



# Temperature patterns along the migration routes of European eel larvae towards the south of the Iberian Peninsula

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## ABSTRACT

This study analysed the variations in sea surface temperature patterns along the two main migration routes of European eel larvae from their spawning grounds (Sargasso Sea) to the southern coasts of the Iberian Peninsula. For this purpose, monthly time series of sea surface temperature associated with theoretical locations along the migratory routes from January 1984 to December 2006 were analysed. The results indicate that regardless of the migration route followed, the temperature pattern was characterized by two periods of maximum temperatures. Likewise, in both routes, surface temperature anomalies indicated the presence of a regime change in the mid-1990s that significantly correlated with glass eel abundance anomalies in the south of the Iberian Peninsula. Along both routes, strong negative anomalies (mid-1980s, early-1990s and mid-1990s) were associated with positive anomalies of glass eel abundance. In contrast, from the mid-1990s, the negative anomalies of glass eel abundance were associated with a period in which the SST anomalies were clearly positive. These results support the hypothesis that SST is highly important for the recruitment of glass eels in the European coasts.

## 1. Introduction

The European eel (*Anguilla anguilla* Linnaeus, 1758) is a catadromous, semelparous and panmictic species with a complex life cycle whose continental distribution zone includes the estuaries and freshwaters of an extensive area from the Scandinavian Peninsula to Morocco and from the Iberian Peninsula to all countries bordering the Black Sea (Deelder, 1984). Despite this wide distribution and a great capacity to adapt to different aquatic ecosystems, scientific reports issued at the beginning of the 21st century indicated that its population had drastically diminished. This situation led the European Commission to organise two regional workshops in 2003 and 2004, to debate specific objectives to set and immediate actions to be taken seeking to recover its population (Commission of the European Communities, 2005). The main consequence of these workshops was the promulgation of Council Regulation 1100/2007 of September 18, 2007 establishing measures for the recovery of the stock of European eel. This regulation established that European Union Member States should develop Eel Management Plans (EMPs), designed to allow at least 40% of the silver eel biomass to escape to the sea.

In 2014, the European Commission published the first report on the implementation of the EMPs (Commission of the European Communities,

2014) in which it highlighted that the 81 Eel Management Units (EMUs) initially established in the EMPs had made significant progress but, in general, it remained difficult to assess the performance of EMPs in relation to the target established in Council Regulation 1100/2007. Nowadays, in spite of efforts by EU Member States, the annual recruitment of glass eel to European waters remains low at 0.6% of 1960–1979 geometric mean in the North of Europe and around 5.5% of that level in the rest of Europe, while the annual recruitment of young yellow eel to European waters is around 19% of the 1960–1979 geometric mean, this being indicative of the difficulty of implementing management plans to reduce the mortality of this species. Therefore, 20 years after the first workshop organised by the EC, the status of eel remains critical (ICES, 2022).

The EMPs established by each EU Member State propose actions to reduce eel mortality in relation to variables that have been reported to be the main factors responsible for the observed decline in European eel populations. Among these, we should highlight the effects of habitat loss and migration barriers, such as dams and hydroelectric plants (Feunteun, 2002; Winter et al., 2006; Acou et al., 2008; Kettle et al., 2011), water quality and pollutants (Belpaire and Goemans, 2007; Guimarães et al., 2009; Geeraerts and Belpaire, 2010; Quadroni et al., 2013; Amilhat et al., 2014; Privitera et al., 2014) and regulated and

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unregulated exploitation and trade of glass, yellow and silver eels (Amilhat et al., 2008; Arribas et al., 2012).

On the other hand, Council Regulation 1100/2007 also required each Member State to report the level of mortality factors unrelated to anthropogenic activities that, in some way, might help improve our understanding of the biology of this species and ultimately strengthen the implementation of management plans. In relation to this, several authors have identified diverse natural factors that may contribute to the observed increase in mortality. For example, some studies have focused on the increase in eel predators (Carpentier et al., 2009; Martino et al., 2011; Wahlberg et al., 2014), some on the energy available for migration (Böetius and Böetius, 1980; Svedäng and Wickström, 1997) and numerous others on the effect of various diseases and parasites (De Charleroy et al., 1990; Vettier et al., 2003; van Ginneken and van den Thillart, 2000; van Ginneken et al., 2004; Palstra et al., 2007; Haenen et al., 2010; Haenen et al., 2012; van Beurden et al., 2012; Amilhat et al., 2014; Armitage et al., 2014; Bandín et al., 2014).

Although all these factors have an impact on eel recruitment, none of them alone explains the strong decline in European eel populations. In fact, the weight and explanatory capacity of each one of these factors and their interactions and synergies are only partially known. Nonetheless, several authors have suggested that the common thread connecting all these factors is the global change in atmospheric and oceanic conditions. This plausible hypothesis is based on the synchronous decrease in all the main eel species (*A. anguilla*, *A. rostrata* and *A. japonica*) in the North hemisphere (Bonhommeau et al., 2008; Miller et al., 2009). Specifically, several authors have shown eel abundance or glass eel recruitment to be significantly correlated with various different atmospheric and oceanic parameters (Castonguay et al., 1994; Kettle and Haines, 2006; Bonhommeau et al., 2008; Miller et al., 2009, 2015; Durif et al., 2011; Arribas et al., 2012; Gutiérrez-Estrada and Pulido-Calvo, 2015).

All atmospheric/oceanic factors must be linked, one way or another, to one or several primary factors which serve as the driving force behind the changes at oceanic level. In the mid-1960s, Bjerknes (1964) analysed air-sea interactions in the North Atlantic and concluded that the warming trend during the first quarter of the last century was linked to a change in ocean conditions rather than air-sea energy exchange. Later, this hypothesis was supported by other authors (e.g., Rodwell et al., 1999) who suggested that sea surface temperature (SST) characteristics are transmitted to the atmosphere in various ways leading to changes in the modes of variability in the global atmosphere, such as, for example, the North Atlantic Oscillation (NAO).

Therefore, taking into account that the larval phase of the European eel is oceanic and that water temperature plays a key role in oceanic conditions, the objective of this study was to determine and analyse the SST and SST anomalies patterns along the migration routes of European eel larvae. In particular, we analyse the monthly temperature patterns

along the traditional migration route (along the Gulf Stream) and the proposed by McCleave (1993) and Desaunay and Guerault (1997) to the coasts of the south of the Iberian Peninsula in the period between 1984 and 2006. For that, we consider the location of the spawning area determined by Tesch (1982) and Tesch and Wegner (1990), the spawning season (Schmidt, 1922; Miller et al., 2015; Pacariz et al., 2014) and the time elapsed between the larvae hatching in the Sargasso Sea and their arrival to European coasts (Lecomte-Finiger, 1994; Arai et al., 2000; Wang and Tzeng, 2000; Kettle and Haines, 2006; Bonhommeau et al., 2009; Arribas et al., 2012; Pacariz et al., 2014).

## 2. Material and methods

### 2.1. Study area

The study area is a section of the Atlantic Ocean extending from 45°N-75°W, close to Baccaro Point (Canada) and Cape Cob Bay (USA), to 23°N-6°W, close to the Gulf of Cintra in Western Sahara (Fig. 1). This section includes the European eel spawning area proposed by McCleave and Kleckner (1987) and McCleave et al. (1987) and the possible migration routes of European eel larvae from this spawning area to the Guadalquivir Estuary in the south of the Iberian Peninsula (from 36° 47'N-06° 22'W to 37° 04'N-06° 05'W).

### 2.2. Sea surface temperature data sets

The SST data for the Atlantic Ocean section analysed in this work were downloaded using griddap on the website of the Environmental Research Division's Data Access Program (ERDDAP), a research division of the National Oceanic and Atmospheric Administration (NOAA) (<http://coastwatch.pfeg.noaa.gov/erddap/index.html>). Specifically, the data used are included in the Pathfinder Version 5.0 Sea Surface Temperature dataset which is a reprocessing of global SST data from NOAA's Advanced Very High Resolution Radiometer aboard NOAA's Polar Operational Environmental Satellites.

