



Contribution to the Theme Section 'Latest advances in research on fish early life stages'

# The box-balance model: a new tool to assess fish larval survival, applied to field data on two small pelagic fish

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**ABSTRACT:** This work develops a new method, the box-balance model (BBM), to assess the role of hydrodynamic structures in the survival of fish larvae. The BBM was applied in the northwest Mediterranean to field data, on 2 small pelagic fish species whose larvae coexist in summer: *Engraulis encrasicolus*, a dominant species, and *Sardinella aurita*, which is expanding northwards in relation to sea warming. The BBM allows one to quantify the contribution of circulation, with significant mesoscale activity, to the survival of fish larvae, clearly separating the effect of transport from biological factors. It is based on comparing the larval abundances at age found in local target areas, associated with the mesoscale structures (boxes), to those predicted by the overall mortality rate of the population in the region. The application of the BBM reveals that dispersion/retention by hydrodynamic structures favours the survival of *E. encrasicolus* larvae. In addition, since larval growth and mortality rates of the species are required parameters for application of the BBM, we present their estimates for *S. aurita* in the region for the first time. Although growth and mortality rates found for *S. aurita* are both higher than for *E. encrasicolus*, their combined effect confers a lower survival to *S. aurita* larvae. Thus, although the warming trend in the region would contribute to the expansion of the fast-growing species *S. aurita*, we can confirm that *E. encrasicolus* is well established, with a better adapted survival strategy.

**KEY WORDS:** *Engraulis encrasicolus* · *Sardinella aurita* · Mortality · Growth · Fish larvae · NW Mediterranean

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## 1. INTRODUCTION

Understanding how processes acting during the early life of fishes determine recruitment has been a key issue in fisheries science since the early 20<sup>th</sup> century (Hjort 1914, 1926, Cushing 1990). A complex mix of biological (feeding and predation) and physical factors (advection in or out of a sampled region) and their interactions, which control larval survival, can easily generate high variability in recruitment via small effects on mortality rates during the egg and larval stages (Houde 2008). One of the difficulties in mortality estimates is to assign the relative contribution of biological and physical processes on

perceived changes in population abundance (Pepin et al. 2002). Field studies conducted to estimate the role of physical processes in fish larval mortality estimates have been developed based on Lagrangian (Fortier & Leggett 1985, Pepin et al. 2002) or Eulerian approaches (Taggart & Leggett 1987, Kim & Bang 1990, Pepin et al. 1995). Some of these studies concluded that the relative contribution of dynamical processes to the variations in larval fish abundance are likely to be scale dependent, with an increase in the relative importance of advective losses as the area of study decreases (Taggart & Frank 1990, Pepin et al. 1995). Another kind of approach, which was applied in a field study with reasonable confidence,

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was proposed by Helbig & Pepin (1998a,b), who developed a theoretical framework to study the relative importance of advection in larval mortality estimates.

Variability in fish larval survival has been linked to variability in larval growth rates (Campana 1996, Allain et al. 2003, Takasuka et al. 2004a). It is generally considered that faster-growing larvae experience lower mortality as a result of increased size-at-age (Miller et al. 1988, Pepin 2016a) and decreased duration of the vulnerable larval stage (Houde 1987, Anderson 1988). For this reason, accurate measurements of mortality and growth rates are fundamental in determining the factors that influence the survival of fish at early life stages (Helbig & Pepin 1998b). However, despite the potential importance of growth and mortality rates in determining early life survival, there are few works where both were studied simultaneously (Pepin 2016b).

In the NW Mediterranean, the anchovy *Engraulis encrasicolus* and European sardine *Sardina pilchardus* are the most important small pelagic fishes in terms of both biomass and commercial fisheries (Lleonart & Maynou 2003). The reproductive period of these 2 dominant species takes place in completely opposite periods of the year: spring–summer for anchovy and autumn–winter for sardine (Palomera et al. 2007), thus minimizing competition during the early life stages. Round sardinella *Sardinella aurita* is a thermophilic small pelagic species that extends into tropical and subtropical waters of the western and eastern Atlantic Ocean and into the Mediterranean, where it is particularly frequent in the warmer waters of the eastern and southern basins (Ben-Tuvia 1960, Whitehead 1985). However, in the last 2 decades, an increasing abundance and gradual expansion northward of *S. aurita* has been documented in the northern sectors of the Mediterranean, in relation to progressive seawater warming (Sabatés et al. 2006, Tsikliras 2008). Round sardinella reproduces in summer, when surface waters reach the highest temperature of the year (Palomera & Sabatés 1990, Somarakis et al. 2002). Therefore, during this period, larvae of anchovy and round sardinella coexist and dominate the ichthyoplanktonic fraction in neritic areas of the Mediterranean coasts (Sabatés et al. 2007, Somarakis et al. 2011, Cuttitta et al. 2016).

