Physical–biological interactions in the life history of small pelagic fish in the Western Iberia Upwelling Ecosystem

A. Miguel P. Santos [a,*], Alexandra Chícharo [b], Antonina Dos Santos [a], Teresa Moita [a], Paulo B. Oliveira [a], Álvaro Peliz [c], Pedro Ré [d]

[a] *INIAP-IPIMAR, Av. Brasília s/n, 1449-006 Lisboa, Portugal*
[b] *FCMA/CCMAR, Univ. Algarve, Campus de Gambelas, 8005-139 Faro, Portugal*
[c] *Dept. Física/CESAM, Univ. Aveiro, Campus de Santiago, 3810-193 Aveiro, Portugal*
[d] *FCUL, Laboratório Marítimo da Guia, Est. do Guincho, 2750-374 Cascais, Portugal*

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Abstract

This paper reviews relevant investigations conducted in the Western Iberia Upwelling Ecosystem (WIUE) on the dynamics of small pelagic fish (SPF), its relationship to climate changes and processes related to the 'ocean triad' (enrichment, concentration, transport/retention). In the last decades, a decline in the productivity of several SPF species (e.g., sardine and horse mackerel) was observed in the WIUE, which is partially explained by environmental variability (e.g., changes in coastal upwelling). The main mechanism proposed to explain this decline is the increased frequency and intensity of upwelling events during the spawning season (winter) of these species, which is typically a period when convergence conditions prevail. Thus, this 'anomalous' situation promotes egg and larval dispersal away from the favourable coastal habitat (the shelf) and consequently has a negative impact on their survival and recruitment. However, the variability of local features like the Western Iberia Buoyant Plume (WIBP) and the Iberian Poleward Current (IPC) introduce important fluctuations in the transport patterns of the region, and could modulate the impact of these winter upwelling events in the survival of larvae. The retention on the shelf of larval sardine along convergence zones formed by the interaction of these two features plays an important role in their survival. Furthermore, the WIBP is a suitable environment for the growth of phytoplankton and for larval fish survival. From these findings it is clear that simplified Ekman transport models could not explain larval fish transport/retention patterns in this region and more realistic biophysical models should be used to simulate the local oceanographic conditions to understand larval dynamics and the success of recruitment of SPF in the Western Iberia.
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[*] Corresponding author. Tel.: +351 213 027 193; fax: +351 213 015 948.
E-mail addresses: amsantos@ipimar.pt (A. Miguel P. Santos), mchichar@ualg.pt (A. Chícharo), antonina@ipimar.pt (A. Dos Santos), tmoita@ipimar.pt (T. Moita), pbo@ipimar.pt (P.B. Oliveira), apeliz@fis.ua.pt (Á. Peliz), pedro.re@mail.telepac.pt (P. Ré).

1. Introduction

The Western Iberia Upwelling Ecosystem (WIUE) comprises the northern limit of the Canary Current Upwelling System (Fig. 1), one of the world's four major Eastern Boundary Currents. This ecosystem is dominated by the European sardine *Sardina pilchardus* (Fig. 2) and is subject to the influence and perturbation of the North Atlantic Oscillation – NAO (Borges et al., 2003; Santos et al., 2005). The NAO is the principal climate influence at middle and high latitudes of the North Atlantic Ocean (Hurrell et al., 2003) and induces changes in sea surface temperature – SST (Ottersen et al., 2003; Visbeck et al., 2003), variations in upwelling patterns (Borges et al., 2003; Santos et al., 2005), and changes in various marine trophic levels (Drinkwater et al., 2003) of the Eastern North Atlantic.

Populations of small pelagic fishes (SPF), such as sardine and anchovy, show evidence of important long-term natural fluctuations in their abundance (Lluch-Belda et al., 1989), which have implications for medium and long-term forecasting of catches. These fluctuations seem to be related, among other factors, to large-scale climate variability (Beamish, 1995; Bakun, 1996; Alheit and Hagen, 1997), raising important scientific and eco-
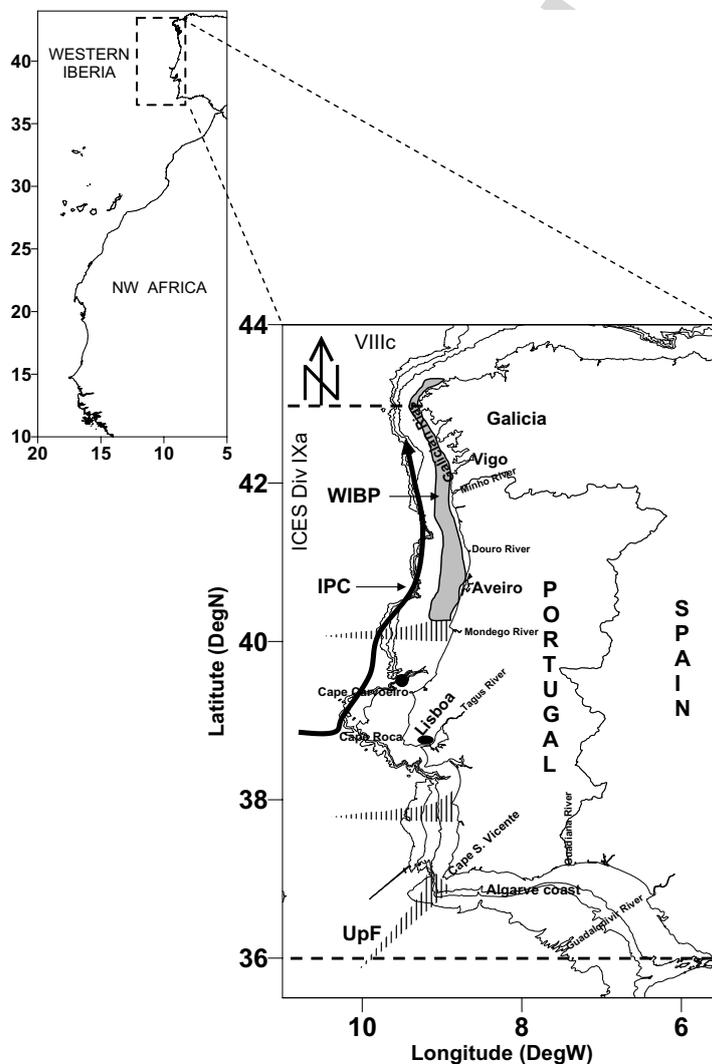

