (2.30%), *Sardina pilchardus* (2.05%), *Parablennius pilicornis* (1.21%), *Ammodytes tobianus* (1.19%), *Liza ramada* (1.04%) and *Solea senegalensis* (1.01%) were less common species with seasonal peaks spread along the year. The pattern observed was similar to the ones previously reported in the Mondego estuary (e.g.: Ribeiro, 1991; Marques et al., 2006; Primo et al., 2011), and in other Portuguese estuaries (Faria et al., 2006; Ramos et al., 2006). In fact, one or two dominant species and a variety of occasional ones in lower abundancies, is a characteristic feature portrayed in estuaries worldwide (Whitfield, 1990; Harris & Cyrus, 1995; Tolan, 2008;). Gobies' success in these ecosystems may be explained by an advantage of their reproductive strategy. They are capable to release multiple batches of demersal eggs within a spawning season which, added to their male parental care, may increase their survival success (Bouchereau & Guelorget, 1998; Laur et al., 2014). Also, their demersal eggs constitute a successful adaptation to estuarine environments, reducing the probability of being dragged out of the estuary thus decreasing mortality risks and increasing their abundance (Whitfield et al., 1990; Laur et al., 2014). Furthermore, their protracted spawning periods give rise to more than one spawning peak, mainly during years with warm summers and in highly productive habitats (Newton, 1996; Mazzoldi & Rasotto, 2001). This was previously observed in the Mondego estuary where *Pomatoschistus microps* presented three periods of recruitment (January, April and June/July) (Dolbeth et al., 2007; Nyitrai et al., 2013).

Along the study period it was noticed a strong seasonal pattern despite the climate condition. Indeed, higher abundances of fish larvae occur during warmer months, in spring and summer, a pattern widely described on the literature (Marques et al., 2006; Faria et al., 2006; Ramos et al., 2006; Primo et al., 2011; Costa & Muelbert, 2017). This seasonal pattern is related with the spawning period of most of the taxa and to favourable conditions to a rapid growth (Whitfield, 1990; Faria et al., 2006).

The wet climate condition showed the highest larvae abundance, with a great number of not only estuarine species, but also marine stranglers. Alterations on freshwater flow affect not only the saline gradient inside the estuary but also dissolved oxygen content, turbidity, suspended solids content, nutrients and detrital input, and consequently, primary and secondary production, as well as the extend of the estuarine plume, which sends mainly olfactory cues responsible to signal marine larvae species their way into the nursery estuarine ground (Whitfield, 1990; Meynecke et al., 2006; Baptista et al., 2010; González-Ortegón et al., 2010; Williams et al., 2013). During years of low freshwater flow (dry years), the plume will reach a reduced costal area, failing on signalling more larvae into the estuary (Chícharo et al., 2006). On the contrary, during years with a greater flux of river drainage (wet years), the estuarine plume will penetrate widely on to the coastal area signalling more larvae that spawn at coast and lead their way into the nursery ground, resulting in high rates of recruitment of marine species (Vinagre et al., 2007).

Results showed that both dry and wet climate conditions present similar seasonal abundance peaks: a smaller during spring and a maximum during summer. However, during wet years, the first smaller peak occures sooner, starting during late winter/early spring, and the later during late summer. Other systems demonstrate a delay on peak abundance inherent to climate conditions (Jenkins et al., 2018). Indeed, Primo et al. (2011) had already observed this alteration of timing on seasonal peaks according to climate conditions on the Mondego estuary. Postponement of the second peak of abundance during wet years may be due to an increase in water flow during the winter and spring period, delaying the optimal conditions of salinity for spawning until late summer (Jenkins et al., 2018). Phenological changes may influence the ecosystems functions, mainly the trophic chain, through disruptions on the timing of food availability for fish larvae in the environment through Cushing's match/mismatch hypothesis (Cushing, 1975; Edwards & Richardson, 2004; Genner et al., 2010). Indeed, many studies point out the influence of climate change on the larval and juvenile fish communities via bottom-up control, through changes on the food web, either on delayed timing of food abundance, or quantity or quality of the food available on the environment (e.g.: Reid et al., 2001; Beaugrand et al., 2003; Pitois et al., 2012; Lynam et al., 2017; Capuzzo et al., 2018). Nevertheless, Newton, (1996) indicates that the match/mismatch hypothesis is more relevant in a marine environment or for marine species, since most estuarine species are well adapted to the changing hydrological regimes of the estuary.