Pathfinder processing uses a modified version of the non-linear SST algorithm (Walton et al., 1998). Kilpatrick et al. (2001) introduced changes in the algorithm including: an improved atmospheric correction, better cloud masking, and monthly recalculation of algorithm coefficients based on a match-up database of *in situ* SST measurements (moored and drifting buoys). The data are mapped to an equal-angle grid (0.05° latitude by 0.05° longitude) using a simple arithmetic mean to produce individual and composite images of various durations. Composite images are generated using only the pixels of the highest quality and are available at 4-km resolution (with an accuracy of 0.3 °C) in a monthly composite from September 1981 to December 2009.

Additionally, the time series of water temperature in the spawning area were obtained from the Simple Ocean Data Assimilation v 3.3.1

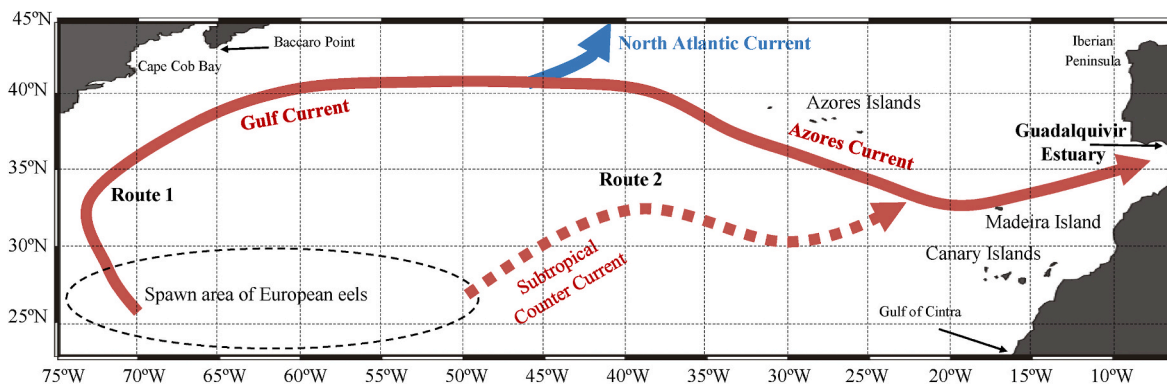


Fig. 1. Study area that includes the spawn area of the European eels (McCleave and Kleckner, 1987; McCleave et al., 1987) as well as two approaches to possible migration routes of the leptocephalus larvae to the south of the Iberian Peninsula.

reanalysis data set (<https://www.atmos.umd.edu/~ocean/index.htm>). This data set contains monthly ocean data remapped in 3D to a horizontal 1/2° x 1/2° Mercator coordinate grid with 50 vertical levels (Carton et al., 2018).

### 2.3. Characterisation of SST in the study area

To characterise the variability the SST in the study area, SST mean for each month and pixel ( $\overline{SST}$ ), SST anomalies (SSTa) around the  $\overline{SST}$  and SST anomaly rate were calculated. To estimate the SST mean, a SST base period of 27.8 years was used (from September 1981 to December 2009). The SST anomaly was calculated as:

$$SSTa_{x,y,t} = SST_{x,y,t} - \overline{SST}_{x,y,T} \tag{1}$$

where  $x$  is the latitude,  $y$  is the longitude,  $t$  is the month ( $1 \leq t \leq 12$ ) and  $T$  is the set of  $t$  months corresponding to the base period. Additionally, to determine the spatial structure of the dominant mode of variability in SST an empirical orthogonal function (EOF) analysis was carried out (Preisendorfer, 1988).

### 2.4. SST and SSTa time series along the migration routes

SST time series were constructed considering migration periods of 24 and 18 months along each route (Route #1: 24 months; Route #2: 18 months). In the case of the longest route (Route #1), the approximate position of a larva in month  $t$  was approached from the results of the model proposed by Kettle and Haines (2006) (KH model). The KH model estimates that eel larvae that reach the southwest of the Iberian Peninsula are born in the western part of the spawning area in the Sargasso Sea (around 73°W-27°N). From there, the larvae enter the Gulf Stream and are transported northeast taking approximately 6 months to reach 60-50°W 39-42°N. Six months later, the larvae that reach 40-33°W 35-39°N are transported by the Azores Current to south of the Iberian Peninsula where the larvae reach the Guadalquivir Estuary (36°47'N-6°22'W) 12 months later (Table 1). On the other hand, for Route #2, the approximate positions of larvae were estimated from the results of the model proposed by Pacariz et al. (2014) which considers a

**Table 1**  
Theoretical monthly locations of leptocephalus larvae along the two routes considered. Route #1 corresponds to the classic migration route that takes advantage of the displacement of the Gulf current. Route #2 is suggested by McCleave (1993) and Desaunay and Guerault (1997) (See Figs. 1 and 2).

Reference points (months)	Route #1 (Latitude-Longitude)	Route #2 (Latitude-Longitude)
1	26° 00'N-70° 00'W	26° 30'N-52° 30'W
2	29° 30'N-70° 30'W	27° 00'N-50° 00'W
3	33° 00'N-71° 00'W	28° 00'N-47° 40'W
4	35° 40'N-71° 00'W	30° 00'N-45° 00'W
5	38° 20'N-67° 20'W	32° 00'N-42° 00'W
6	41° 00'N-63° 40'W	32° 00'N-38° 00'W
7	41° 00'N-52° 40'W	31° 40'N-35° 00'W
8	41° 00'N-45° 20'W	31° 20'N-33° 40'W
9	41° 00'N-38° 00'W	30° 00'N-31° 00'W
10	40° 00'N-36° 20'W	30° 20'N-28° 00'W
11	39° 00'N-34° 40'W	31° 20'N-25° 40'W
12	38° 00'N-33° 00'W	32°30'N-23° 30'W
13	37° 20'N-31° 00'W	34° 00'N-22° 20'W
14	36° 40'N-29° 00'W	33° 30'N-21° 10'W
15	36° 00'N-27° 00'W	33° 00'N-20° 00'W
16	35° 30'N-25° 50'W	34° 00'N-15° 40'W
17	35° 00'N-24° 40'W	35° 00'N-11° 20'W
18	34° 30'N-23° 30'W	36° 00'N-7° 00'W
19	34° 00'N-22° 20'W	
20	33° 30'N-21° 10'W	
21	33° 00'N-20° 00'W	
22	34° 00'N-15° 40'W	
23	35° 00'N-11° 20'W	
24	36° 00'N-7° 00'W	

maximum drift time of 18 months.

For each reference point (Table 1), the mean and standard deviation of SST and SSTa were estimated from 200 pixels randomly selected around each reference point (Fig. 2). For each reference point beyond 20°W, all pixels selected were included in a circular area with a radius of 360 km. This distance was selected because around each reference point a large proportion of possible larvae trajectories were contained in a circle delimited by this radius (see Fig. 2 in Kettle and Haines, 2006 and Fig. 5 in Pacariz et al., 2014). Likewise, the diameter of this circle (720 km) has a similar scale to the baroclinic eddies (with approximately wavelengths of 800 km) confined in the Subtropical Convergence Zone (Halliwell et al., 1991). Below 20°W, the radius around the reference point was reduced to 300 km because from this longitude the variation range of the possible trajectories is narrower. For the last position located near the mouth of the Guadalquivir river, a radius of 100 km was considered.

Particular attention was paid to the analysis of reference points where the SSTa was more than twice the standard deviation above or below ( $\pm 2\sigma$ ) the mean SST (Hansen et al., 2012). From this analysis it is possible to obtain the temporal distribution of the times at which the temperature is abnormally above or below the mean SST (TGSD), which allows the comparison with the anomaly of glass eel density in the Guadalquivir River (Gutiérrez-Estrada and Pulido-Calvo, 2015). This way, it is possible to obtain common behaviour patterns of both series.