Fig. 1. The Western Iberia Upwelling Ecosystem (WIUE). The small map represents the whole Canary Current Upwelling System, in which the location of the WIUE is represented by the dashed rectangle. The main oceanographic features referred in the text are represented, namely the Western Iberia Buoyant Plume (WIBP), the Iberian Poleward Current (IPC) and upwelling filaments (UpF). The isobaths of the 200, 500 and 1000 m are also presented to locate the shelf break. The black dot near Cape Carvoeiro show SST data location presented in Fig. 6. ICES Divisions are also presented and their limits are represented by the dash straight lines.
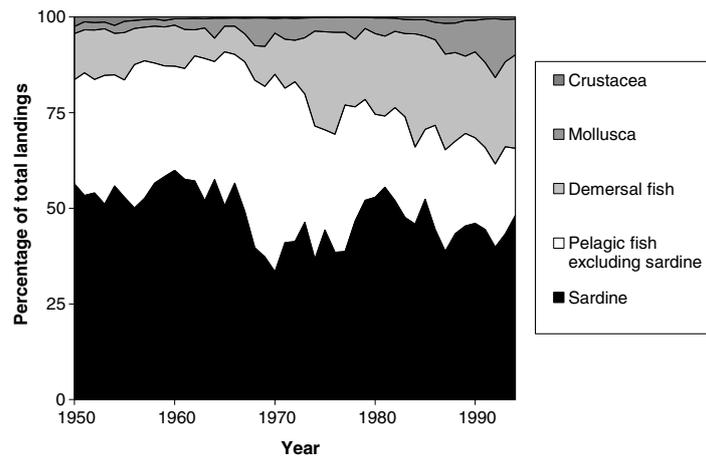
Fig. 2. Relative percentage of sardine and other marine species catches in Western Iberia (Source data: FAO).

nomic concerns. Evidence that these fluctuations are related to environmental variability will be presented for sardine in the WIUE (Section 2).

Understanding the processes affecting recruitment is a fundamental objective of fisheries biology. It is commonly assumed that recruitment variability is largely determined by survival during the larval and juvenile stages. Several hypotheses were postulated to link larval fish survival (and thus future recruitment) with physical and biological conditions during the larval stage. These include Hjort's (1914) "critical period", Cushing's (1975, 1990) "match-mismatch", Lasker's (1975) "stable ocean", Sinclair's (1988) "member-vagrant" and Bakun's (1996) "ocean triad" hypotheses. Thus, to understand recruitment variability of SPF it is necessary to study the underlying physical processes (e.g., related to larval transport/retention), as well as the complex food web processes that sustain fish, particularly the diversity, dynamics and interactions of the plankton. Examples of these studies in the WIUE will be presented in Sections 3–6, including some modelling experiments already performed (Section 4).

2. Decadal changes in small pelagic fish (SPF) and climate variability

SPF populations (e.g., anchovy, sardine, sardinella, and horse mackerel) are of great socio-economic importance for the countries of the Canary Current Upwelling Ecosystem (Portugal, Spain, Morocco, Mauritania and Senegal). Fluctuations in their productivity cause important problems for fisheries management and policies in the region.

Sardine is the main SPF in this ecosystem (Fig. 2). It has a wide distribution around both NE Atlantic waters (from Mauritania up to the North Sea) and in the Mediterranean Sea. Nevertheless, in Atlantic waters, it is only a target species for the Moroccan, Spanish and Portuguese fishing fleets. Moroccan annual catches average around 500 thousand tonnes (Belvèze and Erzini, 1983; Kifani, 1998), while the combined catches for the Iberian Peninsula (Portugal and Spain) fluctuated around 150 thousand tonnes (Fig. 3), with a historical maximum of about 250 thousand tonnes in 1961 (ICES, 2005). As in other parts of the world, cyclic fluctuations in SPF productivity in the WIUE were observed, with peaks in the early 1940s, 1960s and 1980s (Fig. 3). Since 1985, there has been a decline in catches, more pronounced in NW Spain (Cendrero, 2002; Carrera and Porteiro, 2003), with a historical minimum around 86 thousand tonnes in 2000 (Fig. 3).

The WIUE main spawning and recruitment area is located in the Portuguese NW coast (Ré et al., 1990), where young fish (age groups 0–2) are mainly caught (Marques et al., 2003). The analysis of the recruitment (defined as age group-0) time series (1978–2002; Fig. 4a) showed that strong year classes were observed with a periodicity of about 4 years (Fig. 4b). Minimum recruitment levels were observed in the period 1993–1999 (Fig. 4a).

Important fluctuations in the productivity of other SPF species were also reported (data not shown). Horse mackerel (*Trachurus trachurus*) has shown a dramatic decrease in their catches since the early 1970s off
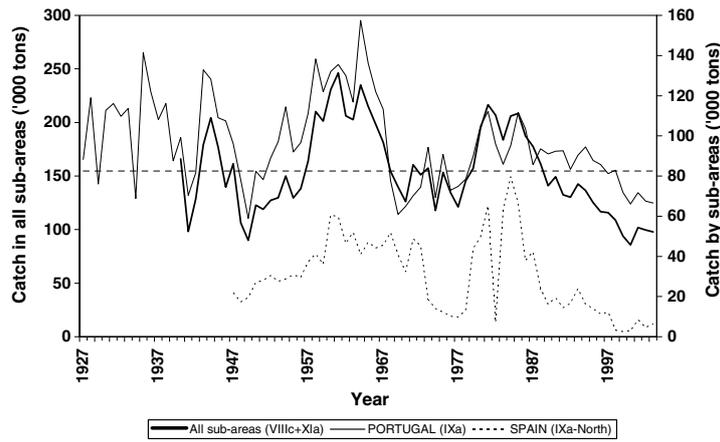
Fig. 3. Annual landings of sardine in ICES sub-areas corresponding to the Western Iberia Upwelling Ecosystem (Source data: ICES, 2005 and IPIMAR, unpublished data; see Fig. 1 for the location of ICES divisions). The horizontal dashed line is the mean value of "All sub-areas" time series.
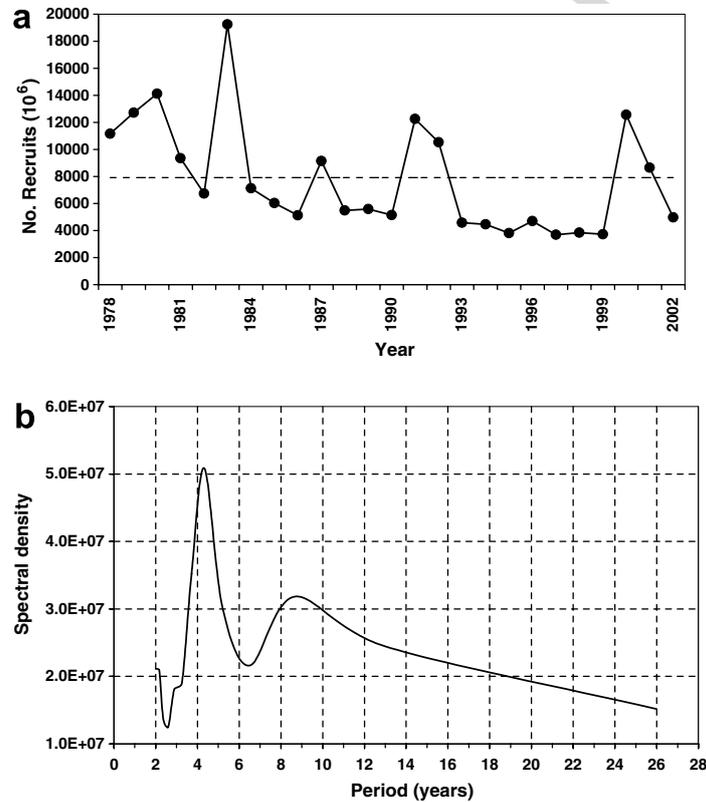