The NW Mediterranean is quite oligotrophic in summer. This period is characterized by a stratified water column, with a marked thermocline that limits vertical mixing. Consequently, primary production remains concentrated at the deep chlorophyll maximum, a thin layer at the deepest levels of the photic zone (Estrada 1985). Surface productivity is restricted

to some coastal zones (Atienza et al. 2016) and to areas under the influence of runoff waters, mainly the Rhone and the Ebro (Salat 1996) that spread above the thermocline, supplying nutrients that maintain surface planktonic production over wide areas (Salat et al. 2002, Ribera d'Alcalà et al. 2004). In this environment—and taking into account that larvae of anchovy and round sardinella occupy the upper levels of the water column and share similar diets (Morote et al. 2008, 2010, Sabatés et al. 2008)—competition for trophic resources is likely to occur. However, there is some degree of spatial segregation between species. The spawning of *E. encrasicolus* takes place all over the continental shelf, and their larvae are found scattered on the whole continental shelf, being particularly abundant over the shelf break (Palomera et al. 2007, Sabatés et al. 2018). The spawning of *S. aurita* takes place close to the shore, associated with coastal productive waters, with a more coastal distribution of their larvae (Sabatés et al. 2009, Maynou et al. 2014, Cuttitta et al. 2018).

The dynamics of the northwestern Mediterranean basin are characterized by a general cyclonic circulation contouring the entire northern continental slope of the basin. This current, called the Northern Current, is in geostrophic equilibrium with a shelf-slope density front that runs along its path, and leaves fresher and cooler waters on its coastal side (Font et al. 1988, Millot 1990). The current, which extends down to a depth of 300–400 m, flows southwestwards along the Catalan coast at approximately 30–50 cm s<sup>-1</sup>, at the surface (Castellón et al. 1990, Salat 1995). The Northern Current shows high mesoscale variability that causes oscillations, meandering and eddy generation (Flexas et al. 2002, Rubio et al. 2005).

Different studies in the Catalan Sea evidenced the role played by the mesoscale dynamics in the distribution of larvae of anchovy and round sardinella, such as the transport of anchovy larvae to the shelf by the Northern Current (Sabatés et al. 2007, Ospina-Alvarez et al. 2015), and the retention of both species by the anticyclonic eddies, which would favour their survival (Sabatés et al. 2013). However, this last study could not offer a quantitative comparison of survival between larvae of *E. encrasicolus* and *S. aurita*, as it lacked an appropriate methodology.

To address this issue and to identify suitable (or unsuitable) areas for larval development, we created a new tool, the box-balance model (BBM), that was conceived to quantify larval dispersion and retention by mesoscale dynamics. The model is based on the larval population dynamics, and can be applied to several species simultaneously. For each species, the

BBM compares the population abundance at age in local areas (boxes) with their abundances predicted by the respective mortality parameter. In this work, the BBM was applied in the NW Mediterranean to the abundant and widely distributed *E. encrasicolus* and *S. aurita* larvae, using the same field data as in Sabatés et al. (2013). The specific objectives of the present work were (1) to describe how the BBM is built, (2) to assess the role of the hydrodynamic structures as larval retention and dispersion areas using the BBM and (3) to analyse the larval survival of these 2 species in the region by combining their individual growth and mortality rates and the BBM results.

## 2. MATERIALS AND METHODS

### 2.1. Field sampling

The study area was located in the Catalan Sea, NW Mediterranean (Fig. 1). Three oceanographic surveys were performed in the summer of 2 consecutive years, coinciding with the spawning period of *Sardinella aurita* and *Engraulis encrasicolus* in the western Mediterranean (Palomera & Sabatés 1990): 18–25 July 2003, 23 June–1 July and 21–29 July 2004). In each survey, 66 sampling stations were located on transects perpendicular to the shoreline, from near

the coast to the slope. The distance between transects was 18.5 km and, on transects, stations were separated by ~14 km (Fig. 1). At each station, vertical profiles of basic hydrographical parameters, i.e. temperature, salinity and fluorescence, were obtained with a Neil Brown Mark III-CTD (World Ocean Circulation Experiment standard) equipped with a Sea Tech fluorometer. The vertical profiles were interpolated to 1 m depth intervals. Geostrophic circulation was estimated from the dynamic height at the stations with a 600 m reference level, and where depth was lower, dynamic heights were extrapolated using the continuity equation applied to the deepest level of 3-station clusters (cf. Hidaka 1940). More details and a full description of the oceanographic methodology can be found in Sabatés et al. (2013).