Once the mean SST values for each reference point were calculated, the time series of SST for each cohort was constructed (March, April, May, June, and July cohorts). The time series of SST associated to each cohort was averaged to obtain a single pattern of temperature variation along each migration route. On the other hand, time series of SSTa mean were also constructed for each reference point in order to identify areas and periods with an atypical behaviour. To facilitate the identification of the most important periods in SSTa time series, a high-frequency noise removal procedure consisting of a centred quasi-annual moving average was applied:

$$SSTa_{smooth,t} = \frac{\sum_{j=t-5}^{t-1} SSTa_j + SSTa_t + \sum_{j=t+1}^{t+5} SSTa_j}{J} \tag{2}$$

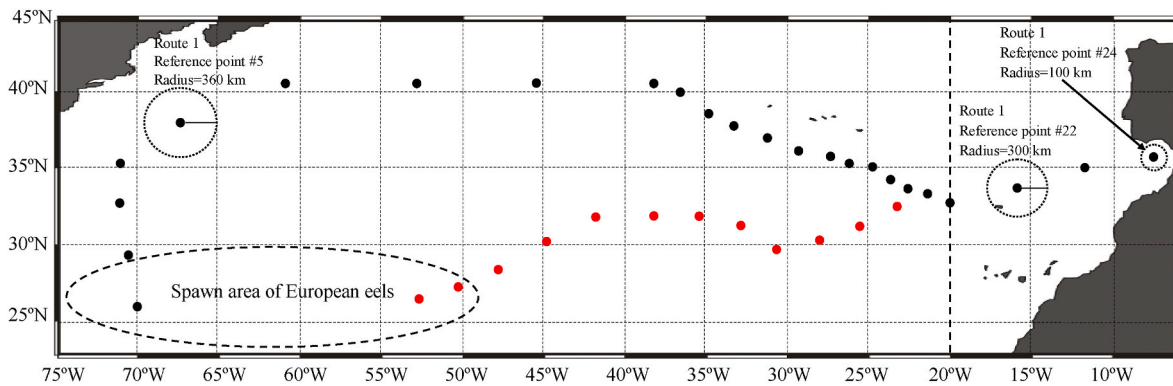
where  $t$  is the month and  $J$  is the number of months to be averaged. In our case  $J = 11$ . Fig. 3 shows an example of how the mean SST time series associated to the first migration year of the cohort born in May 1985 and SSTa time series associated to the reference point #8 can be constructed.

## 3. Results

### 3.1. SST in the study area

Fig. 4a shows the time series of the mean SST in the study area for the period January 1984 to December 2006. The linear tendency of this series indicates that the averaged SST increased 0.9 °C over this period. On the other hand, Fig. 4b clearly shows that there was an interdecadal change in the study area SSTa in the mid-1990s. In this Atlantic area, SSTa changed from negative during the period 1984–95 to positive during the period 1996–2006. Further, this abrupt change is detected in the anomaly ratio time series (Fig. 4c).

The two first EOFs explained almost 37% of the total variance (Fig. 5a). The principal component associated with the first EOF was characterised by two clear maxima in 1988 and 1994, with a third maximum being detected in 2006. The first component explained 21.5% of the total variance and the spatial pattern associated with this mode (Fig. 5b) was characterised by the presence of a dipole structure with strong intensities close to the bifurcation of the Gulf Stream in the North Atlantic and the Azores Current (45-60°W 40-45°N). On the other hand, the principal component associated with the second mode of variability showed a maximum in mid-1994 and explained a total of 15.3% of the



**Fig. 2.** Theoretical monthly positions of the leptocephalus larvae along the two suggested routes. The black dots correspond to Route #1 and their positions are associated to an approximation obtained from the results of Kettle and Haines (2006). The red dots correspond to Route #2 which was approximated from the model proposed by Pacariz et al. (2014). The dotted circles correspond to areas containing different trajectories around the reference point. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

variance. The spatial mode of this second principal component (Fig. 5c) was also characterised by a dipole pattern in which the high intensities were shifted westward (50–70°W) and southward (close the eel breeding area), and with strong intensities along the second migration route (from the breeding area to the Iberian Peninsula and Africa coasts).

The time series of water temperature in the spawning area is shown in Fig. 6. Significant positive correlations were detected for all depth gradients between 98.6 and 287.6 m (Table 2). In the period between 1984 and 1993, the water temperature increased slightly in the depth range considered. In 1993, a strong decrease in temperature was clearly observed between 98.6 and 201.3 m, and also at 287.6 m, where the temperature decreased from  $18.8 \pm 0.38$  °C to  $18.2 \pm 0.26$  °C ( $t = 6.66$ ,  $p < 0.001$ ). From that year, the water temperature increased until 1997; subsequently, the temperature showed a tendency to decline until 2001; and then again, after a clear ascent, the temperature tended to decrease at all depths.

### 3.2. Route #1. Migration period of 24 months

Along Route #1 and considering a migration period of 24 months, the average SST patterns for the March, April and May cohorts show a similar double bell profile (Fig. 7a). The three profiles have two maxima, each of which shows a time lag of approximately 1 month with respect to the others. The absolute maxima means were found between 35° 40'N–71° 20'W and 38° 20'N–67° 40'W (reference points 4 and 5, respectively). From here, the mean temperature tends to progressively diminish to reference points 10 to 13 (around to 37° 20'N–31° 00'W) subsequently to increase again until locations south of the Azores Islands (reference points 16 to 18). Finally, from this area, the mean temperature drops until the vicinity of the Guadalquivir river mouth.

The periods in which the SSTa were higher or lower than  $\pm 2\sigma$  from the mean value are shown in Fig. 7b. Along this route, the positive and negative anomalies were grouped into two different phases. All negative anomalies (except one in October 1997) were detected between 1984 and 1994 while all the positive anomalies were observed from 1995 onwards. In the negative phase, particularly at the end of 1985 and 1994, the anomalies were significantly low and persistent in time. For example, in October 1985, the larvae born in March found temperatures 2.4 °C below the mean SST in the area around reference point 8 (41° 00'N–45° 20'W), which implies a SST 3.3 times the standard deviation (TGSD) below the mean SST in the area. This cohort found similar environmental conditions in November and December 1985 (reference points 9 and 10; 41° 00'N–38° 00'W and 40° 00'N–36° 20'W, respectively). Specifically, in November (Fig. 7c), the SST was 2.3 times the standard deviation below the mean SST and in December this cohort found a mean SSTa 2 °C below the mean SST (2.9 times the standard

deviation below the mean SST in the area around reference point 10).

These environmental conditions contrast with those detected some years later. In November 2000 (Fig. 7d), the cohort of larvae born in April found a mean SST 1.7 °C above the mean SST at reference point 8 (41° 00'N–45° 20'W), which implies a SST +2.0 times the standard deviation above the mean SST in the area. The complete set of figures showing reference points with SSTa higher or lower than twice the standard deviation are shown in Supplementary Fig. S1.

The time series of mean SSTa for each reference point (Supplementary Figs. S2a and S2b) show an alternation between negative and positive anomalies with a clear tendency to positive anomalies from the mid-1990s. This tendency starts to be significant from reference points 7 and 8 and very evident when the Azores Current runs near the Azores Islands (reference points 12 and 13) (Fig. 8).

### 3.3. Route #2. Migration period of 18 months

Like in Route #1, in Route #2 a double bell SST pattern for each cohort (May, June and July) was observed. Further, the three profiles have two maxima: the first between reference points 2 and 4 (27° 00'N–50° 00'W and 30° 00'N–45° 00'W); and the second between reference points 14 and 16 (33° 30'N–21° 10'W and 34° 00'N–15° 40'W) (Fig. 9a). Compared to the SST profiles observed along Route #1, the SST profiles of Route #2 are smoother, that is, along Route #2 the mean SST oscillated between 27.6 °C and 17.8 °C (a range of 9.8 °C), a narrower range than along Route #1 (a range of 11.2 °C).