Fig. 4. Sardine recruitment in ICES divisions VIIIc and IXa (see Fig. 1 for the location of ICES divisions): (a) time series for 1978–2002 (Source data: ICES, 2005) and corresponding (b) density spectrum. For the spectral analysis the series was detrended by a simple linear model, tapered by 10% and smoothed by a Hamming filter (window width = 5). The horizontal dashed line in (a) is the mean value of the time series.

Portugal and since the late 1970s off northern Spain (ICES, 2004a), and snipefish (*Macroramphosus* spp.), with peaks of abundance off Portugal in the 1970s and 1990s, reported low abundances in the 1980s and early 2000s (Marques et al., 2005). The abundance of the latter species seems to oscillate in opposite phase to sardine (Marques et al., 2005). However there is no clear evidence that this constitutes an alternating regime similar to the replacement patterns described for sardine and anchovy in other marine ecosystems (Lluch-Belda et al., 1989; Schwartzlose et al., 1999).

These SPF fluctuations over the last decades of the 20th century, especially the decreasing trends of sardine observed in NW Iberia, were also preceded by changes in wind and upwelling patterns (Santos et al., 2001a; Borges et al., 2003). According to the first climatological analyses using wind and SST datasets for periods prior to 1970, maximum coastal upwelling occurs in summer months, from July through September, and minimum in winter/spring (Wooster et al., 1976; Fiúza et al., 1982). However, after the 1970s several changes in this pattern were reported, namely a delay to the spring in the peak of intense upwelling-favourable winds (Dickson et al., 1988; Moita et al., 1998; Palma et al., 1998). At the same time, some authors found an increasing trend in upwelling intensity (Dickson et al., 1988; Bakun, 1990, 1992), but others reported a decreasing trend (Dias, 1994; Dias et al., 1996; Lavin et al., 2000). These changes in upwelling intensity during spring-summer need to be further investigated. A more consistent change in the patterns and intensity of coastal upwelling off W Iberia was the increase in the frequency and intensity of northerly winds (upwelling-favourable) in winter (Dias, 1994; Dias et al., 1996; Borges et al., 2003; Santos et al., 2005) during the period of 1947–2001. Since winter is the main spawning season of SPF in the WIUE (Figueiredo and Santos, 1989; Ré et al., 1990; Borges and Gordo, 1991; Farinha and Borges, 1994; Zwolinski et al., 2001; Marques et al., 2005), these events can have a negative impact on the survival of their first developmental stages through increased offshore transport to unfavourable areas.

There is also evidence that some of these alterations could be related to the NAO (Borges et al., 2003; Santos et al., 2005) and were part of large-scale patterns affecting the whole Canary Current Upwelling System (Santos et al., 2005). Since the beginning of the 1970s, the NAO has been in a positive dominant phase, reaching unprecedented high positive values in the 1990s (Fig. 5).

Borges et al. (2003) found highly significant positive correlations between the NAO and the frequency and intensity of upwelling favourable wind conditions (northerlies) during wintertime off Western Iberia, and a significant correlation between the wind conditions and sardine catch. The climatic changes before and after the 1970s, i.e., the shift in the wind conditions during the winter in phase with NAO trends, was coincident with the trends observed in sardine catches, i.e., a cycle of high catches before the 1970s and a period of lower catches in the following years (Borges et al., 2003). However, Borges et al. (2003) only found a very weak linear correlation ($p = 0.06$) between the NAO and sardine catches. This could be explained by the complexity (e.g., see below Section 3.2) and non-linearity of the relationships between environment, recruitment and fish stock abundance (e.g., Rothschild, 2000; Werner and Quinlan, 2002). Guisande et al. (2004) observed a non-linear relationship between NAO and sardine juvenile landings at Vigo harbour (SW Galicia, Spain) and proposed that NAO and Ekman transport could be combined in an Optimal Environmental Window concept (Cury and Roy, 1989). Another aspect to take into account is that the NAO index only reflects the winter situation and thus the survival conditions during the spawning season but could not explain the conditions occurring during the feeding season.

The lowest landings in the region since the late 1940s and the lowest sardine recruitments were observed during the 1990s in association with a shift in the intensity of upwelling between the 1980s and the 1990s, both in winter and summer (Santos et al., 2001a; Santos et al., 2005). Changes in other components of the ecosys-
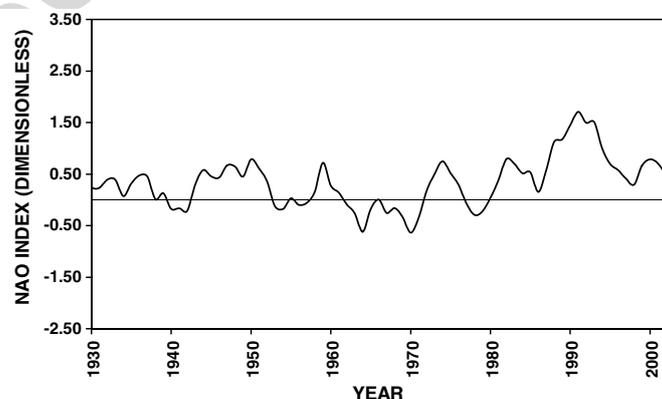

