Influence of oceanic and climate conditions on the early life history of European seabass *Dicentrarchus labrax*

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ABSTRACT

Understanding how marine fish early-life history is affected in the long-term by environmental and oceanographic factors is fundamental given its importance to population dynamics and connectivity. This work aimed at determining the influence of these processes on the interannual variability in hatch day and early-life growth patterns of European seabass, over a seven-year period (2011–2017) in the Atlantic Iberian coast. To accomplish this, otolith microstructure analysis was used to determine seabass hatch day and to develop early-growth correlations. In most years, hatching occurred from February to April, with two exceptions: in 2012, hatching started in early-January, and in 2016 an exceptionally long hatching period was registered. Using generalized additive models (GAM), we observed that sea surface temperature (SST), the North Atlantic Oscillation index (NAOi) and Chlorophyll-a (Chla) were the main drivers behind the inter-annual variability in seabass hatch day. Analysis of correlations between growth increments allowed assessing important periods of seabass growth and how future growth is affected. Since seawater temperature is among the main drivers for seabass recruitment and growth, its life cycle may be hampered due to ocean warming and an increasingly unstable climate, with consequences for the natural marine stocks and their harvest.

1. Introduction

Many marine fish species have complex life histories, in which transitions between life stages often coincide with shifts in habitat use (Able, 2005; Dambrine et al., 2021). These are shared by several coastal species, where spawning takes place offshore, after which newly hatched larvae are transported into shallow coastal and estuarine areas, remaining for varying periods, prior to their migration back into coastal areas. In this sense, connectivity, i.e., the exchange of individuals amongst geographically separated units, is a key feature for the population dynamics of these species (Cowen, 2000; Gillanders et al., 2012). Still, quantifying the scale and extent at which fish larvae are able to disperse remains a challenge (Morat et al., 2014).

Recruitment of marine fish is among the most important issues in fisheries ecology (Rijnsdorp et al., 2009), and is mainly influenced by density-independent factors (Miller et al., 1991; Rijnsdorp et al., 1995; Cabral et al., 2007), with consequences for the natural populations and

their harvest (Jennings and Pawson, 1992). Previous studies have described the effect of several oceanographic factors on marine fish life cycles, such as sea surface temperature (SST), the North Atlantic Oscillation (NAO), Eckman transport, upwelling events and the extension of river plumes (Van Der Veer et al., 2000; Attrill and Power, 2002; Santos et al., 2004; Martinho et al., 2009; Tanner et al., 2017), which can deeply affect time of hatching and larvae migration and thus, can affect the ability for marine fish to successfully recruit (Rijnsdorp et al., 1995; Beraud et al., 2018).

Over the past decades, otoliths have become a key tool to uncover further information in this field. Located on the fish's equivalent to the inner ear, otoliths are calcium carbonate structures formed in the beginning of the ontogenic process (Stevenson and Campana, 1992). Biologically, they are crucial for hearing (Stevenson and Campana, 1992), detecting movement, maintaining balance and ultimately for orientation (Comerford et al., 2013). The two main properties that grant these structures their current applications in marine ecological studies

are the non-skeletal and continuous growth through biomineralization, and never being subject to resorption, even in periods of starvation (unlike scales or bones) (Campana and Thorrold, 2001). Indeed, otolith microstructural analysis can be a powerful tool to unveil many species' early life history traits such as hatching day, mouth opening and first feeding, settlement, metamorphosis, age and growth patterns, and even migration (e.g. Campana and Neilson, 1985; Fox et al., 2007; Martinho et al., 2013; Rodríguez-Valentino et al., 2015; Nanami, 2017; Joh and Wada, 2018; Vaz et al., 2019). Determining the timing and duration of key events is very important to understand the fish life cycle, which is highly crucial for fisheries management. These life-history traits are initially recorded in bipartite structures on a microstructural level, forming daily growth bands or growth rings (Rodríguez-Valentino et al., 2015) which are the basis for age and growth back-calculation (Neuman, 2001; Stevenson and Campana, 1992).

This study focuses on the European seabass *Dicentrarchus labrax,* a demersal euryhaline and eurythermic species which inhabits coastal lagoons and estuaries as well as open sea and coastal waters (Cardoso et al., 2015; Bento et al., 2016). Its geographical distribution ranges from the North Sea, in Norway, to the coast of Senegal, including the Mediterranean and Black seas (Cardoso et al., 2015; Bento et al., 2016). The life cycle of the European seabass can be characterized as a typical marine fish with ontogenic migrations and oceanic and estuarine phases (Pickett et al., 2004; Martinho et al., 2009; Reis-Santos et al., 2013) clearly delimited in time. Despite this species popularity for both recreational and professional fisheries, granting it a high economic relevance, few are the studies focusing on its otolith microstructure (see Gutiérrez and Morales-Nin, 1986; Planes et al., 1991; Regner and Dulcic, 1994), and those are nearly three decades old. Therefore, new insight in this field is required. In the western Atlantic, some studies have focused on the effects of water temperature and photoperiod on its spawning period (Vinagre et al., 2009), and on the control exerted by climate patterns on juvenile abundance within estuarine nurseries (Bento et al., 2016). Hence, there is a clear lack of knowledge on the long-term effects of climate and oceanographic conditions on the early life cycle of *Dicentrarchus labrax* on the northeast Atlantic. Particularly, the stock structure in the Atlantic Iberian waters is virtually unknown (ICES, 2019a,b), which hinders the implementation of management measures.

Studies focusing on inter-annual hatching variability and species/climate interactions are essential to understand early life history ecology, providing key information for the development of management and protection plans for fish and their fisheries. This will ultimately contribute to a sustainable harvest of marine resources. The present work aimed at determining the interannual variability of seabass hatch day distributions and early-life growth induced by environmental and oceanographic factors in the Iberian coast over a 7-year-period (2011–2017).

2. Materials & methods

2.1. Study area

Located on the western edge of the Iberian Peninsula, the Portuguese coast is characterized by a temperate climate and by the occurrence of seasonal upwelling. As one of its most important traits, upwelling is prevalent during the spring and summer seasons driven by the steady northerly winds between April and September (Garrido et al., 2009). During the winter months, winds often switch between southerly and northerly, promoting both upwelling and downwelling events (Santos et al., 2004; Martinho et al., 2009). The Western Buoyant Iberian Plume (WIBP) and the Iberian Poleward Current (IPC) are other important features of the Portuguese coast. The WIBP is surface water lens which is more prevalent during the winter, fed by the runoff of several rivers (Peliz et al., 2002; Garrido et al., 2009), while the IPC is a warmer and saltier current that flows poleward and prevents seaward extension of the WIBP (Santos et al., 2004; Garrido et al., 2009).

Located on the west coast of continental Portugal, the Mondego estuary (Fig. 1) is characterized by a continental temperate climate. This small estuary is composed of a northern and southern arm, formed when the river splits in half, about 7 km from the sea (Pardal et al., 2002). Both arms re-join near the river mouth. The northern arm is the deepest, with a 5–10 m depth during the high tide, being the main navigational channel, while the southern arm is shallower, with a 2–4 m depth during the high tide where intertidal mudflats constitute about 75% of its area (Pardal et al., 2002). The Mondego estuary has long been recognized as an important nursery area for many marine fish species (e.g. Cabral et al., 2007; Martinho et al., 2009; Primo et al., 2013; Bento et al., 2016; Primo et al., 2021).