Spatial patterns in the estuary seems also to be affected by different climate conditions with increased presence of marine species during dry winter periods. In fact, marine stragglers reach upper zones of the estuary in high densities during dry winters and summers. This pattern was previously observed in the Mondego estuary particularly for marine migrants (Primo et al., 2011). The increased abundances of marine species during dry years is caused by higher incursion of seawater, due to low precipitation and river flow (Martinho et al., 2007), creating a more suitable environment for these species that typically spawn in coastal zones. This process

was named the 'marinisation' hypothesis by Pasquaud et al. (2012) which observed a similar trend on the Gironde estuary, caused by increased seawater intrusion which may favour the nursery function for marine juvenile fishes in upstream areas of the estuary. During regular summers, marine stranglers reach the upper sampling station of the south arm, yet in lower numbers. During summer this area present reduced river flow, changes on daily salinity are low and the water is highly rich in nutrients resulting in a high zooplanktonic abundance enabling marine strangles to prevail on this arm (Marques et al., 2006).

Along the study period, the community assemblages behave on different ways according to each climate condition. Generally, during regular conditions, the assemblages structure changed along the year, while during extreme climatic periods, dry and wet conditions, summer and spring were similar. Furthermore, six different assemblages were observed. Despite climate conditions, *Pomatoschistus* spp., *A. tobianus*, *P. microps* and *S. pilchardus* were the most important species in the assemblage during winter, and *Pomatoschistus* spp., *P. microps*, and *G. niger* during spring. Main differences observed between climate condition occurred in summer and autumn assemblages. During regular and dry summers, the assemblages was mostly constituted by Gobiidae species, *E. encrasicolus* and *P. pilicornis* while the latter two species decrease considerable during wet summers. The decrease of anchovy during high water flow periods has already been documented and is mainly related with the increase of freshwater flux which drag their pelagic eggs and small larvae out of the nursery zone, compromising their survival (Faria et al., 2006; Tolan, 2008). On the other hand, *P. pilicornis* presents demersal eggs (Resgalla, 2000), an adaptative strategy to prevent the eggs being dragged. This species presence inside the Mondego estuary has been recorded previously mainly on the upstream area of the estuary during summers with low river flow (Primo et al., 2012a). Therefore, the low salinity levels during high river flow periods may act as a barrier for this marine strangler to enter the estuary, resulting in a reduction of their abundance during wet years (Marshall & Elliott, 1998). During wet and dry autumns, the assemblage was mainly constituted by Gobidae species as well as *S. senegalensis* and *B. luteum*. In regular autumns, there is a decrease in the abundancies of both flatfish species. In fact, during autumn, wet and dry condition periods presented similar precipitation regimes, with higher values than regular autumn conditions. This precipitation will contribute to an increased river plume. Flatfish species are known to have a strong relationship with the extent of the river plume, essential to signal larvae their way into the estuary (Vinagre et al., 2007).