Fig. 5. Five year running mean of the winter (December–March) NAO index (Source data: CRU-University East Anglia, UK: http://www.cru.uea.ac.uk/~timo/projpages/nao_update.htm).
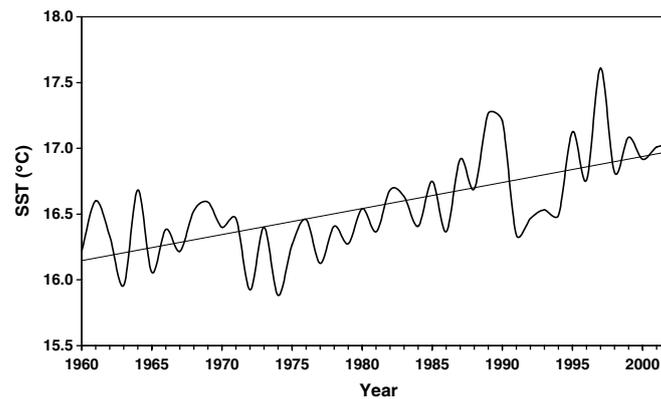
Fig. 6. Sea surface temperature (SST) at (39.5°N; 9.5°W; see Fig. 1 for location) obtained from data extracted from the International Comprehensive Ocean–Atmosphere Data Set (ICOADS) provided by the NOAA's Climate Diagnostics Centre (CDC). The thin line is the overall linear trend.

tem were also associated with environmental changes in wind and upwelling. The distribution and abundance of sardine eggs and larvae in the main spawning grounds changed significantly between the 1980s and the 1990s, with a significant decrease of the area from 11,800 km^2 in 1988 to 7000 km^2 in 1997 (Stratoudakis et al., 2003). These changes are in phase with the ones previously described for sardine landings, as well as for the area of distribution and abundance of sardine estimated by Portuguese and Spanish acoustic surveys (Stratoudakis et al., 2003; ICES, 2002). Changes in sardine maturation between the 1980s and the 1990s (e.g., an increase in the duration of the spawning season and a decrease of the length at 50% maturity-L$_{50}$) were also documented by Silva et al. (2006).

Finally, the increase in water and air temperatures during the last decades (Fig. 6) led to a subsequent change in fish species composition in several North Atlantic ecosystems (Quero et al., 1998; Brander et al., 2003). An increase of tropical fish species and a decrease of boreal species from 1980s to the 1990s were observed in the WIEU (Borges et al., 2004). A comparative study of the fish community on the southern Portuguese coast (~37°N) between the 1980s and the 2000s suggests that warm water species have been extending their range into this region (Brander et al., 2003), in particular species whose distribution was previously limited to the Mediterranean and/or NW Africa. Santos et al. (2001b) and ICES (2002) mention a northern expansion of species (e.g., *Boops boops* and *Scomber japonicus*) with a more subtropical distribution during the 1990s based on trawl data from acoustic surveys performed in the period 1982–2000. An increase in the abundance of subtropical species and the decrease of species whose southern distribution limit is the Portuguese coast have also been observed in the Tagus estuary from early 1980s to late 1990s (Cabral et al., 2001).

3. The "ocean triad": processes of enrichment, concentration and transport/retention in the Western Iberia Upwelling Ecosystem

The dominant oceanographic processes along the Western Iberia coast are seasonal upwelling of nutrient-rich waters in summer, and poleward slope currents carrying warm and saline waters and buoyant plumes from river discharge during winter (e.g., Peliz et al., 2005; Relvas et al., 2007). According to the "ocean triad hypothesis" (Bakun, 1996), nutrient enrichment, concentration of larval food and retention of larvae are the three main factors required for successful recruitment of SPF. In this section we review some studies of physical–biological interactions showing how the "ocean triad hypothesis" operates in the Western Iberia marine ecosystem.

3.1. Enrichment and concentration

The main enrichment process in the Western Iberia is related to the intensity and persistence of coastal upwelling conditions that occurs in spring and summer (Fig. 7a and b), which promote the enrichment of
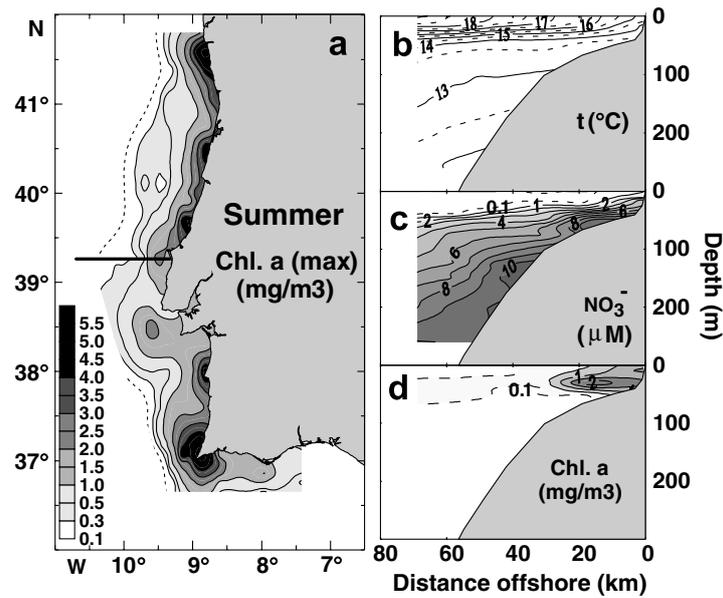
Fig. 7. Horizontal distribution of maximum concentration of chlorophyll-*a* (a) along the Portuguese coast and vertical distributions of temperature (b), nitrate (c) and chlorophyll-*a* (d) off Cape Carvoeiro during summer (adapted from Moita, 2001). The black line in panel (a) presents the location of the vertical distributions.

the euphotic zone with nutrients (Fig. 7c and 8c) and permit phytoplankton growth (Nogueira et al., 1997; Moita, 2001) (Fig. 7a and d) that sustain the high zooplankton production observed from early spring to late autumn (Cunha, 1993a,b).