Fish larvae were sampled by means of oblique tows, from a maximum depth of 200 m to the surface, using a Bongo net with a 60 cm diameter opening and mesh sizes of 300 and 500  $\mu\text{m}$ . The volume of filtered water was estimated by means of a flowmeter fitted in the centre of each net mouth. Zooplankton samples from the 300  $\mu\text{m}$  net were preserved in 5% formalin buffered with borax. On board, anchovy and round sardinella larvae were sorted from the 500  $\mu\text{m}$  net and frozen in liquid nitrogen for shrinkage correction, due to formalin preservation, and otolith analyses. Larval abundances were estimated from the 300  $\mu\text{m}$  net and standardized to individuals per 10  $\text{m}^2$ .

### 2.2. Age-length relationship

In the laboratory, larvae were sorted and identified from the preserved 300  $\mu\text{m}$  net samples. Larvae of *S. aurita* and *E. encrasicolus* collected at each station were counted, and the standard length (SL) of at least 100 individuals of each species per haul was measured to the nearest 0.1 mm.

As preservation in formalin causes significant reduction in larval fish length, and the degree of shrinkage depends on the larval size (Theilacker 1980, Hay 1982), the SL of preserved larvae was corrected for shrinkage due to preservation. To that, the length of larvae, sorted and frozen in liquid nitrogen on board, was measured and larvae were then transferred to formalin for 3 mo. After preservation, all larvae were measured again to perform a linear regression of the initial vs. preserved larval length.

To estimate the growth of each species, we used a total of 80 *E. encrasicolus* larvae (6–20 mm SL) and 93 *S. aurita* (6–15 mm SL). Sagittal otoliths were ex-

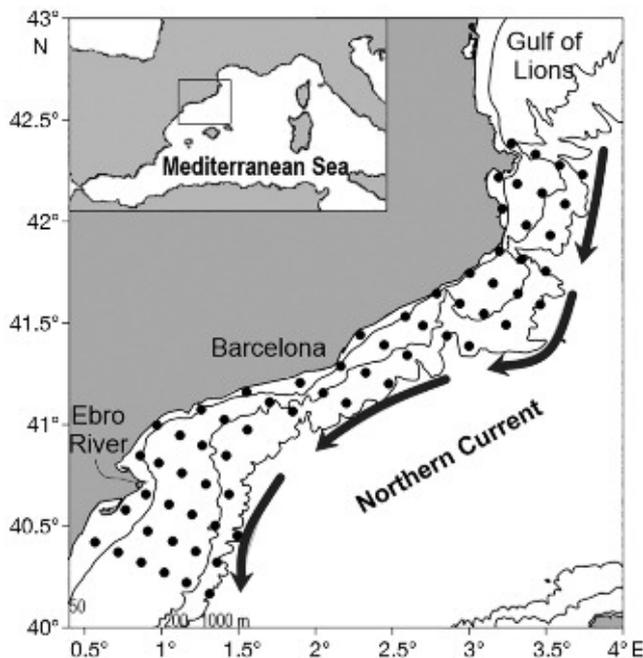


Fig. 1. Study region, *R* (see Sections 2.3 and 2.5 for details), in the NW Mediterranean, showing the sampling stations. Arrows indicate the typical path of the Northern Current along the continental slope

tracted under a dissecting microscope equipped with polarized light, and mounted on a clear medium. Prior to otolith removal, the SL of each individual was measured to the nearest 0.1 mm. Increment counts were made for both otoliths under a light microscope (Axioplan, Zeiss) coupled to an image-analysis system (ProgRes CapturePro 2.0), at 400–1000× magnification. Increments were assumed to be daily, with the first increment laid down at hatching (Aldanondo et al. 2008, Costalago et al. 2011). Assuming linear growth, the equations to convert length to age were obtained by linear regression of age vs. SL of the selected larvae of each species. The larval growth rates, i.e. the daily length increase, were obtained by inversion of the slope of the age–length relationship.