2.2. Sample acquisition and processing

Seabass samples were obtained in the Mondego estuary from January 2011 to December 2017 at five sampling stations, guaranteeing the representation of the whole estuarine system (Fig. 1). The Mondego monitoring programme consists of three hauls performed per station in each fishing campaign using a 2-m-wide beam trawl and at the speed of two knots, covering at least 500 m^2. Hauls were performed at night, so fish would not be able to see the net and evade it. In the laboratory, all seabass specimens were measured (total length in cm; TL) and weighted (wet weight in g; WW). From the obtained samples, 0-group seabass with total length (TL) under 9 cm were selected (n = 214) to ensure that they were born in each respective year, and that a representative sample of the existing size range was obtained (based on previous work by Dolbeth et al. (2013) and Bento et al. (2016)). From the selected fish, sagittae otoliths were extracted, cleaned and stored dry in eppendorfs until further analysis. Fish handling protocols were approved by the Portuguese National Authority for Animal Health (DGAV; Ref 0421/000/000/2017).

2.3. Otolith microstructure analysis

Sagittae otoliths were mounted on microscope slides with Crystalbond 509 resin and then polished in the sagittal plane using P4000 (3 μm) Buehler silicon carbide grinding paper until clear visibility of the daily rings was obtained from the core to the edge. Digital images of each otolith were captured with a light microscope Leica DM2000 LED; the former was attached to a Leica ICC50 W camera connected to an external computer, using Leica LAS V4.8 software. At least two photos per otolith were taken (Fig. 2): one for the otolith core with a magnification of 400×, and another for the outer otolith area, with a magnification of 100×. In some cases, the 1000x amplification was used to observe more difficult otolith cores and, in larger otoliths, additional photos at 100x or 50x amplification were required to capture the whole otolith microstructure and/or facilitate microstructural analysis. Daily rings were counted in the whole otolith, and increment measures were performed only for the pelagic larval duration (PLD) until fish reached metamorphosis (according to Regner and Dulcic, 1994), using the ObjectJ plugin for ImageJ software (Schneider et al., 2012).

2.4. Environmental data

Environmental variables with different temporal resolutions, obtained from various online sources, were used as predictors with the purpose of evaluating their effect on seabass hatching over the study period. The North Atlantic Oscillation index (NAOi) was chosen as a predictor for fish hatching due to its large-scale environmental influence on western Europe and the North Atlantic. NAOi data were included in two different temporal resolutions: 30-day (hereafter 30 d) and 8-day (hereafter 8 d) means, and were acquired from the National Weather Service, Climate Prediction Centre (https://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao.shtml; accessed on April 29, 2019).

The East Atlantic pattern (EAP) is the second most influential
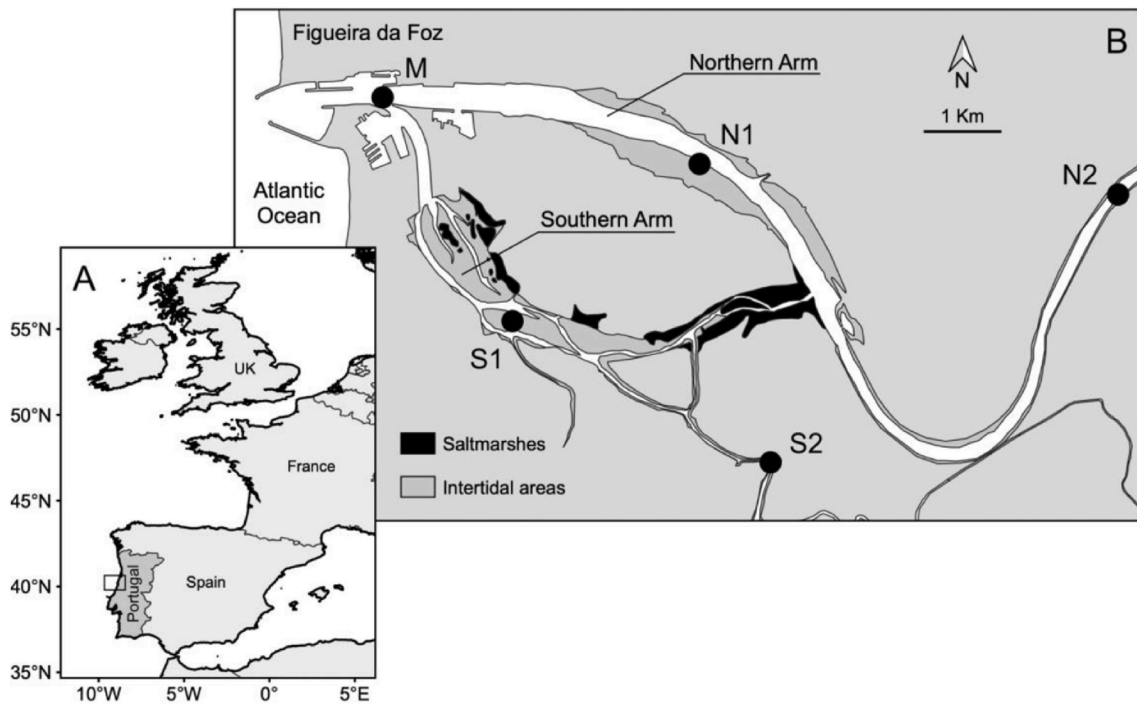
Fig. 1. Geographical location of the Mondego estuary (A) and five sampling stations representative of the whole estuarine system (B). M corresponds to the station close to the river mouth; S1 is representative of Mondego's southern arm, while S2 is representative of the Pranto river which itself holds influence over the southern arm; N1 represents the northern arm, while N2 represents the upper reaches of Mondego estuary.
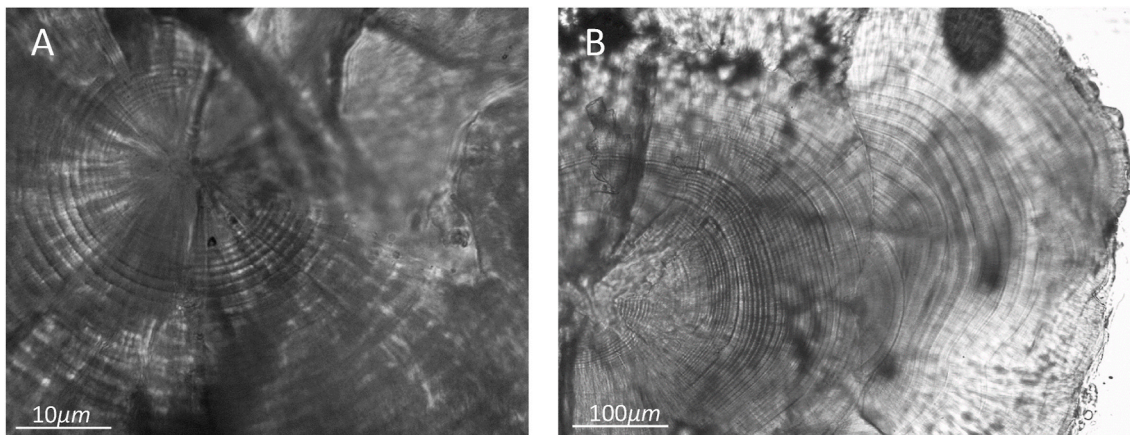
Fig. 2. Photograph of a 0-group *Dicentrarchus labrax* sagittae otolith, revealing its microstructure. Observation of an otolith core at 1000x magnification (A); otolith outer growth rings, at $100\times$ magnification, with the core visible in the centre left of the image (B).

atmospheric pattern in the North Atlantic. Yet, as its centre of activity is in the southeast North Atlantic, EAP behaves in a distinct manner comparing to NAOi (Barnston and Levezey, 1987). EA data only included a 30 d mean resolution, and were acquired from the National Weather Service, Climate Prediction Centre (https://www.cpc.ncep.noaa.gov/data/teledoc/ea.shtml; accessed on August 16, 2019).