During early spring, when strong upwelling events and weak thermal stratification are recurrent, phytoplankton blooms are advected from the coast and can occur on the oceanic side of a poorly developed upwelling front (Fig. 8a,b and d). Under these conditions, chlorophyll maxima are often found in an area of convergence or retention formed by the Iberian Poleward Current (IPC), which serves as a barrier to shelf-
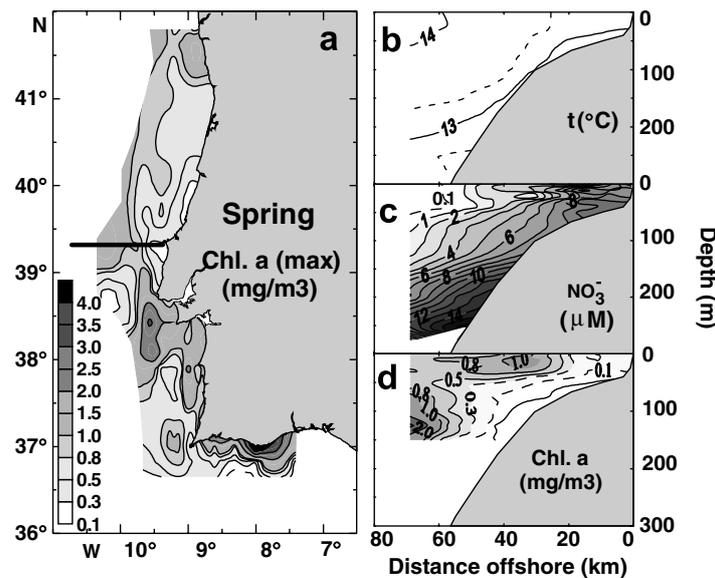

Fig. 8. Horizontal distribution of maximum concentration of chlorophyll-*a* (a) along the Portuguese coast and vertical distributions of temperature (b), nitrate (c) and chlorophyll-*a* (d) off Cape Carvoeiro during spring (adapted from Moita, 2001). The black line in panel (a) presents the location of the vertical distributions.

ocean exchange of upwelled waters (Moita, 2001; Santos et al., 2004) and constitute a zone of concentration of food in the coastal habitat of larval and juvenile sardine.

In summer, the main feeding season of adult sardine, a regular band of high chlorophyll concentration is found near the coast associated with upwelled waters (Fig. 7a and b). Strong cross-shelf gradients separate upwelled from oceanic waters. Concentration maxima occur near the coast in surface waters, whereas offshore these extend in a subsurface maximum within the nutricline (Fig. 7c and d) (Moita, 2001; Tilstone et al., 2003). Pulses of weak to moderate upwelling disrupt stratification and bring nutrients into the photic zone allowing phytoplankton growth on the inshore side of a well-developed thermal front, at the same time that stratified oceanic waters are poor in phytoplankton due to nutrient depletion in the surface layer. These conditions during the feeding season will be fundamental for the optimal fat content and gonadal development of sardine leading to better quality and viable eggs, since phytoplankton is an important component of the dietary of sardine in the Western Iberia in spring and summer (Garrido et al., 2006).

In winter, short events of strong northerlies can occur, but apparently most times they cannot disrupt the haline stratification on the NW Iberia coast where river discharges are important. Under these conditions, phytoplankton productivity is enhanced by the higher nutrient availability related to river discharge and/or regeneration (Alvarez-Salgado et al., 2000; Moita, 2001). In this case, the presence of the Western Iberia Buoyant Plume-WIBP, a recurrent lens of less saline water (< 35.8) fed by the winter discharges of several rivers of the NW Iberian coast (Peliz et al., 2002; Peliz et al., 2005), allow the growth and concentration of phytoplankton (Ribeiro et al., 2005), and is a suitable environment for larval survival in the NW Iberia (Santos et al., 2004, 2006b).

3.2. Transport and retention

As described in Section 2, environmental variability contributes to explaining the observed fluctuations in the productivity of sardine. The main hypothesised mechanism is that northerlies in winter increase upwelling during the spawning season with strong and frequent events being unfavourable for sardine recruitment. However, Santos et al. (2004) showed that the variability in local features, such as buoyant plumes from river discharge (WIBP) and poleward currents (IPC) could introduce important fluctuations in the transport patterns, and modulate the impact of winter upwelling events in the survival of larvae.

During "typical" winter conditions (i.e., without coastal upwelling) the WIBP is bounded to the area of the shelf close to the coast and more pronounced to the north of the Mondego river's mouth (Peliz et al., 2005). In situations of coastal upwelling, the WIBP can extend far beyond the limits of the shelf break, forming a thin surface layer of about 25 m depth over the IPC (Ribeiro et al., 2005). The latter could be very important in the definition of the advection patterns of fish larvae (Santos et al., 2004), as a complement of the transport due to the wind, because it can: (i) induce convergent areas on the continental shelf; (ii) work as a regulating factor in the alongshore transport; and (iii) constitute a mode of exchange between the shelf and the open ocean, taking into account mesoscale features (e.g., eddies) associated with it.

Based on observations of these features, complemented with ichthyoplankton sampling, Santos et al. (2004) proposed a mechanism for transport and retention of fish eggs and larvae in NW Iberia. Retention on the shelf of ichthyoplankton in general, and of larval sardine in particular, along convergence areas formed by the interaction of these local structures, plays an important role in their survival. Sardine larvae are also retained vertically inside the WIBP (Santos et al., 2006b), where high food concentrations exist (Chícharo et al., 2003; Ribeiro et al., 2005) allowing for the survival of larvae and subsequent recruitment success, even in conditions (e.g., upwelling conditions during the spawning season) and places (e.g., offshore distribution) away from the favourable coastal habitat. Moreover, the IPC induces a modulation of the transport northward, thus it is expected that this could contribute to alongshore dispersal of larvae towards the Galician coast.

Extreme events of offshore transport of phytoplankton inside long filaments (∼400 km) induced by eddy–eddy interactions (Fig. 9) occur in SW Iberia (Peliz et al., 2004). Estimated offshore water transport of one of these events was about 58 km^3 day^{-1} with a development time of 20 days, and corresponding to a phytoplankton biomass transport of 8 t day^{-1}. These conditions lead to a dramatic phytoplankton growth inside the filament, enriching the oligotrophic oceanic waters. The magnitude of these extreme events can be several times
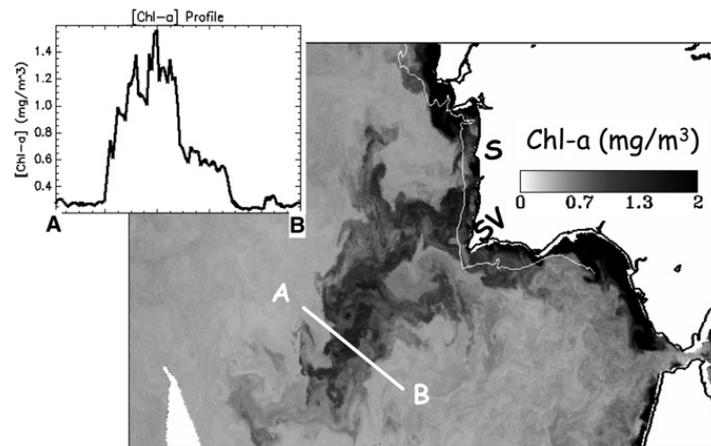
Fig. 9. SeaWiFS-derived chlorophyll-*a* distribution in SW Iberia in 12 February 2001. The inset plot shows the chlorophyll-*a* values across the filament from A to B along the white line of the image. The southwestward filament is about 400 km long (adapted from Peliz et al., 2004).

larger than recurrent upwelling-generated filaments, i.e. 890 t of phytoplankton (Peliz et al., 2004) against 70 t (Cravo et al., 2006).