### 2.3. Theoretical framework

This section describes the basic definitions and theoretical framework that sustain the BBM. Larval populations are known to be subjected to a time decay according to the equation (Houde 2002):

$$\frac{dN}{dt} = -MN \quad (1)$$

where  $N$  is the larval abundance at age  $t$  (expressed in days) and  $M$  is the instantaneous mortality rate. If  $M$  is assumed to be constant, the population decay (Eq. 1) becomes exponential and the parameter  $M$  is known as natural mortality. Therefore, for any  $t$ ,

$$N(t) = N_0 e^{-Mt} \quad (2)$$

where  $N_0$  is the initial population ( $t = 0$ ).

The proportion of the population lost every day,  $D$ , can be directly derived from  $M$ , as:

$$D = 1 - e^{-M} \quad (3)$$

to give a more intuitive and accountable indication of the population decay.

The population within an age interval  $S$ , in a given region  $R$  (Fig. 1), is said to be in steady-state, during the sampling period  $T$ , if:

(1) Mortality,  $M$ , is constant (i.e. the population decays according to Eq. 2)

(2) Daily spawning remains constant (i.e. the number of larvae that incorporates every day to the population in  $R$  is constant)

(3) The region  $R$  is 'closed' (i.e. there is neither external input nor output, or, more generally, the external input of larvae by advection equals the output).

These conditions can be assumed when a region  $R$ , large enough in relation to the mesoscale variability,

is sampled during a short time period  $T$  (i.e. comparable to the age interval  $S$ ).

### 2.4. Mortality estimations

Hereafter, the sampling region  $R$  is assumed to be in a steady-state with a population whose natural mortality  $M$  is within an age interval  $S$ . Under these conditions, and according to Eq. (2),  $M$  can be estimated from a pool of all samples in  $R$  as the slope of the linear regression of the whole log abundances at age within  $S$ .

The first step is to determine the age interval  $S$  where the natural mortality  $M$  can be assumed to be constant, for each species and survey. Assuming that the small and large individuals are not efficiently sampled due to extrusion and avoidance, the youngest and oldest larvae must be excluded in the mortality estimates. The remaining larval size range, considered to be fully sampled, has to be converted to the age interval  $S$ , using the age–length relationship previously established.

The abundances at age of collected larvae may not be comparable among day and night samples, since fish larvae can escape from the net during daylight, and this ability increases with length. Therefore, the abundance of older larvae collected during daylight hours can be underestimated, which would cause a bias in the mortality estimates towards higher values when abundances of larvae collected during the day are included in the mortality estimates (Morse 1989). Since the balance estimations require a mortality estimate independent of the sampling light conditions, abundances must be homogenised by catchability factors at age.

The catchability factors at each age are defined as follows. Let  $X_i$  be the real abundance of larvae at age  $i \in S$ , and  $C_i$  the observed abundance of larvae at this age (larvae actually caught), then  $q_i = C_i / X_i$  ( $0 \leq q_i \leq 1$ ) is the catchability factor for age  $i$ . According to the definition, these factors can be directly obtained from the age–length relationship as the ratios between abundances at length of all daylight samples and all night samples.

However, it may happen that none of the larger larvae would be caught during daylight hours, even if they are present. Hence, there is no way to estimate the real abundance of such large individuals from daylight samples. Therefore, to have comparable values among samples, required for the BBM, we must use the catchability factors to convert all samples to the daylight conditions.

Accordingly, 2 mortality rates are presented in the results: (1) the mortality rate estimated from the abundances converted to the daylight conditions, only to be used as a parameter in the BBM, and (2) the mortality rate using the uncorrected abundances, suitable for comparison with other studies, since it was not overestimated.