The choice of sea surface temperature (SST, °C) as a predictor for hatch day derives from the extensive research data pointing to SST as a key driver in *Dicentrarchus labrax* life cycle (Jennings and Pawson 1992; Henderson 2002; Vinagre et al., 2012a, b; Cardoso et al., 2015; Beraud et al., 2018). SST data were obtained for a radius of 20 km off the coast of Mondego estuary, in two temporal resolutions: 30 d means and 8 d means, from NASA Oceancolor Web (https://oceancolor.gsfc.nasa.gov/l3/; accessed on May 12, 2019). Chlorophyll-a (Chla; mg m^{-3}) often used as a proxy for primary productivity, since it is considered the base for the marine food web. Similar to SST, Chla data were collected in a 20

km radius off the coast of the Mondego estuary from NASA Oceancolor Web (https://oceancolor.gsfc.nasa.gov/l3/; accessed on May 12, 2019).

Upwelling is known to affect larval transport towards inshore nurseries (Santos et al., 2004, 2007). Upwelling index (UI, m^3 s^{-1} Km^{-1}) data were obtained from the Spanish Oceanographic Institute (IEO) (http://www.indicedeafloramiento.ieo.es/index_UI_es.html; accessed on May 11, 2019), at 30 d resolution.

2.5. Data analysis

2.5.1. Biological data

For all individuals (n = 214), the relation between TL (cm) and otolith length (OL) (µm) was assessed to determine whether otolith growth is well related to fish growth. For each fish, otolith microstructure was analyzed, and the measurement of the total number of daily increments provided the fish age (FA; in days). Hatch day was then back-

calculated by subtracting the previously measured FA to the capture age (after Fox et al., 2006; Martinho et al., 2013; Vaz et al., 2019). After this, linear regressions were fitted to the relationship between TL (cm) and FA (days), accounting also for the YoC. Differences in the slopes between years were analyzed by estimated marginal means for specified factors, computed using the *lsmeans* package (Lenth, 2016) in R software (R Development Core Team, 2018). Differences occurred whenever there was a significant interaction between FA x YoC in the previous model (obtained by ANOVA; p < 0.05), after which a pairwise comparisons procedure was performed. Model validation was performed through visual inspection of the absence of discernible patterns in the residuals.

Differences in hatch day distributions between years were assessed by Kruskal-Wallis ANOVA followed by Wilcoxon multiple comparisons tests with Bonferroni correction. These analyses were also performed in R software (R Development Core Team, 2018).

2.5.2. Effects of environmental variables on hatch day distributions

Generalized additive models (GAM) were developed to assess the relationship between biological and environmental variables, given the existence of non-linear relationships between the biological features and environmental factors. During the initial model development process, Chla was log-transformed to reduce skewness of the original data. Next, collinearity between all environmental variables was evaluated with Pearson correlation coefficient. Any variable pair correlated with a correlation coefficient higher than 0.4 was assumed redundant; consequently, the environmental predictor from the pair with the highest Akaike Information Criteria (AIC) value on a univariate analysis was excluded. The effect of the excluded variable on the hatching is further discussed in the Discussion section. GAM development was performed by testing the effects of all possible environmental variable combinations of SST, NAOi and Chla, considering both 30 d and 8 d means with the objective of comparing whether distinct temporal resolutions in environmental factors would provide contrasting responses in biological parameters. For these analyses, seabass hatch day was also grouped in corresponding 30-day and 8-day periods. Model selection was done via AIC criteria. All analyses were performed using the *mgcv* package (Wood, 2011) in R software (R Development Core Team, 2018), considering a level of significance of 5%.

2.5.3. Early growth increment correlations

Forward-lag autocorrelation was used to relate the increment width of day *i* with the increment width of the previous days for each year, using Pearson correlation coefficient, following Dower et al. (2008) and Robert et al. (2014). The rationale behind this procedure is based on the premise that any event experienced in the first days of life may have repercussions on fish growth and survival in the near future. Data analysis was performed using the average daily fish growth during the PLD for each year, which was determined to occur until there was a clear transition phase in the daily ring widths, following Regner and Dulcic (1994) method. Contour plots were created using Sigmaplot 12.5 software, and used to display the Spearman correlation coefficients, ranging from 0 to 1. In 2017, we were not able to successfully correlate seabass PLD growth increments due to the low number of individuals obtained.

3. Results

3.1. Relation between fish age and fish length

For our 214 individuals, we verified the positive relation between TL (cm) and OL (μm), demonstrating that otolith growth is positively related to fish growth (Fig. S1). The present study is based on the analysis of 14035 growth increment measures. In this model, variables Age and Year of Capture (YoC) were significant (p < 0.01), as well as their interaction (p < 0.01). This indicates that regression slopes were different between years, as follows: 2012 was different from 2013 (p < 0.01), 2012 was different from 2017 (p = 0.03) and 2013 was different

from 2016 (p < 0.01) (Fig. 3). Overall, 0-group seabass in 2012 showed a lower TL/FA slope, indicating that at a given age, fish tended to be shorter, as a consequence of slower growth rates (Fig. 3).

3.2. Environmental data

Environmental factors were quite variable throughout the 7-year period (Fig. 4). Sea surface temperature (SST) in the coastal area surrounding the Mondego estuary displayed a typical variation of temperate areas, with warm summer values and colder winters. The highest SST values were observed in 2014, while the lowest were observed in 2015–2016 (winter) (Fig. 4). Chlorophyll-a concentration (mg m^{-3}) was also highly variable throughout the study duration with an exceptional event in 2014, where concentrations reached nearly 15 mg m^{-3} (Fig. 4). Highest NAOi values were observed in 2011 and 2012, while the lowest values were observed in 2015. The year of 2012 registered a particularly long negative NAO phase (Fig. 4). Particularly strong upwelling events occurred in 2013, 2014, 2015 and 2016, and a highly negative value in the end of 2015 (Fig. 4). The EAP displayed an increasing trend between 2011 and 2016 towards more positive values, to decline again in the next years (Fig. 4).

3.3. Seabass hatch day distributions

Seabass hatching dates were significantly different between years (Kruskal-Wallis H = 65.128; p < 0.001) (Fig. 5). The shortest hatching period was observed in 2015, from day 44 to day 85 (Julian days), with a total duration of 41 days. In contrast, the broadest hatching period happened in 2016, from day 14 to day 148, with a total duration of 141 days. The earliest median hatch day was recorded in 2012, while the latest median hatch day occurred in 2016 (Fig. 5). The Wilcoxon pairwise test for multiple comparisons (with Bonferroni correction) indicated the following differences: hatching period in 2011 was different from 2012 (p < 0.01), and similar to hatching in remaining years; in 2012 hatching was different from all years (2013, 2014, 2015, 2016, 2017; p < 0.01). Hatch day in 2014 was different from 2015 (p = 0.01) and hatching in 2015 was different from 2016 (p = 0.02).