The frequency of occurrence of these extreme phenomena is unknown. However, this intense mesoscale activity observed in the SW Iberia could explain why this is not considered a favourable recruitment area for sardine (Bernal et al., 2007) and other species. Dos Santos and Peliz (2005), based on 15 years of plankton data from the Portuguese coast, showed that early larval stages of deep-water species, e.g. the Norway lobster *Nephrops norvegicus*, could be transported along the coast and be retained over the shelf during their development. This mechanism may be similar to the ones used by larval SPF, and so it will be interesting to refer to it here. Larval *Nephrops*, like larval sardine are present in the plankton of Iberia during winter months. In the northwestern coast, larvae are only found over the shelf shoreward of the adult distribution. During winter, the W Iberian coast is usually influenced by southerly winds promoting coastward transport within the Ekman layer and retention of larvae over the shelf. Although this mechanism is the same in both NW and SW coasts, larvae are not found over the latter shelf. In that area, the shelf is narrow and intense eddy activity is observed, thus these factors could contribute to enhance cross-shelf exchange and be responsible for the observed larval absence.

4. Physical modelling and larval transport/retention

The first modelling experiment aimed at understanding the processes of dispersion of larval sardine off NW Iberia was reported in Santos et al. (2004). The authors discuss the relevance of different physical dynamics driving the sardine larvae distribution in the winter of 2000. A simple lagrangian transport model was developed that included surface Ekman velocities, measured shelf currents and slope geostrophic flow estimates. The particles (eggs and larvae) mainly aggregated within a meridional band along the shelf break as was observed in nature. This distribution pattern was associated not only with the Ekman dynamics but also with the cross-shore variation of the along-shore flow. Santos et al. (2004) demonstrate that simplified Ekman models could not explain the transport/retention of larvae in this region and more realistic models should be used to simulate the local oceanographic conditions to understand larval dynamics in the region. Furthermore, the results of Santos et al. (2006b) on the vertical behaviour of larval sardine show the difficulty to provide a realistic larval transport model, but also practical information about the degree of vertical resolution needed in the circulation models.

Barotropic tides have little influence on the net dispersal of larvae at the shelf scale off NW Iberia (Marta-Almeida et al., 2006). The contributions of additional supra-inertial dynamical processes (from internal waves to baroclinic tides) to the plankton transport on this shelf zone are almost unknown. These sub-inertial characteristics prompted the need for a modelling framework that comprises the large to small scale processes to

achieve realistic simulations of larval dispersal. Model domains should be sufficiently large to include the large-scale circulation that force the slope flow (Peliz et al., 2003a,b), and need to be of sub-mesoscale resolution to reproduce accurately the small scale structure induced by the joint action of wind and river plumes (Santos et al., 2004; Ribeiro et al., 2005).

A first effort to develop such a framework is described in Peliz et al. (2007). The authors have adopted a nested approach to accommodate large domains with locally high resolutions using the Regional Ocean Modeling System with Adaptive Grid Refinement in Fortran (Roms-Agrif; Penven et al., 2006) to produce model configurations with one-way on line nesting (larger grids passing information to high resolution smaller grids). Fully realistic capabilities were included to simulate river outflow plumes and atmospheric fluxes using NCEP re-analysis. A simulation was conducted for the spring of 1991 because it coincided with WOCE observations (hydrology and currents; Hagen, 1994) and a plankton survey off NW Iberia (Queiroga, 1996) that allowed the validation of the model. Comparisons between survey data and model output were in good agreement, considering that an exact correspondence between model and observations in a system with strong meso- and sub-mesoscale activity is difficult to achieve even in assimilation experiments (Wilkin et al., 2005). The model represented all the major features of the flow field, namely the jets and eddies associated with the IPC, the low salinity lenses and its offshore drift due to the upwelling events, and the low salinity filaments generated by interaction of the salinity plume with the slope eddies (Peliz et al., 2007). Horizontal and vertical diffusion plays a comparable role in the net transport and were also studied by Peliz et al. (2007). For a correct implementation of a lagrangian dispersal sub-model, different configurations were coded and tested for the horizontal and vertical diffusion (Ross and Sharples, 2004), as well as for the vertical diel migration.

A first application of this model with larval crab revealed that the model reproduces well the plankton patches obtained in the survey (Peliz et al., 2007). Thus, these results, and the high realism and resolution already attained by the circulation model give confidence to set up, in a near future, a model of the dynamics of larval SPF for the NW Iberia that should include also parameterizations of larval vertical distribution and vital rates (see next sections).

5. Larval growth and otolith microstructure of sardine and anchovy

The linkage between rates of mortality, growth nutrition and predation are key components of survival of marine fish (Houde, 1987; Lasker, 1987; Bailey and Houde, 1989). The knowledge of the ontogenic events and the time when they occur is crucial before starting any larval survival modelling study, namely using Individual Base Models coupled with Hydrodynamical Models.

Growth rings in otoliths have been used to age larval fish and to establish life history events. In Portugal a number of studies dealing with otolith microstructure, growth and detection of life history events were performed with sardine (Ré, 1983a,b, 1984, 1986) and anchovy *Engraulis encrasicolus* (Ré, 1986, 1987, 1994, 1996; Ribeiro and Gonçalves, 1996). Otolith microstructure increments are deposited on a daily basis (e.g., Ré, 1984, 1986). The *sagittae* of larval sardine exhibit a clear nucleus, which corresponds to the yolk-sac stage. The first increment appears after yolk-sac absorption when the mouth and the digestive tract become functional. On a given otolith the width of the daily increments can vary significantly expressing different daily growth of the individual. Near the nucleus, the first 8–10 growth units are comparatively narrower and less intense (Fig. 10). Microgrowth units become wider from ring 13 onwards. Larval anchovy *sagittae* are similar to those of sardine. A clear nucleus is apparent and daily microgrowth increments also vary in width and intensity being wider and sharper after a certain age.