Fig. 9b shows the periods in which the SSTa were more than  $\pm 2\sigma$  from the mean value along Route #2. Like in Route #1, the positive and negative anomalies were grouped into two different phases. All negative anomalies were observed between 1984 and mid-1997 while the most marked positive anomalies were detected from mid-1995. Further, between 1985 and mid-1995 three periods with positive anomalies appeared among the negative anomalies: June 1985 (larvae born in May, SSTa = +1.0 °C, 2.2  $\sigma$  above the mean); September 1987 (larvae born in July, SSTa = +1.1 °C, 2.5  $\sigma$  above the mean); and September 1991 (larvae born in May of the previous year, SSTa = +1.2 °C, 2.2  $\sigma$  above the mean). The negative anomalies were particularly significant in 1985, 1990 and 1993. For example, in April 1990, the larvae born between May and July found temperatures 2.2–2.6  $\sigma$  below the mean SST (Fig. 9c). By contrast, significant positive anomalies were detected in May 1995 (Fig. 9d). In this case, the larvae of the May, June and July cohorts of the previous year found temperatures 3.1–3.5  $\sigma$  above the mean SST, this corresponding to mean SST anomalies higher than +2.2 °C.

In addition, this alternation between negative and positive anomalies is detected in the smoothed SSTa time series for each reference point

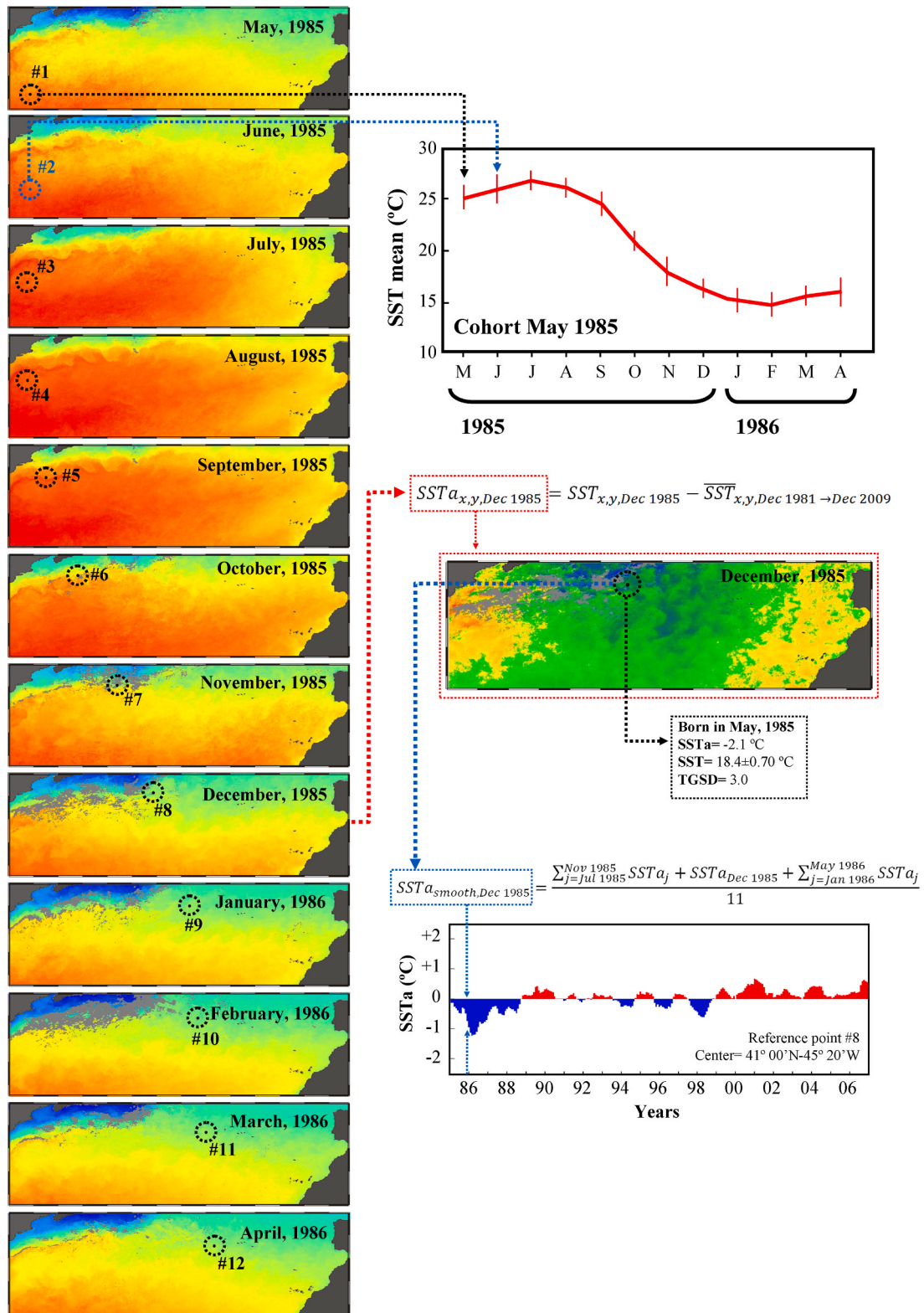
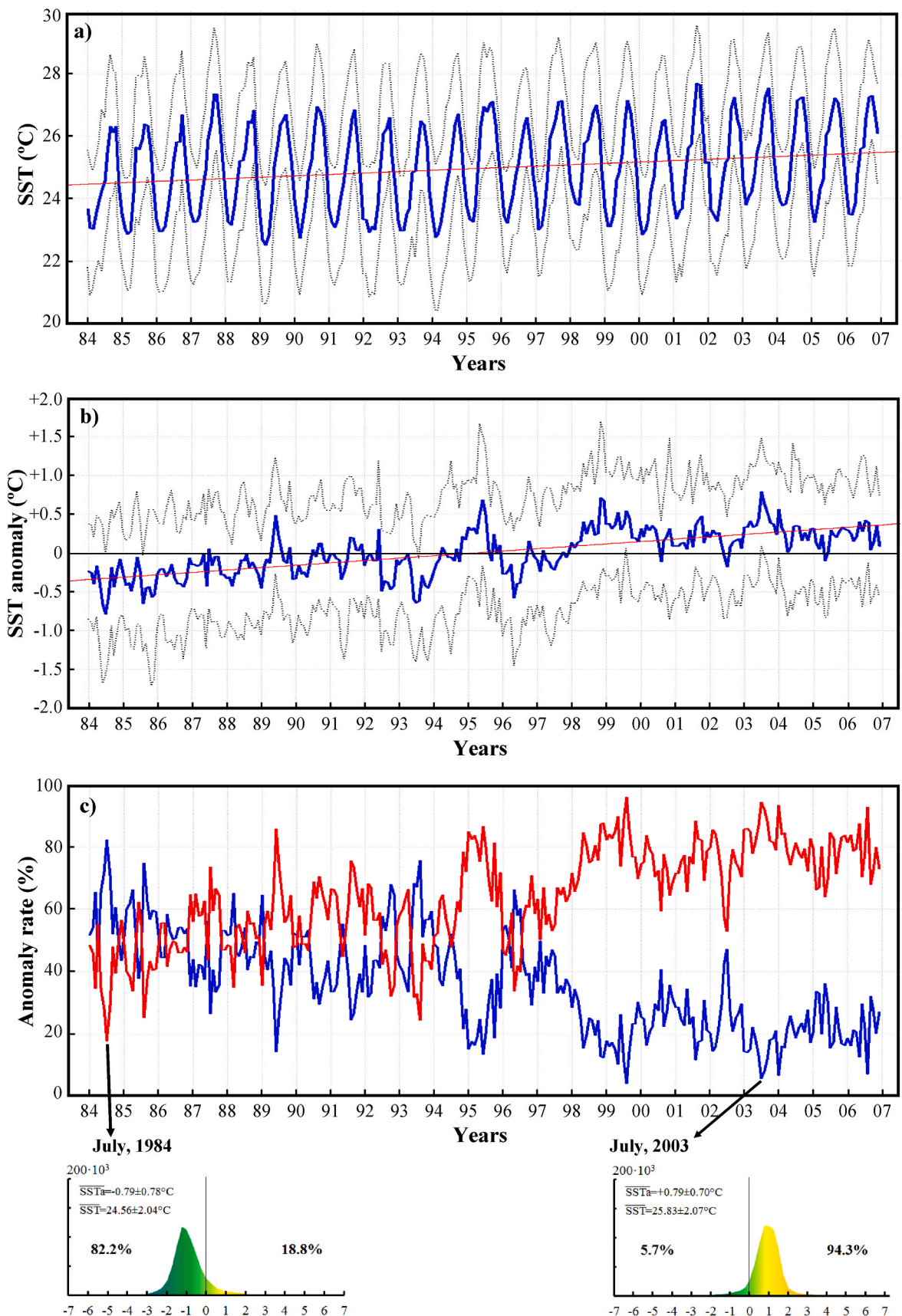