3.4. Effect of abiotic variables in seabass hatching

A collinearity test between variables resulted in the exclusion of the upwelling index and EAP data, who were positively correlated with the NAOi and Chla, respectively. The influence of environmental factors on hatch day was inferred via GAM (Fig. 6). Overall, GAMs presented a good predicting capability (Tables 1–4): the 30 d GAM (Fig. 6 B, D & F) explained 78.9% of the deviance, while the 8 d GAM (Fig. 6 A, C & E) explained 41.8% of the deviance. In all models, there was a significant effect of YoC, indicating that the influence of the environmental variables varied throughout the study period. We also observed a high level of concordance between 30 d and 8 d models, with SST, NAOi and LogChla comprising the group of significant environmental predictors. Overall, the NAO was negatively related with hatching in seabass in both the 8 d and the 30 d models, in contrast to SST which presented a positive relation with hatching. Hence, hatch day occurred earlier with lower SST and higher NAOi values and were delayed by higher SST and lower NAOi values. In the 30 d model, SST had a slight u-shaped pattern at 14.5 °C (Fig. 6B). There was also a negative effect of LogChla on seabass hatching throughout the study period observed in both models.

3.5. Fish otolith early growth

The PLD was highly variable between years, with 2012 registering the longest individual PLD (97 days) and 2016 registering the shortest (43 days). Longest average PLD occurred also in 2012 (70.8 ± 11.7 days) and shortest average PLD occurred in 2017 (55.7 ± 3.8 days) (Table 5). We observed similar early larval otolith growth patterns when
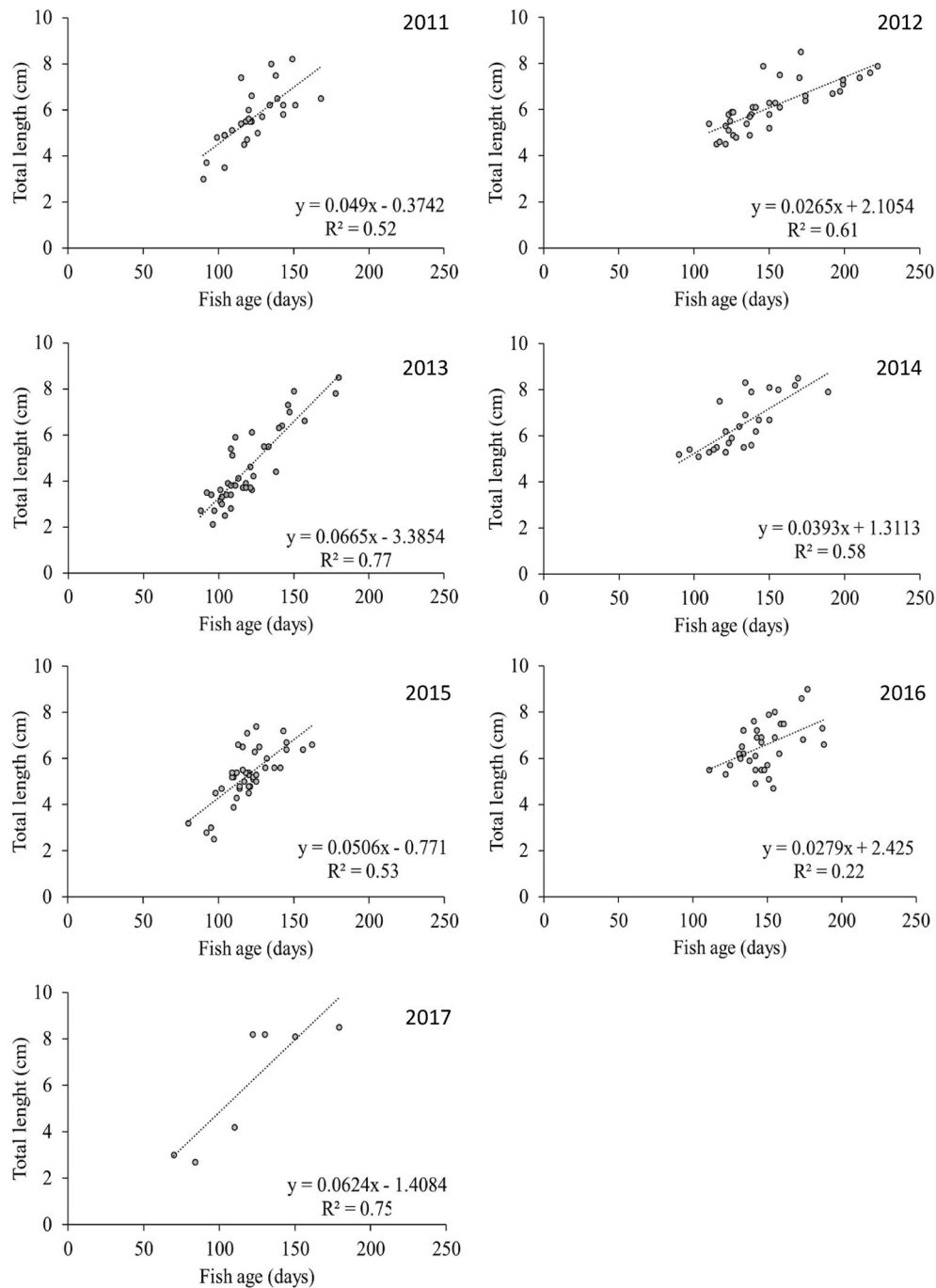
Fig. 3. Relationship between TL (cm) and estimated age (days) for 0-group juvenile *Dicentrarchus labrax* from the Mondego estuary for the period between 2011 and 2017.

comparing individual years (Fig. 7). In particular, growth over the PLD was fairly steady and slow, characterized by low variability, particularly during the first 40 days. In the end of the PLD, we observed an increase in growth rates, as well as increased variability. In 2012, lower growth rates were observed at the first days of life when comparing with the remaining years (Fig. 7).

Forward-lag autocorrelations in the early life growth of seabass showcased some variability among years (2011–2016; Fig. 8). Overall, growth in seabass at a given day seemed to have a stronger impact in the short-term (few days) rather than in the long-term. In all years, correlations were stronger in the first 3–5 days and gradually tended to diminish. However, it is still possible to split the 6 years in 2 different groups. A first group, including 2011, 2015 and 2016, where growth

remains strongly correlated (correlation value > 0.6) for periods of up to 20–30 days, and a second group including the years of 2012, 2013 and 2014, which presented overall lower growth correlations. In the latter case, after around 10 days growth correlations become much weaker, rarely exceeding the 0.6 threshold.