The first transition in the microstructure of the otolith is related to the onset of exogenous feeding. The wider rings are related to the onset of a diel rhythm of swim bladder inflation and also with the existence of more pronounced rhythms of feeding and vertical migrations. Based in these information it is possible to date the main ontogenic events of larval sardine, which are presented in Table 1.

The integrated growth of sardine larvae can be estimated from the relationship between body size and the number of daily growth increments enumerated from the otoliths (Fig. 11a). Sardine larval growth varies from 0.41 to 0.57 mm day^{-1} (Ré, 1984). Growth of anchovy larvae can also be adequately described, up to an age of about 30 days, using regression analysis (Fig. 11b). Integrated daily growth rates of larval anchovy vary from 0.25 to 0.41 mm day^{-1} (Ré, 1994, 1996) and its main ontogenic events are presented in Table 2.
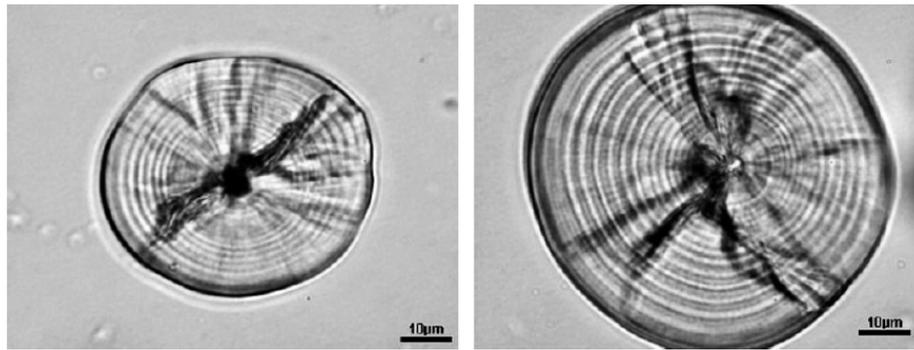
Fig. 10. Sardine larval otolith.

Table 1
Main ontogenetic events in larval sardine (*Sardina pilchardus*)

Age (days)	Length (mm)	Main ontogenetic events
1	4	Eclosion, newly hatched larva (3.3–4 mm)
4	5	Yolk completely absorbed, larva (4.0–5.5 mm)
5	6	Typical larval pigmentation
9	8	Beginning of development of the dorsal fin (7.5 mm)
12	10	Swim-bladder formation
14	11	Flexion of notochord (11–12.5 mm)
17	13	Diel rhythms of swim-bladder inflation (12.5 mm). More pronounced rhythms of feeding and vertical migration
30	20	First appearance of pelvic fins (level with pylorus)
40	26	Dorsal fin with complete number of fin rays
	28	Anal fin with complete number of fin rays
	40	Beginning of metamorphosis

6. Larval feeding and nutritional condition of sardine

It is accepted that starvation during the first-feeding period is one of the main causes of mortality during the larval stages (Hewitt et al., 1985). Starvation weakens larvae, decreasing their capacity to avoid attacks by predators, hence increasing their mortality by predation (Purcell et al., 1987). Starvation also leads to slower growth rates (Buckley, 1982, 1984), thus larvae spend more time in length classes that are more vulnerable to predators (Folkvord and Hunter, 1986; Rice et al., 1993). Therefore, evaluation of food availability and nutritional condition of marine fish larvae is important for a better understanding of the processes affecting survival during the early life stages.

Zooplankton concentration or biomass estimates may underestimate prey availability when zooplankton production is being consumed as quickly as it is being produced (Hunter, 1981), thus the estimation of egg production rates of copepods could be a useful technique to determine food availability for larval fish survival. The first estimations for *Calanus helgolandicus* daily egg production (DEP) in the Portuguese coast were presented by Chícharo et al. (2003). DEP was determined for NW Iberia on shipboard incubations using the techniques described by Harris et al. (2000). Egg production rates in February 2000 ranged from 2 to 31.5 egg fem^{-1} d^{-1} (Fig. 12). The mean value ($\sim$14 egg fem^{-1} d^{-1}) is similar to the values of previous studies reported for this species in its distribution area and for the same period of the year (Bonnet et al., 2005).

In the W Iberia, the above estimates probably do not reflect a generic copepod egg production because other copepod species are also very abundant, particularly *Euchaeta hebes* (Cruz dos Santos, 1992) and *Acartia* spp. (Santos et al., 2006a). Thus, these species should also be considered in future studies in the area to prevent an underestimated of DEP of copepods.

Accurate assessment of nutritional condition in fish larvae has been hampered by the difficulty of capturing and rearing larvae in the laboratory. However, the introduction of biochemical methods (enzymatic activity,
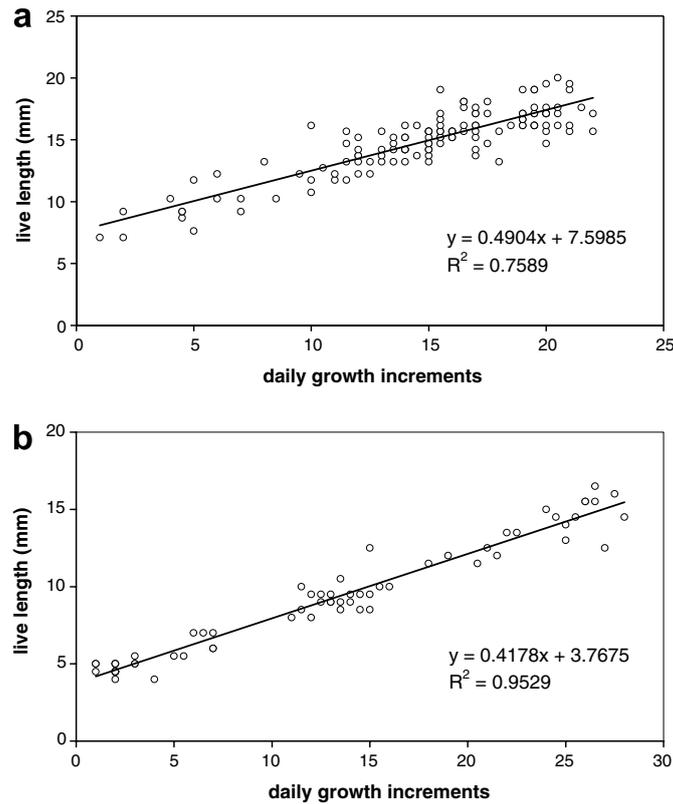
Fig. 11. Age-length relationship for (a) larval sardine (*Sardina pilchardus*) and (b) larval anchovy (*Engraulis encrasicolus*) based on otolith daily growth increments.