Fig. 3. Time series of SST associated with the first migration year for the cohort born in May 1985 along the Route #1. On the left, each figure shows the reference point and the circular area in which 200 pixels were randomly selected to estimate the mean SST. For December 1985 the SSta is showed. Also the smooth time series of mean SSta corresponding to the reference point #8 is showed.

(Supplementary Figs. S3a and S3b). A clear tendency to positive anomalies is observed from the mid-1990s, this being particularly evident from the reference points located east of the reference point number 4 (Fig. 10).

### 3.4. SST patterns and eel recruitment in the south of the Iberian Peninsula (Guadalquivir River)

The correlation between the time series of annual moving average of TGSD and the annual moving average of abundance anomalies time



**Fig. 4.** a) Monthly mean SST ± standard deviation in the area of study. The red line indicates the linear trend; b) Monthly SSTa ± standard deviation. The red line indicates the linear trend; c) Time series of the percentage of number of pixels with temperatures below (blue line) and above (red line) the mean for each month. For July 1984 and July 2003 the mean SST and mean SSTa are indicated. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

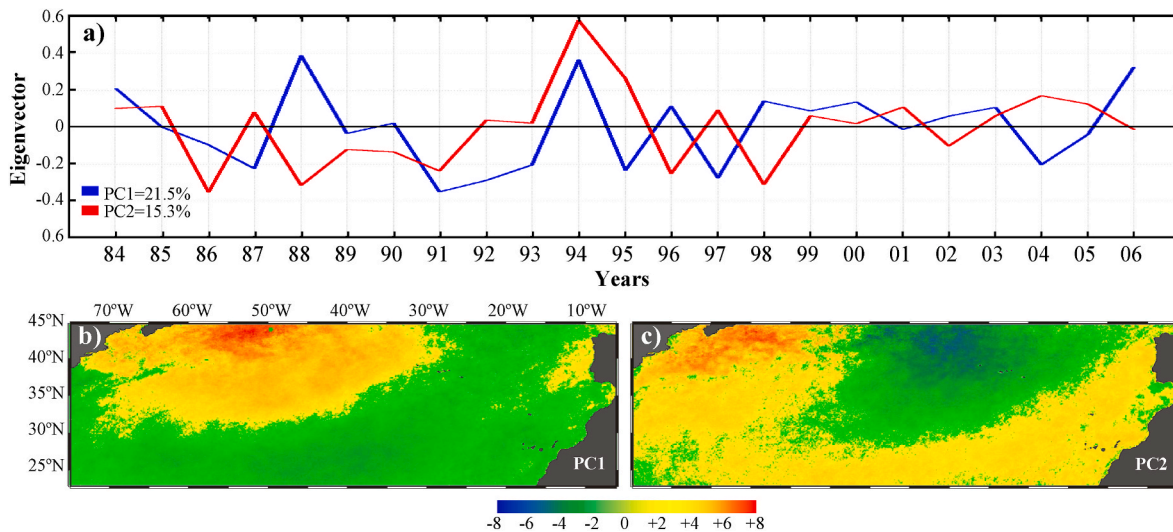


Fig. 5. a) Principal component 1 (PC1) and principal component 2 (PC2) of Empirical Orthogonal Function (EOF) of SSTa annually averaged; b) spatial representation of PC1; c) spatial representation of PC2.

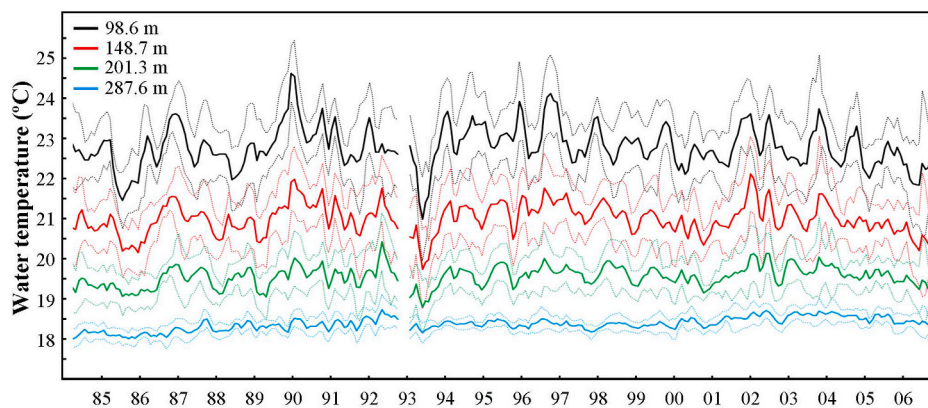


Fig. 6. Time series of mean water temperature ± standard deviation in the spawning area for four different depths.

Table 2

Correlation matrix between time series of water temperature at different depths in the European eel spawn area. In all cases  $p < 0.001$ .

Depth	98.6 m	148.7 m	201.3 m
148.7 m	0.73		
201.3 m	0.48	0.85	
287.6 m	0.21	0.40	0.67

series of glass eel recruitment in the Guadalquivir River (south of the Iberian Peninsula) was significantly negative (Route #1:  $R = -0.57, p < 0.01$ ; Route #2:  $R = -0.62, p < 0.01$ ) (Fig. 11). Along both routes, strong negative anomalies (mid-1980s, early-1990s and mid-1990s) were associated with positive anomalies of glass eel abundance in the Guadalquivir River. In contrast, from the mid-1990s, the negative anomalies of glass eel abundance were associated with a period in which the SST anomalies were clearly positive.