4. Discussion

This study is among the first to describe the long-term effects of environmental and oceanographic conditions on hatching of European seabass *D. labrax*, indicating a strong control exerted by seawater temperature and the North Atlantic Oscillation. Although some studies had already reported the effects of climate variability on the duration of the
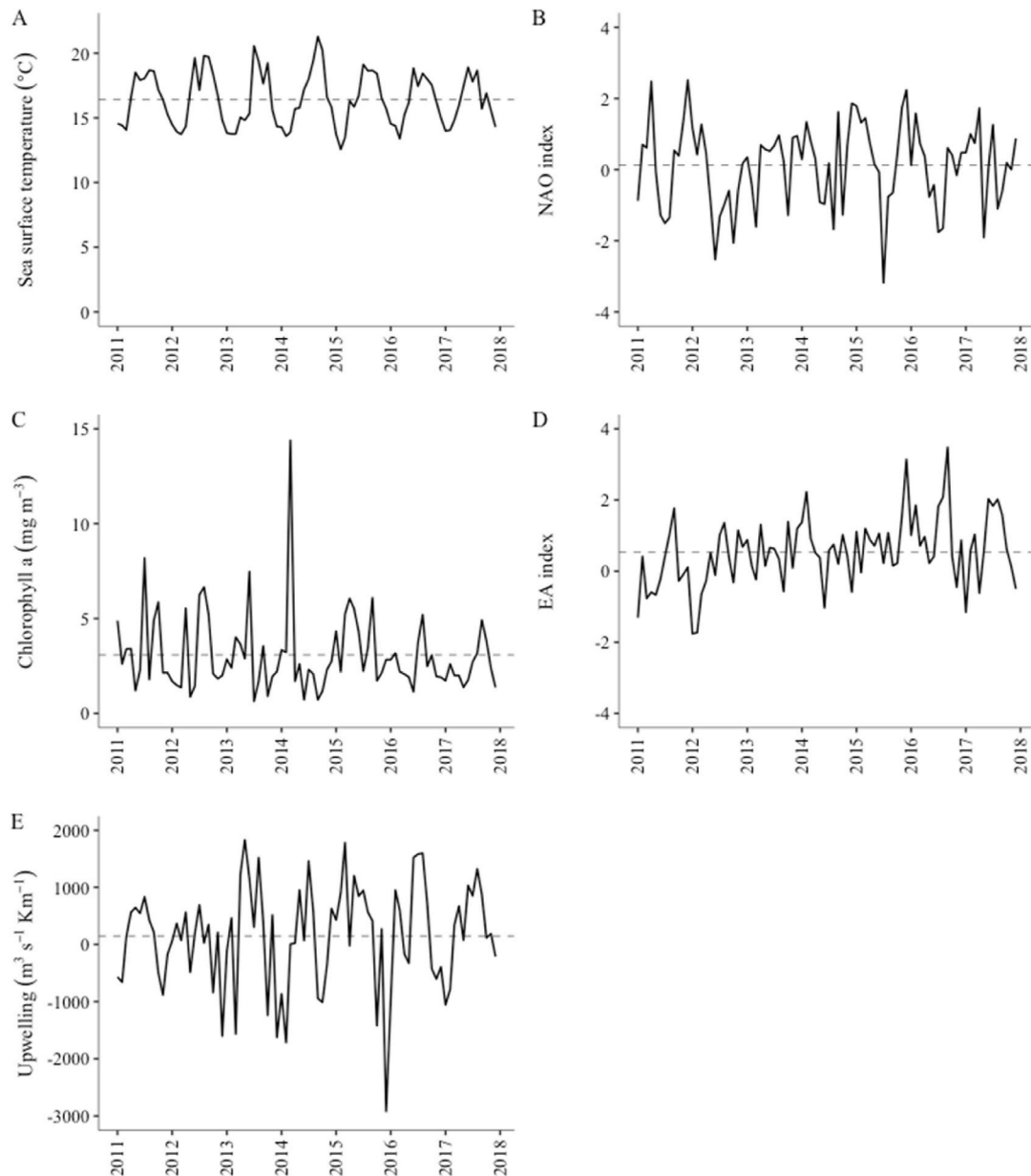
Fig. 4. Monthly average for the five environmental variables used - Sea Surface Temperature (A), North Atlantic Oscillation index (B), Chlorophyll-a (C), Eastern Atlantic pattern (D) and Upwelling index (E) from 2011 to 2017. Dashed line represents the mean value for the studied period of each environmental variable.
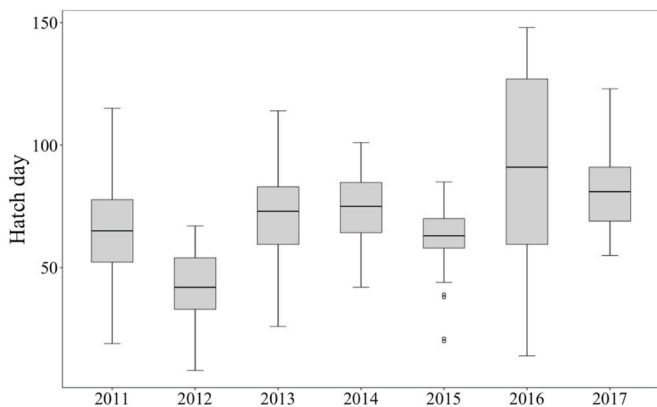

Fig. 5. Hatch day (in Julian days) distribution for juvenile *Dicentrarchus labrax* between 2011 and 2017 in the Eastern Atlantic.

spawning season (Vinagre et al., 2009) and the juvenile abundance within an estuarine nursery (Bento et al., 2016), there was still a clear lack of knowledge on how climate drives early life history in such an ecologically and economically important species, whose landings have been following a downward trend in the last years in the Atlantic (ICES, 2019a; 2019b). Indeed, understanding the effects of climate and oceanic variability on early life stages such as larvae and juveniles is key to better understand the drivers for recruitment variability, particularly in over-wintering and nursery coastal and estuarine habitats.

According to our results, seabass larvae hatched between 12 and 17 °C. Additionally, SST values near 13.5 °C led to hatching around mid-February (Julian day 50), near winter's end and early spring. This also matches previous data from the Portuguese coast, where seabass spawning occurred around winter's end and early spring, when SST is usually at its lowest (Vinagre et al., 2009). In the Portuguese coast, lowest SST values also overlap with this period, linking seabass reproduction with a drop in water temperature near winter's end and early spring (Vinagre et al., 2009). Thus, our results suggest that a decrease in
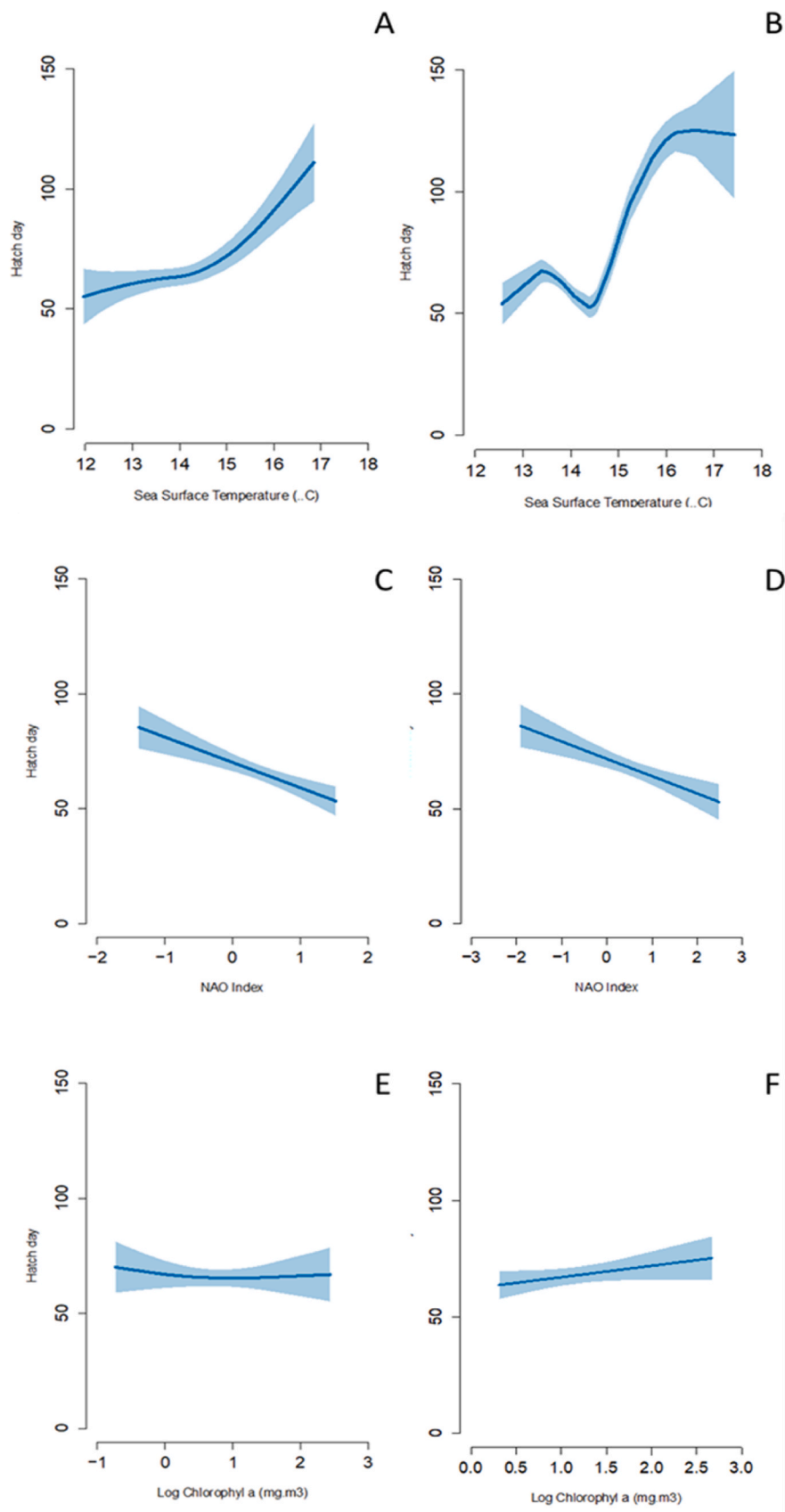
Fig. 6. Effects of environmental processes on *Dicentrarchus labrax* hatch day distribution, obtained by GAM. A, C & E represent the effect of 8 d means for SST, NAOi and Chl a respectively, while B, D & F represent the effects of 30 d means for these same variables. Shaded areas are the 95% confidence intervals.