Table 2
Main ontogenetic events in larval anchovy (*Engraulis encrasicolus*)

Age (days)	Length (mm)	Main ontogenetic events
1	3	Eclosion, newly hatched larva (3.0–4 mm)
5	4	Yolk completely absorbed, larva (4.0–5.0 mm)
9	5	Typical larval pigmentation
11	6	Beginning of development of the dorsal fin
13	7	Swim-bladder formation
18	9	Flexion of notochord (9–10 mm)
20	10	Diel rhythms of swim-bladder inflation
22	11	Dorsal and anal fin rays developed
30	15	Pelvic fins appears on level with pylorus
	35	Beginning of metamorphosis (35–40 mm)

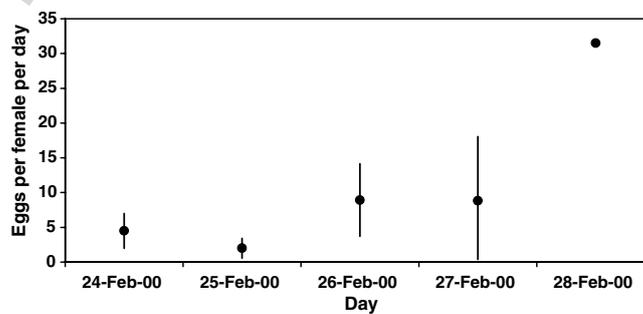
Fig. 12. Daily egg production (means ± standard deviation) for the copepod *Calanus helgolandicus* in the Portuguese west coast during February 2000 (Data source: Chícharo et al., 2003).

Table 3
Summary of results of major nutritional studies with sardine fish larvae in the Western Iberia Peninsula

Study area	Study year/ season	NAO	Up welling event	SST	N	Length (mm)	RNA/DNA	AFDW	% Starvation	Project/references
N Iberia	1991/spring	1.03	Yes	12.4–12.6	84	13.7 ± 5.67	3.95 ± 2.02	0.18 ± 0.11	0.05	Chícharo et al. (1998a,b)
W Iberia	2000/winter	2.8	Yes	13–14	156	16 ± 3.65	5.61 ± 2.17	0.21 ± 0.17	0.64	Chícharo et al. (2003)
S Iberia	1992/spring	3.28	No	14.4–17.4	302	12 ± 4.53	3.27 ± 1.45	No data	4.8	Chícharo (1997a,b)

SST = sea surface temperature, N = number of analysed sardine larvae, AFDW = zooplankton biomass expressed in ash free dry weight (mg m^{-3}). North Atlantic Oscillation (NAO) index from the American Climate and Global Dynamics Division (http://www.cgd.ucar.edu/cas/jhurrell/indices.data.html#naostatdjfm).

RNA/DNA ratios, and lipid content) to assess nutritional condition of individual fish larvae has facilitated this assessment. In particular, nucleic acid determination (for reviews see Ferron and Leggett, 1994; Bergeron, 1997; Buckley et al., 2000) is the recommended nutritional condition index by ICES (2004b) for recruitment monitoring studies. To assess starvation it is necessary to determine the level of RNA/DNA ratio, below which larvae will be classified as starving. Robinson and Ware (1988) defined the "critical ratio" when larval protein growth rate is zero. According to Clemmesen (1994) and Chícharo (1997a) this level is close to one for SPF.

SPF nutritional condition based on RNA/DNA ratios in the WIUE has only been determined for sardine (Chícharo, 1997a,b; Chícharo et al., 1998a,b; Chícharo et al., 2003). The general results of RNA/DNA ratios showed that most of the larvae captured were in good condition, but the highest values of this index were registered off NW Iberia, compared to surveys in the southern or in the northern areas (Table 3).

The condition of sardine larvae in northern Spain was estimated using histological methods (McFadzen et al., 1997), and using gut content analysis (Conway et al., 1991). The former showed that most specimens were in medium or good condition and the latter suggested that in all months food was generally sufficient. Chícharo et al. (1998b) found that zooplankton biomass explained part of the variation of RNA/DNA ratios, which was revealed by the significant correlation between this index and the potential prey of sardine larvae, in agreement with several other studies (Canino et al., 1991; Bailey et al., 1995; Suthers et al., 1996).

Very low starvation percentages were registered during the studies mentioned in Table 3, varying between 0.05–4.8%. The highest starvation percentages were registered off southern Iberia (Table 3). In the WIUE, important sources of coastal water fertilization are freshwater runoff (including river inflow) and upwelling events, and even during some periods the synergies between both seemed to keep SPF larvae in good condition in coastal waters off Iberia (e.g., Chícharo et al., 2003). Low condition values registered together with high starvation percentages found off Algarve coast (southern Iberia) in May 1992, could be explained by low values of river discharges (very positive NAO index) and seem to coincide with an absence of upwelling events. The highest values of nutritional condition, together with low starvation percentages of sardine larvae found off Aveiro (W Iberia) could be linked to the freshwater runoff affecting the shelf and slope, as described in Section 3.1.

7. Conclusions

Partitioning the environmental effects on marine populations from human-induced changes is crucial for the understanding of global change. Atmospheric forcing (e.g., wind) is important to predict natural changes because it is measured operationally and in a systematic way (unlike other ocean parameters). However studies in NW Iberia reviewed here show that this is not enough for understanding such a complex system. Better knowledge of the interplay between the different oceanographic processes and scales, their interactions with land processes (e.g., riverine fluxes), and multiple impacts in the biological systems (from the individual to populations), is necessary to move forward in the study of Global Ecosystem Dynamics.

The lack of consistent time series on dynamical ecological processes and the difficulty to conduct at-sea experiments to study physical–biological interactions in the ocean makes models a powerful tool to study these

interactions on appropriate spatial and temporal scales. Models can also support the design of sea experiments that in turn will provide the necessary data for model validation, essential to obtain reliable simulations. There are no good models without good observations.

The recent development of very realist circulation models for the WIEU, their application to larval dispersal studies and the knowledge of the biology and ecology of larval sardine acquired in the last years, suggest that in a near future we could develop biophysical models to study sardine larval dynamics capable of resolving abundance fluctuations of SPF. However, the processes linking environment, growth and survival of larval sardine are still poorly understood and in situ studies with field-derived vital rates of larvae together with small scale physical observations are still needed in order to validate biophysical models.

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