#### 4. Discussion

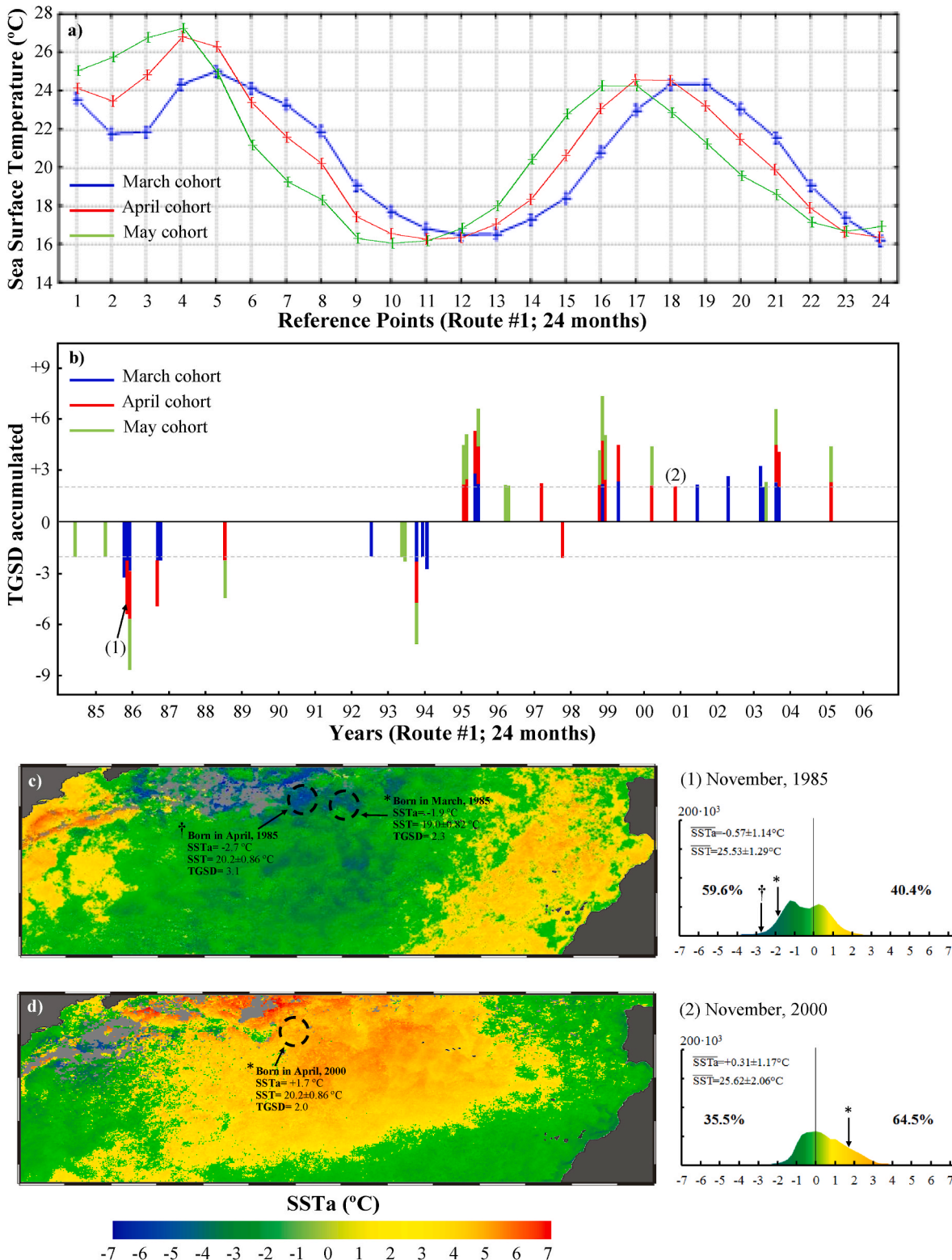
European eel populations have drastically decreased in recent years, and there is increasing interest among the scientific community and European institutions in the analysis of the causes underlying this trend as well as strategies to follow to implement effective recovery plans. There is an absence of fundamental information on basic life-history

patterns, ecological characteristics, behavioural factors, functional relationships with environmental parameters, and long-term data on eel stocks as well as, notably, the scarce data on the oceanic conditions in which the eel larvae migrate from the spawning areas to the European coast. This lack of data strongly hinders an accurate assessment of the causes of variability in glass eel recruitment and, therefore, the capacity to establish management actions is significantly reduced.

##### 4.1. Sea surface temperature (SST) in the study area

In the study area, the SST experienced an abrupt change around 1994/96. In this period, the temperature anomalies had a clear positive tendency which was reflected in an increase in the temperature anomaly rate with occasional inversions. This change is consistent with the results previously reported by other authors for the North Atlantic as well as other locations. For example, Flatau et al. (2003) reported this change in the winter of 1994/95 in the Nordic Seas and Gang et al. (2014) detected a similar pattern of SST anomaly variation in the South Pacific. Trenberth and Dai (2007) and Balmaseda et al. (2013) associated the oscillations with natural phenomena such as the eruption of Mount Pinatubo in 1991 and the El Niño events in 1991/92, 1997/98 and 2002/2003. These events decrease the radioactive imbalance at the top of the atmosphere which leads to a temporary cooling of the sea surface.

These phenomena are also reflected in the eigenvector time series of the EOF of the global SST anomalies analysed in this study. This series



**Fig. 7.** a) SST patterns for the March, April and May cohorts along the Route #1; b) Periods in which standard deviation is higher or lower to twice de mean SST (TGSD), (1) correspond with November 1985 and (2) November 2000; c) SSTa in November 1985; d) SSTa in November 2000.

provides an SST anomaly pattern characterised by pronounced positive anomalies confined around 40-45°N-50-55°W and, to a lesser extent, negative anomalies around 40°N-35°W (close to the Azores Islands), which delimits a band of positive anomalies that extends along Route #2. This pattern corresponds approximately to that described by other authors despite the area considered in this work being constrained to the

migration routes from the spawning area to Guadalquivir Estuary. Czaja and Frankignoul (2002) indicated that the forcing SST pattern for a positive NAO phase has a positive SST anomaly southeast of Newfoundland along 40°N and a negative SST anomaly to the northeast and southeast, which corresponds to our PC1 mode. This SST configuration precedes a positive NAO phase for several months, while to a



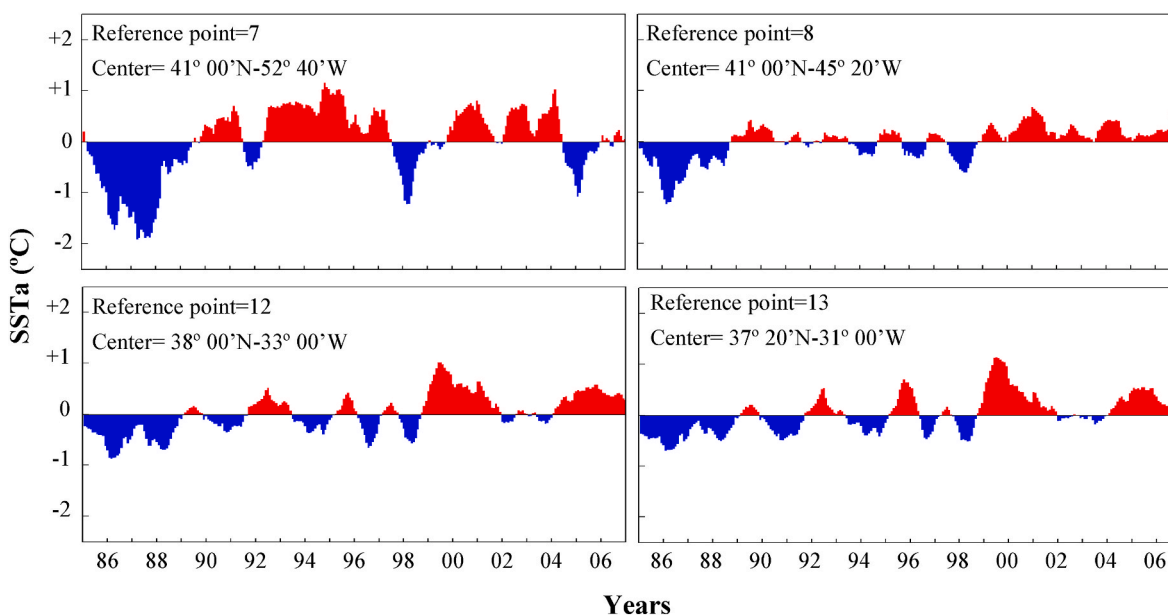


Fig. 8. Time series of mean SSTa for the reference points number 7, 8, 12 and 13 in the Route #1.

lesser extent, negative NAO phases are associated with positive SST anomalies centred around 10°N-20°W (outside our area of analysis) and negative SST anomalies around 40°N-35°W, which approximately correspond to our PC2 mode.