## 2.5. BBM

We define the concept of 'box' as an area  $A$  within the region  $R$  (Fig. 1). If the population in box  $A$  were in a steady-state, conditions 1 to 3 (see Section 2.3) would hold so that the distribution of larval abundances at age in the box would present the same 'shape' as the whole population in  $R$  (i.e. the mortality estimated using only the data of the population in  $A$  would not be significantly different from  $M$ ). Otherwise, it would be at least one age,  $i$ , whose abundance  $N_i$  would be different than the value expected by Eq. (2). This 'local anomaly' in the abundances at age observed in box  $A$ , with respect to the whole population in  $R$ , indicates that the box  $A$  was not 'closed'. That is, input of larvae at age  $i$  advected into the box is not compensated by the output or vice versa. We thus could say that the box imports (exports) larvae of age  $i$  if the abundance at this age showed a positive (negative) local anomaly. The above mentioned anomalies in comparisons among 'shapes' of the local abundances at age in a given box with respect to those of the whole region  $R$  can be used to estimate the behaviour of this box, in terms of retention (if imports are larger than exports) or dispersion (in the opposite case) of larvae, by looking at all of the anomalies in the abundances at age. In summary, the general assumptions 1 to 3 for the overall sampled region are required as a frame of reference for the population, since the losses or gains in small areas (boxes) by advection are estimated by comparing the local observed abundances at age with what would be found if the local population were in a steady state.

For instance, let us consider a box  $A$ . Let  $N_t$  be the abundance at age  $t$  in  $A$  and let  $m$  be the lowest age of the interval  $S$  (initial age). According to Eq. (2), for any age  $i \in S$ ,  $i > m$ , the expected population at this age in the box will be  $P_i = N_m e^{-M(i-m)}$ . The local anomaly in the box at this age will be  $X_i = N_i - P_i$ . Then, if  $X_i > 0$ , we can say that the box 'imported'  $X_i$  larvae of age  $i$ , and if  $X_i < 0$ , the box 'exported'  $X_i$  larvae of age  $i$ .

The sum of  $X_i$  over all  $i \in S$ :

$$B = \sum_{i \in S} X_i \quad (4)$$

is called the balance of larvae in box  $A$ , as an expression of the overall behaviour of the box in terms of retention or dispersion of larvae. Therefore,  $B > 0$  indicates retention and  $B < 0$  indicates dispersion of larvae. According to the above statements, the sizes of the boxes should be clearly smaller than the whole region, and its lower limit is a single station, provided that there is sufficient larval abundance to have a balance estimation. Nevertheless, the BBM is intended to explain how the mesoscale affects the larval distributions observed in a survey so that relevant quantitative results are expected when the size of boxes is comparable to the mesoscale structures. In order to explain how the mesoscale affects the larval distributions, we present the results of the BBM in 2 ways: (1) To have a quick look at the region to locate zones of dispersion and retention, the balance station-by-station (i.e. each box contains a single station) was determined when possible, and these values were then mapped using kriging as the gridding method in SURFER 13.0 (Golden Software 1994). (2) An accurate quantitative balance determination in some selected areas that can be associated with oceanographic structures as identified in the circulation maps. Note that this last analysis is much more accurate and may not necessarily support the quick-look information provided by the station-by-station maps. To help possible users, a detailed method for applying the BBM to field data is described in the Appendix.

## 2.6. Statistical analyses and significance levels of the estimations

All calculations involved in the balances are subjected to the statistical uncertainties associated with the linear regressions used in the mortality estimation. Since the anomalies at age depend on the estimated value of  $M$ , we calculated the confidence intervals for  $M$  for a given significance level  $\alpha$ , and the associated projections  $P_{\max}$  and  $P_{\min}$  at each age. To minimize the uncertainty associated with the balances (Eq. 4), import and export were estimated with  $P = P_{\min}$  and  $P = P_{\max}$ , respectively for each age. Overall, the significance level was set to  $\alpha = 0.05$  (see Appendix for details).

To test differences between species and among surveys for all parameters estimated in this work, the most appropriate statistical analysis was performed using the IBM SPSS Statistics 25 tools: ANOVA,  $t$ -test and ANCOVA, when it was possible, and non-parametric tests (Wilcoxon rank-sum test) when the abun-

Table 1. Summary of the regression analyses for: (1) the correction of the fish larvae standard length (SL) after shrinkage by preservation; (2) the age–length relationship; and (3) the catchability factor ( $q$ ) for day/night sample comparisons (see Section 2.4 for more details). SE( $a$ ) and SE( $b$ ) are the standard error of the coefficients and SE is the standard error of the estimate