Long-term changes on ichthyoplankton community of the Mondego estuary were strongly related with local (river runoff, water salinity and temperature) and regional factors (precipitation, air temperature, SST and SLP). Local variations can lead to changes on reproduction timing, population dynamics, abundance, spatial distribution and interspecific relationships like competition and predation (Ottersen et al., 2001). At a local and regional scale, the relationship between precipitation, runoff and salinity seems to play a key role on the spatial distribution and

abundance of estuarine species (Faria et al., 2006; Drake et al., 2007; Martinho et al., 2009 ; Primo et al., 2011; Williams et al., 2013; Maynou et al., 2020). In fact, precipitation and runoff were previously described as the main drivers influencing the fish community off the Mondego estuary, being inversely related with the ability of young larvae and eggs to be retained and their survival success (Martinho et al., 2009; Primo et al., 2012; Primo et al., 2015). Temperature influence is related with seasonal spawning of the species, since higher values is related with an increase in food availability, namely, higher zooplanktonic abundance (Faria et al., 2006; Marques et al., 2006). Also, SST was positively related with the abundance of some subtropical species which use the Mondego estuary as a nursery ground, like *P. flesus* and *B. Luteum* (Martinho et al., 2010).

In agreement with our results, previous studies in the Mondego estuary also evidenced a lack of relation between NAO and the local communities due to reduced time and space scale of the sampling or to seasonal character of this index (e.g.: Martinho et al., 2009; Primo et al., 2012). NAO influence varies from location to location, and it could not be a good proxy of hydroclimatic variation on the western coast of the Iberian peninsula (Ottersen et al., 2001). Furthermore, this influence can also be species specific. Attrill & Power, (2002) found no correlation between NAO and juvenile estuarine fish species, but strong influence on marine juveniles. Since larvae fish community of the estuary is mainly comprised by estuarine species, this can explain the lack of relationship with NAO. Furthermore, often large scale factors as NAO operate indirectly, affecting regional processes which then shape the physical environment affecting the communities (Marques et al., 2018; Bindoff et al., 2019).

The recent climatic alterations in terms of precipitation documented on the Mondego estuary have impacted several trophic levels of the estuarine community (Marques et al., 2007, 2014; Martinho et al., 2007; Primo et al., 2009, 2015; Baptista et al., 2010; Nyitrai et al., 2012). The results, either on zooplanktonic community or on juvenile and adult fishes, were a depletion of estuarine and freshwater species and increase on marine species during years of low precipitation and reduced river flow, as observed in the present study. Dry condition periods were relatively short (maximum 2 years) and a longer time scale with the same condition may be needed in order to observe dramatic and more permanent changes. Short term drought periods can have lower influence on the community since fish species have a delayed time response to alterations (Primo et al., 2011). Prolonged extreme events, like severe drought regime, will certainly have consequences on the ecosystem function. Low freshwater flow is associated not only with high saline intrusion but also with less nutrients circulating in the water, therefore less productivity, resulting in planktivorous fish being replaced by piscivorous marine species on the downstream estuarine areas (Chícharo et al., 2006). This changes will have enormous impacts on the food web in the relationship prey-predator, possible niche overlapping and increase competition (Baptista et al., 2010; Pasquaud et al., 2012; Nyitrai et al., 2013; da Silva Lima et al., 2020). Furthermore, species response to environmental variability can be complex and very

specie/stage-specific and different combinantions of environmental factors will have different consequences among the larval community (Harris & Cyrus, 1995).

In conclusion, along the 13 years duration of this study, main changes on the ichthyoplanktonic community of the Mondego estuary were related with species seasonality and phenological changes as well as a reduction on total larval abundance and an increase of marine species during extreme events. Local and regional environmental variables were strongly related with the larval fish community structure while large scale index NAO could operate in a more indirect way. Indeed temperature seem to affect the larvae abundance seasonality, while estuarine salinity and river runoff play a key role on their distribution and presence inside the estuary. The higher abundance of fish larvae in the assemblages occurred during wet conditions periods however, during dry periods occurred an increase of marine species presence inside the estuary. Seems likely that the increase duration and severity of extreme weather events will affect the ecology of the larval fish community leading to severe impacts on the fish recruitment and fishing stocks availability. Therefore, the current study present an important contribution to better understand the impact of environmental changes over the ichthyoplanktonic community on the Mondego estuary.

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