Likewise, the changes detected at the surface are reflected at deeper layers in the spawning area. This is a consequence of the temperature variation in the top 700 m depending on heat content in this depth range (Levitus et al., 2012). Lyman et al. (2010) and Balmaseda et al. (2013) indicated that the evolution of the oceanic heat content is dominated by a clear warming trend from 1975 with different cooling episodes in the mid-1980s and mid-1990s, which also is consistent with our results.

#### 4.2. Direct effects of water temperature on recruitment of glass eel

The SST is an essential parameter for the study of marine ecosystems (Emery, 2015). This is because the vast majority of aquatic organisms are ectotherms, whose abundance, development stage and biological activity depend on water temperature (Blaxter, 1992; Thomas et al., 2004). Some studies have concluded that the variations in water temperature are especially important for the early life stages, such as eggs and larvae (Pörtner and Farrell, 2008). In general, this is due, on the one hand, to these stages having a small biomass, which in the case of larvae hinders selection of a migration route towards an adequate habitat, and on the other, to them having high standard metabolic rates and lower energy reserves. Therefore, the early life stages are more vulnerable to mortality during periods of adverse environmental conditions, like periods with markedly high or low water temperature.

Recently, there have been important advances in knowledge on the effects of temperature on gene expression and morphological development of European eel larvae (Politis et al., 2017). Specifically, it was found that temperature influenced the incidence of larval deformities at hatching (around 7 mm length), where larvae reared at 18 °C showed significantly fewer deformities than those reared at 16 °C, 20 °C or 22 °C. Likewise, larvae reared at 22 °C were significantly smaller, showed less efficient yolk utilization and had a reduced growth compared to those in all the other temperature conditions. Therefore, 18 °C seems to be the optimal temperature for the early development of European eel larvae.

Overall, this temperature (18 °C) matches the average water temperature found at 287.6 m depth in the spawning area. Worthington (1953) identified this characteristic of water in the Sargasso Sea at 300

m and called it '18° water'. In higher layers (between 148.7 and 201.3 m) the mean water temperature oscillated between 23 and 18.1 °C from 1984 to 2006, following the frequency of variation in surface temperature. This temperature range is close to the lower and upper thermal tolerance limits of European eel larvae established by Politis et al. (2017) (between 16 and 22 °C). These limits imply a narrow temperature range of only 3.9 °C at these depths.

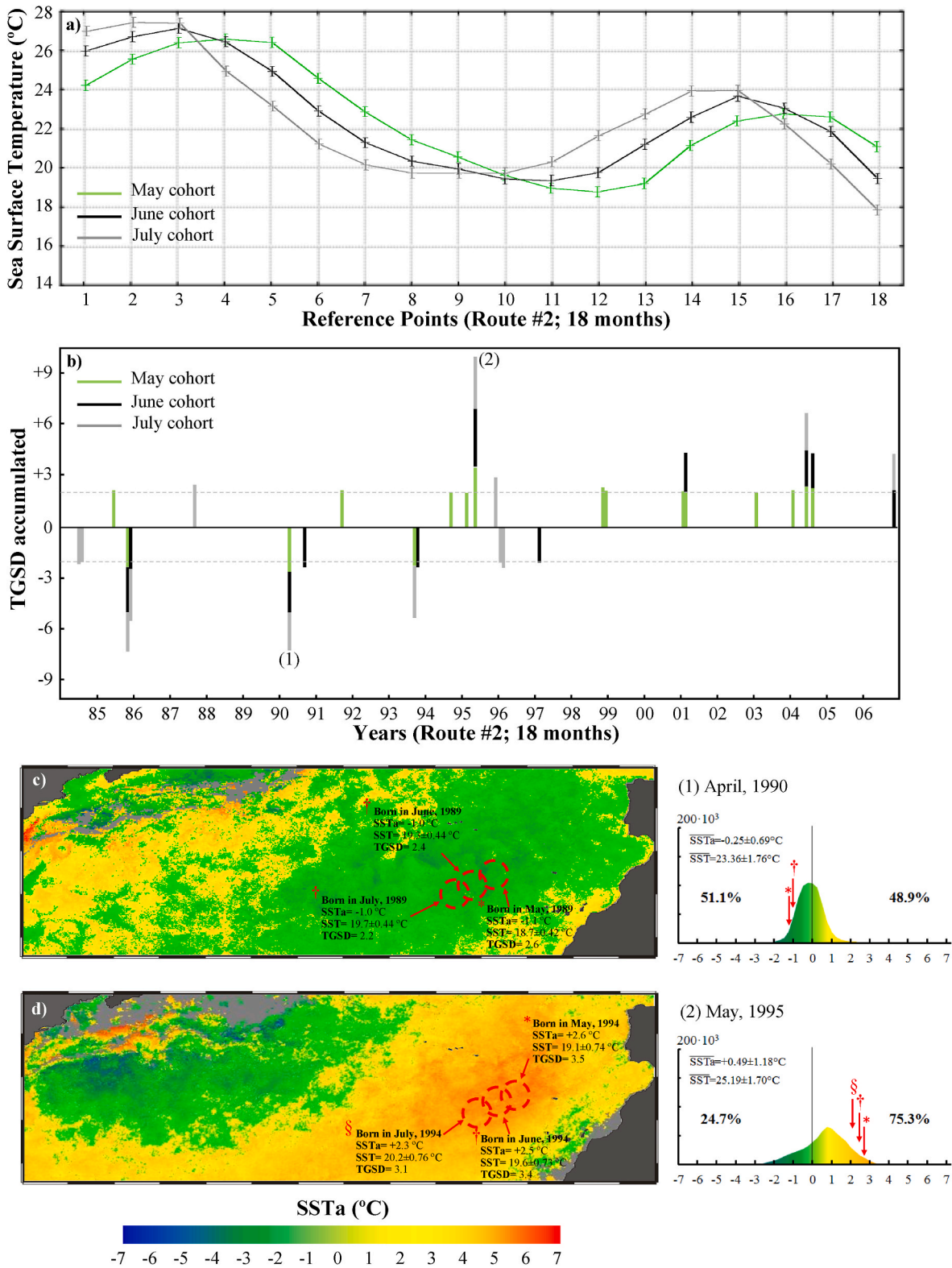
On the other hand, Castonguay and McCleave (1987) reported that the European eel larvae fraction most sensitive to thermal stress (those less than 5 mm) was mainly caught at a depth of between 150 and 200 m. Therefore, the coupling between the surface temperature and water temperature in deeper layers suggests that an increase in SST could further narrow the range at which the larvae do not suffer thermal stress, which could, in turn, increase the mortality rate at this stage and consequently decrease the recruitment of glass eels on European coasts.

Along both migratory routes, a similar double bell shape temperature pattern has been obtained. This, independently of the metamorphosis to glass eel being seasonal and synchronized from year to year, could imply that the intraspecific variability may be modulated by environmental factors, such as temperature. Such a relationship has been observed in the metamorphosis of other fish species. For example, the transformation of some anadromous species as *Lampræta planeri* and *Mordacia mordax* starts in rivers with lower temperature regimes (Potter, 1968; Bird and Potter, 1979) but the first changes occur in larvae exposed to higher temperature regimes (Potter, 1970), which could suggest that the onset of metamorphosis would be more related to the temperature pattern change than to reaching a critical temperature (Potter, 1980).

#### 4.3. Indirect effects of water temperature on glass eel recruitment

Sea water temperature has a persistent influence on the air-sea heat fluxes which modulates the atmospheric variation phenomena such as the NAO and El Niño-Southern Oscillation (ENSO) (Flatau et al., 2003; Gang et al., 2014). These teleconnections, in turn, play a central role in the functioning of oceanic current systems (Frankignoul et al., 2001; Hu and Huang, 2006; Lugo-Fernández, 2007) and in the formation of mesoscale structures such as eddies (Stammer and Wunsch, 1999; Pen-duff et al., 2004; Kelly et al., 2010), which have a strong influence on leptocephalus transport, abundance, and food availability as well as the time of arrival and size of glass eels at the continental coasts.