Table 1
Generalized additive model (GAM) (30 d means), outputs for parametric co-efficients testing the interaction between environmental variables and seabass hatching, for the years of 2011–2017.

	Estimate	Std. error	t-value	p-value
Intercept	77.120	2.918	26.429	<2e-16
2012	−8.366	4.143	−2.019	0.045
2013	−12.432	4.438	−2.801	0.006
2014	−20.995	5.618	−3.737	0.001
2015	−18.661	5.737	−3.253	0.001
2016	2.494	3.660	0.681	0.496
2017	5.034	5.674	0.887	0.376

Table 2
Generalized additive model (GAM) (30 d means), outputs for the smooth terms in the interaction between environmental variables and seabass hatching, for the years of 2011–2017.

	e.d.f	Ref.df	F	p-value
SST	4.637	5.573	59.65	<2e-16
NAOi	1.000	1.000	12.22	0.001
LogChla	1.000	1.000	32.58	3.85e-08

Table 3
Generalized additive model (GAM) (8 d means), outputs for parametric co-efficients testing the interaction between environmental variables and seabass hatching, for the years of 2011–2017.

	Estimate	Std. error	t-value	p-value
Intercept	63.420	3.715	17.071	<2e-16
2012	−29.918	5.587	−5.355	2.43e-07
2013	3.651	6.196	0.589	0.556
2014	17.243	5.900	2.923	0.004
2015	11.473	5.372	2.136	0.034
2016	14.551	5.101	2.853	0.005
2017	6.822	8.402	0.812	0.419

Table 4
Generalized additive model (GAM) (8 d means), outputs for the smooth terms in the interaction between environmental variables and seabass hatching, for the years of 2011–2017.

	e.d.f	Ref.df	F	p-value
SST	1.000	1.000	16.672	6.44e-06
NAOi	1.000	1.000	3.875	0.050
LogChla	1.000	1.000	10.451	0.001

Table 5
Summary table of the biological data used in the present study (mean ± standard deviation; PLD – pelagic larval duration).

YEAR	N	TL (MM)	PLD DURATION (DAYS)	SAMPLING MONTHS
2011	30	56.8 ± 13.6	64.0 ± 9.7	Jun; Jul; Aug
2012	36	61.5 ± 10.8	70.8 ± 11.7	Jun; Jul
2013	39	46.4 ± 16.9	69.0 ± 9.5	Jun; Jul
2014	26	73.3 ± 9.9	66.8 ± 9.9	Jun; Jul; Sep
2015	41	53.0 ± 11.7	62.2 ± 8.4	May; Jul; Aug
2016	35	65.4 ± 10.3	62.9 ± 8.9	Jul; Sep
2017	7	67.9 ± 31.1	55.7 ± 3.8	Apr; May; Jun; Sep

SST might be acting as a trigger for seabass spawning, similarly to what has been documented for the North Sea populations, where a drop in water temperature led to an increase in egg production and to seabass spawning (Beraud et al., 2018). Additionally, laboratory experiments have determined that water temperature and photoperiod are determinant for male seabass spermiation, since the quantity of sperm produced is higher from December to February (Asturiano et al., 2001), as well as

for female gonadal development and egg release (Zanuy et al., 1986). This matches the spawning (Vinagre et al., 2009) and hatching periods (this work) in the Portuguese Atlantic coast, as well as the subsequent estuarine colonization process (Martinho et al., 2007; Dolbeth et al., 2010; Bento et al., 2016).

Overall, we observed a high inter-annual variability in seabass hatch day positively influenced by water temperature, implying that a warming seawater will lead to a later hatching. In particular, 2012 stood out as the year with the earliest hatching. Such high inter-annual variability in early life history has been strongly related with temperature (ICES, 2012), which corroborates our results. Indeed, warmer water temperatures are also responsible for broadening the available area for spawning in the English Channel (Beraud et al., 2018), as well as for the expansion of seabass into higher latitudes such as the Dutch Wadden Sea (Cardoso et al., 2015) and Norway (Colman et al., 2008). These results provide key insights on how this species will cope with a warming ocean, in the context of climate change.

The North Atlantic Oscillation was the second climatic explanatory variable that influenced seabass hatch day distribution. In the present work, we observed a negative relationship between NAO and seabass hatching, indicating that a negative NAO is related with a delayed hatching, while the contrary was observed for positive NAO conditions. The NAO is the major climatic system affecting Western Europe and North Atlantic (Hurrell, 1995; Trigo et al., 2002). At more northern latitudes, the NAO has been correlated with several biological attributes in marine and estuarine fishes, such as community composition, growth and abundance (e.g. Attrill and Power, 2002; Henderson and Seaby, 2005). However, the NAO has a less pronounced influence at more southern latitudes such as the Portuguese Atlantic coast (Trigo et al., 2002), as well as on the marine species that live there (Martinho et al., 2009; Bento et al., 2016). This indirect influence may derive from NAO's combined effect on ocean temperature (Rodwell et al., 1999), as well as wind and water circulation patterns (Hurrell, 1995), which are critical for a successful spawning and larval transport towards inshore nurseries (see Beraud et al., 2018). Still, the NAO had the lowest values in 2012, which in conjunction with the lower SST, was most probably responsible for an earlier hatching. Indeed, low NAO values are associated with poor oceanic conditions like colder water temperature and low primary productivity (Wang et al., 2010; Avalos et al., 2017), while positive NAO are related with warmer temperatures and more food availability, promoting strong year-class by reduced mortality (Henderson and Seaby, 2005). A positive relationship between the NAO and 0-group juvenile seabass abundance, secondary production and day of peak abundance (lagged by one year) has also been observed in the Mondego estuary (see Bento et al., 2016). Even though we did not include the upwelling index in the models due to strong collinearity with the NAO, we can also expect a positive relationship between upwelling and seabass hatching, most probably related with a bottom-up influence on coastal ecosystems due to higher nutrient input and primary productivity (von Biela et al., 2015). Further work should also focus on the effects of wind strength and direction, which are closely related with coastal upwelling. Indeed, stronger recruitment of the common sole *Solea solea* in the Portuguese coast has been associated with a prevalence of upwelling-favourable winds during spring and early-summer (Tanner et al., 2017), providing additional clues on seabass larval transport.

Although seabass hatching is closely linked with climate variability, the possibility of a match-mismatch (*sensu* Cushing, 1975) with primary food sources can also be explored. This hypothesis states that if a mismatch occurs between larval prey and larvae hatching, larvae are unlikely to find enough food to survive. Chlorophyll *a* has often been linked to fish spawning dynamics and early life history (e.g. Beaugrand and Reid, 2003; Coombs et al., 2006; Faria et al., 2006). In our study, we also determined a link between seabass hatching and phytoplankton abundance in both 30 d and 8 d models, possibly indicating a synchrony between seabass hatching and higher food availability. Nonetheless, further studies should focus on the relationship between marine fish
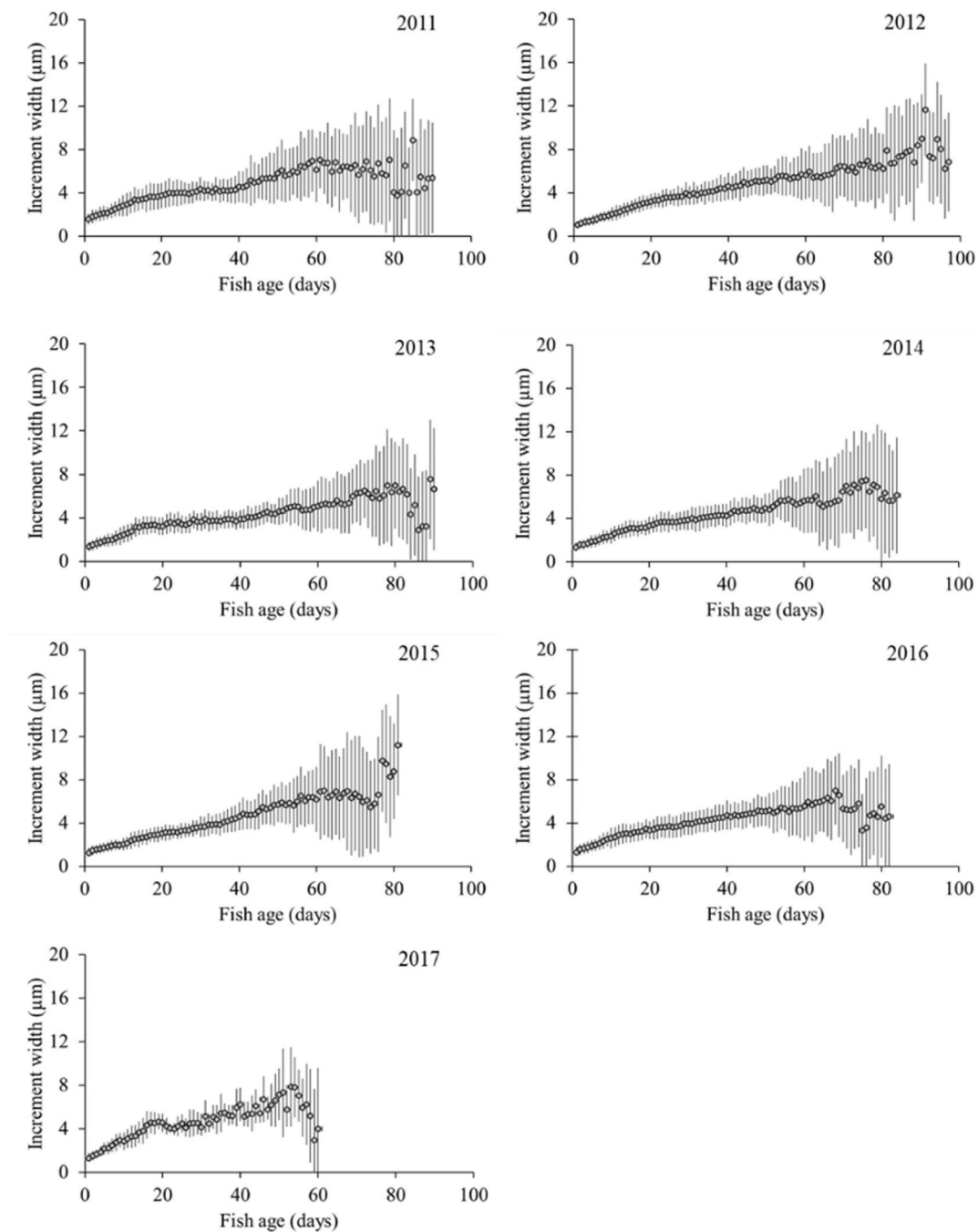
Fig. 7. Average seabass otolith daily growth increments (μm) for the years 2011–2017. Represented increments correspond to growth during the PLD. Circles represent the mean value for each day, and the respective standard deviation (vertical bars).

early-life histories and primary productivity, as chlorophyll *a* forms the base of the food webs in marine ecosystems. Similarly, the EAP (highly correlated with Chl a) also had a mild effect on seabass hatching. The EAP the second most influential atmospheric pattern in the North Atlantic, and directly related with climate patterns in southern Europe like temperature and precipitation (Iglesias et al., 2014). This climate connection process has been related with long-term growth in a marine fish (see Tanner et al., 2017), which suggests the need for more applied research on this topic.

Over the study period, it was verified the existence of variability in seabass otolith growth among years and in the forward-lag correlations. Analysing the 2012 cohort, hatching occurred earlier than expected, as well as a seemingly lower otolith growth in the initial days (Fig. 7).