The interactions of atmospheric/oceanic conditions with the



**Fig. 9.** a) SST patterns for the May, June and July cohorts along the Route #2; b) Periods in which the standard deviation (TGSD) is higher or lower to twice de mean SST, (1) correspond with April 1990 and (2) May 1995; c) SSTA in April 1990; d) SSTA in May 1995.

transport of eel larvae from the spawning grounds to the recruitment areas have been described for most eel species. For example, the Australian species are transported from the Coral Sea to the eastern coastline by the East Australian Current (Jellyman, 1987; Beumer and Sloane, 1990) and this current has a strong signal of decadal variability in temperature which is related to decadal ENSO variability (Hill et al.,

2008). *Anguilla japonica*, distributed from Taiwan to the Pacific coast of Hokkaido Island (Japan), spawns to the west of Mariana Island and the larvae are transport by the North Equatorial and Kuroshio currents to the continental shelves (Tsukamoto, 1992). The pathways of these geostrophic currents are strongly influenced by El Niño and La Niña events just as the East Australian Current is significantly related to the

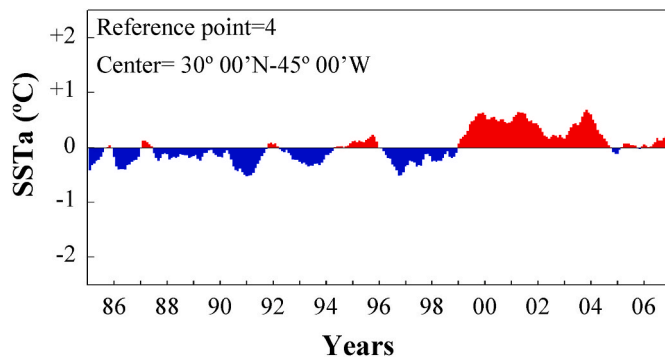


Fig. 10. Time series of mean SSTa for reference point number 4 in the Route #2.

variability of the Southern Oscillation and the Pacific Decadal Oscillation (Han and Huang, 2008; Andres et al., 2009).

Further, in the case of north Atlantic eel species (*Anguilla anguilla* and *Anguilla rostrata*), the interactions of atmospheric/oceanic conditions have been pointed as factors that favour variation in the recruitment of these species on European coasts and the western coast of North America. For example, Knights (2003) found significant negative correlations between the NAO and the Den Oever glass eel recruitment index for the period from 1938 to 1999. The results reported by Knights (2003) were later corroborated by Friedland et al. (2007) using a more extensive data set. Kettle et al. (2008) in a very detailed and robust statistical study concluded that the migration patterns of the European eel are closely associated with the NAO index. These authors obtained statistically significant results which allowed them to establish a plausible link between the NAO index, FAO eel landings, and glass eel catches. Further, Durif et al. (2011) concluded there is an inverse relationship between the decline in eel abundance in Norway and the variation of the NAO index, particularly when considering the NAO values of the 11 previous years. On the other hand, Arribas et al. (2012) analysing glass eel recruitment in the Guadalquivir Estuary (south of Spain) for the period from June 1997 to December 2006 found a highly positive significant correlation with the NAO index. Likewise, Bonhommeau et al. (2008) found clear indications of a coupling between ocean characteristics and European eel recruitment when analysing the correlation between SST in the northern Sargasso Sea and several ICES eel recruitment indices.

More recently, Gutiérrez-Estrada and Pulido-Calvo (2015) calibrated a neural network model which allowed them to explain almost 80% of glass eel recruitment variation in the Guadalquivir Estuary between 1984 and 2006. Perhaps the most interesting aspect of this model was that only SST anomalies in various oceanic clusters were used as explanatory variables. This could explain the significant correlations found in the present work between the time series of SST anomalies of more than

twice standard deviations from the mean and the annual moving average of abundance anomaly time series of glass eel recruitment in the Guadalquivir River and would support the idea that the SST along the migration routes of European eel is a very important factor conditioning recruitment on the southern coasts of the Iberian Peninsula.

Likewise, changes in the Gulf Stream and the formation of oceanic eddies have also been reported as factors that could have a significant impact on changes in European eel abundance (Castonguay et al., 1994; Gutiérrez-Estrada and Pulido-Calvo, 2015). Castonguay et al. (1994) hypothesised that a reduction in the speed of the Gulf Stream is linked to the decline of glass eel recruitment. On the other hand, Gutiérrez-Estrada and Pulido-Calvo (2015) found a highly significant correlation between the annual average SST anomaly in the spawning area and the number of cyclonic eddies which, in turn, is associated with the levels of nutrient production (Palter et al., 2005). Further, Desauany and Guerault (1997) concluded that these open ocean processes indirectly have a significant effect on the body condition of European eel larvae because the leptocephalus food supply is dependent on these processes.

## 5. Conclusions

The processing, interpretation and combination of environmental data with the goal of facilitating the implementation and development of European eel recovery plans is one of the major challenges faced by the managers responsible for the EMUs established in response to Council Regulation 1100/2007. What is the effect of climatic variations and oceanic conditions on eel recruitment on European coasts? What relative weight do these factors have in relation to anthropogenic activities that increase eel mortality? These kinds of questions must be answered if we have to optimize the available resources and develop effective recovery plans for the European eel.

This work provides preliminary results regarding the patterns of sea temperature variation along the spatio-temporal migration routes of European eel larvae from the spawning grounds to the southern coasts of the Iberian Peninsula and changes in glass eel recruitment. From the results of this study, we can conclude that sea temperature in the period and along the migration routes considered has increased significantly with a clear change in regime in the mid-1990s. The results also support the hypothesis, already put forward by Gutiérrez-Estrada and Pulido-Calvo (2015), that SST is highly important for the recruitment of glass eels in the Guadalquivir Estuary.

## CRedit authorship contribution statement

**Juan Carlos Gutiérrez-Estrada:** Writing – review & editing, Writing – original draft, Visualization, Formal analysis, Data curation, Conceptualization. **Inmaculada Pulido-Calvo:** Writing – review & editing, Writing – original draft, Visualization, Data curation, Methodology.

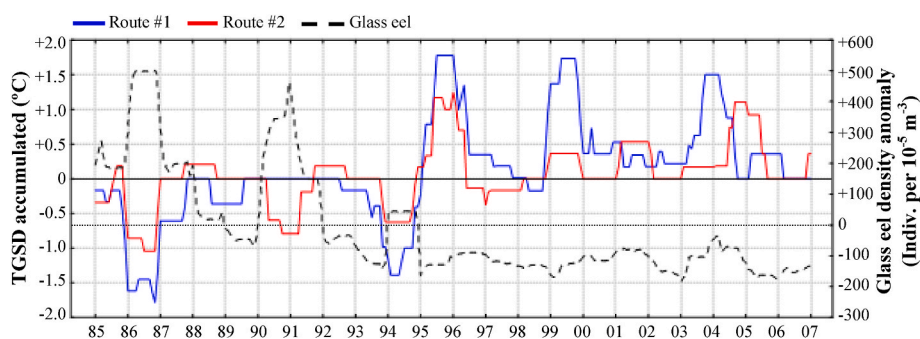


Fig. 11. Annual moving average of TGSD accumulated for Route #1 (blue), Route #2 (red) and glass eel density anomaly in the Guadalquivir River (south of the Iberian Peninsula). This last time serie has been obtained from Gutiérrez-Estrada and Pulido-Calvo (2015). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

## Declaration of competing interest

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

## Data availability

Data will be made available on request.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecss.2023.108297>.

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