Indeed, coupling of an earlier hatching with slower growth might impact on larval migration due to a lower body size attained, as colder temperatures usually result in a longer time to reach a competent settlement size (Beraud et al., 2018). In contrast, the 2017 cohort was characterized by a later hatching period, likely driven by the considerably higher SST values (Fig. 6). At a first glance, an overall higher growth could be noticed, as well as a shorter PLD. However, recruitment in the year of 2017 seems to have been weaker when compared to the remaining period, since the number of 0-group seabass in the estuary was much lower. This points to a possible desynchronization between late hatching and optimal environmental conditions for transport towards the estuary, and highlights the complex species/environment interactions that drive year class strength in marine fishes with complex life cycles such as the
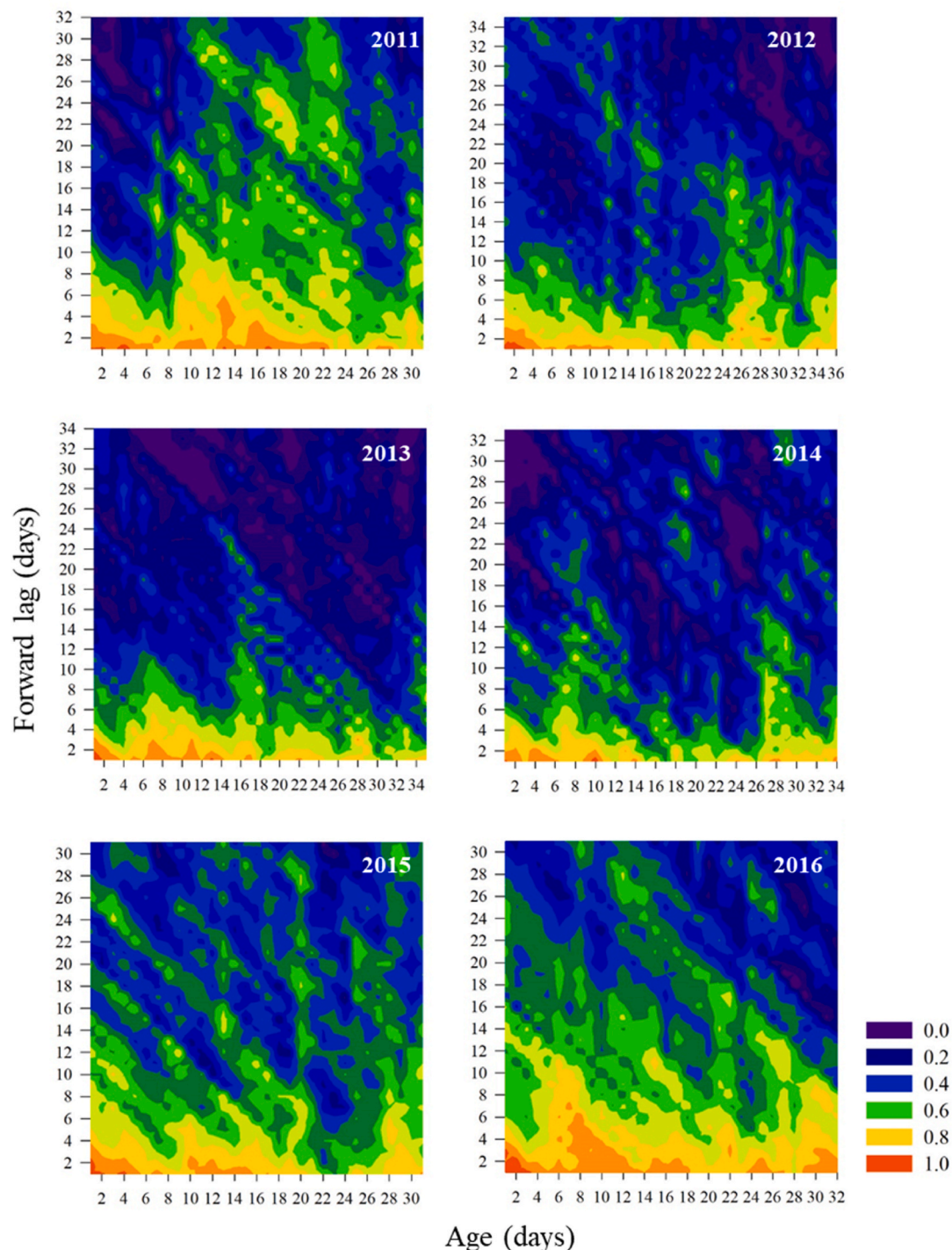
Fig. 8. Contour plot of Pearson correlation coefficients on otolith increment widths of juvenile *Dicentrarchus labrax*. Forward lag corresponds to a number of daily increments after a given otolith increment. R values are represented by the colour scale. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

European seabass.

Besides the possibility of weaker recruitment, desynchronization with suitable environmental conditions may still bring additional challenges to 0-group fish who manage to reach nursery areas. One of the main reasons why fish migrate towards nursery areas is to find shelter and a suitable place for rapid growth (Blaber and Blaber, 1980; Vasconcelos et al., 2010; Martinho 2020). Juvenile seabass have an optimal temperature range from 18 °C to 25 °C (Almeida et al., 2015), at which growth is most favourable. In the case of the Mondego estuary, from June's end onwards, water temperatures often surpass 25 °C (personal

observation), above which temperature can induce thermal stress, increases metabolic and mortality rates, while fish condition and growth rates decrease (Vinagre et al., 2012a, b). Thus, late hatching may undermine fish ability to use this favourable temporal window where fast growth occurs. In this scenario, fish with smaller body size may have lower overwintering survival possibilities.

Our results point out seabass as a fast-growing species, as they tend to exhibit high correlations between otolith growth increments (Pepin et al., 2014). Because seabass growth correlations in the first 2–4 days present extremely high values, these also suggest the existence of a

critical growth period. This critical growth period was first proposed by Johan Hjort (1914), and states that year class strength is determined in the early stages of development, after larvae absorb the yolk and start to actively find their own food; failure to do so will result in a massive mortality (Houde, 2008). Based on our results, two cohort groups can be characterized regarding early growth correlations: one group composed by the 2011, 2015 and 2016 cohorts, which presented overall persistent and stronger correlations over the PLD, and a second group including the 2012, 2013 and 2014 cohorts. According to Robert et al. (2014), a high degree of otolith growth correlations in the larval period suggests that early life events have enduring effects on future growth potential (evident for the 2011, 2015 and 2016 cohorts), and are usually associated with prey availability and the capacity/size of larvae to be able to feed upon them (Robert et al., 2014). Following this rationale, larval fish that attain larger sizes allocate more energy into foraging, allowing them to swim more actively and to escape predators. Energy dispersal pathways at early life stages will ultimately have consequences on fish growth and survival and should be considered when addressing species/environment relationships, particularly in the context of climate change, where changes in seawater temperature, atmospheric and oceanic circulation patterns are envisioned.

Overall, models based on 30-day averaged environmental factors provided more information than the 8-day counterpart, with the first explaining 79% of the associated deviance, compared to the 42% of the deviance explained by the 8-day model. Indeed, we expected that higher temporally resolved data would provide a better description of the relationship between seabass hatch day and the dominant environmental factors; however, our study proved otherwise, which can be an advantage since some data are only available in 30-day means (i.e. upwelling). In this work new insights are provided on seabass hatching in the Iberian Atlantic coast. Still, the present approach was limited by using only data from the Mondego estuary and not accounting for possible spatial/temporal variability along the Iberian coast but in fact, this is the only estuary with such a large temporal coverage in European seabass early life history. Additionally, we would also have benefitted from data on the time and location of adult spawning, which is clearly lacking in the Iberian coast.

5. Conclusions

The present results clearly indicated that seabass early lifecycle is driven by climatic variability, with sea water temperature, the NAO and chlorophyll a as key governing forces. We also suggest that the timing of hatching has the potential to regulate juvenile connectivity and recruitment in estuarine nurseries via synchronization between larval hatching and optimal environmental conditions. In a global warming scenario, changes in water temperature, food availability and oceanic conditions will impact on seabass hatching, with the ever-increasing possibility of altered population structure and connectivity, as well as failure to recruit particularly in more southern European regions.

Credit authorship and contribution statement

Miguel Pinto: Investigation, Formal analysis, Writing – original draft, Writing – review & editing. João Monteiro: Investigation, Writing – review & editing. Daniel Crespo: Investigation, Writing – review & editing. Filipe Costa: Investigation, Writing – review & editing. João Rosa: Investigation, Writing – review & editing. Ana Lígia Primo: Methodology, Writing – review & editing. Miguel Ângelo Pardal: Methodology, Supervision, Writing – review & editing and Funding acquisition. Filipe Martinho: Investigation, Methodology, Supervision, Writing – review & editing and Funding acquisition.

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.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2021.105362.

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