	$y$	$x$	$a$	SE( $a$ )	$b$	SE( $b$ )	N	SE	R <sup>2</sup>	p
<b>Regression <math>y = ax + b</math></b>										
(1) Shrinkage correction factor										
<i>Engraulis encrasicolus</i>	SL	Preserved SL	1.041	0.008	0.791	0.074	145	0.265	0.992	<0.05
<i>Sardinella aurita</i>	SL	Preserved SL	1.009	0.014	1.425	0.108	31	0.154	0.997	<0.05
(2) Age–length relationship										
<i>E. encrasicolus</i>	Age	SL	1.504	0.054	−4.207	0.692	80	1.975	0.909	<0.05
<i>S. aurita</i>	Age	SL	0.908	0.062	−2.215	0.686	93	1.195	0.703	<0.05
<b>Regression <math>y = ae^{-bx}</math></b>										
(3) Catchability factor ( $q$ )										
<i>E. encrasicolus</i>	$q$	SL	1.166	1.112	0.131	0.010	14	0.155	0.932	<0.05
<i>S. aurita</i>	$q$	SL	1.821	1.339	0.208	0.031	9	0.242	0.864	<0.05

dance was too low to assume normal distribution and homogeneity of variances.

### 3. RESULTS

#### 3.1. Age–length relationship

Significant differences in larval shrinkage, due to formalin preservation, were observed between species (ANCOVA,  $p < 0.05$ ). The linear equations found to transform the SL of preserved *Engraulis encrasicolus* and *Sardinella aurita* larvae to their initial SL are presented in Table 1.

The relationship between age, determined from the otolith analysis, and the SL after shrinkage correction can be assumed to be linear in the larval size range considered for *E. encrasicolus* (6.3–20.2 mm SL) and *S. aurita* (6.3–15.1 mm SL). Significant differences in the age–length relationship were found between species (ANCOVA,  $p < 0.05$ ) and the resulting coefficients for each species to convert SL to age are presented in Table 1. The corresponding larval growth rates were 0.66 and 1.10 mm d<sup>−1</sup> for *E. encrasicolus* and *S. aurita*, respectively (Fig. 2).

#### 3.2. Mortality

Significant differences in larval abundance between day and night were found in both species ( $t$ -test,  $p < 0.05$ ). Wilcoxon rank-sum tests also showed that differences were significant in the size intervals 4–16 mm SL and 6–13 mm SL for *E. encrasicolus* and *S. aurita*, respectively (Table 2). At greater sizes, lar-

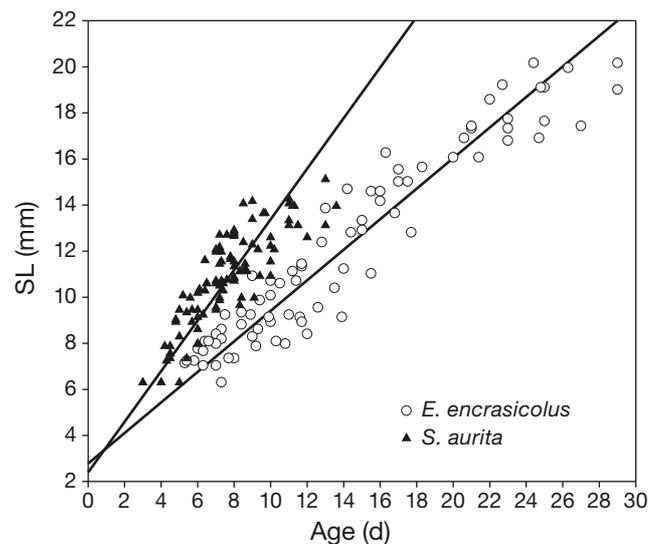


Fig. 2. Age–length relationships of *Engraulis encrasicolus* and *Sardinella aurita* larvae; SL: standard length

val abundances were too low for any statistical analysis (Fig. 3). The catchability factors applied to correct the day/night effects in the abundances are detailed in Table 1.

For each species, the linear regression of the log-abundances at age did not show significant differences in the slopes among surveys (Table 3, Fig. 4). The estimated instantaneous mortality rates were 0.33 and 0.56 for *E. encrasicolus* and *S. aurita*, respectively. These values correspond to a daily population decay of 28 and 43%, respectively, according to Eq. (3). Estimations of instantaneous mortality rates based on the day/night corrected abundances at age, to be used in the BBM (Table 4, Fig. 4) were, as expected, higher than the uncorrected values.

Table 2. Summary of the Wilcoxon rank-sum test for the differences between day and night abundances at length for *Engraulis encrasicolus* and *Sardinella aurita* larvae. SL: standard length

SL class (mm)	Day		Night		p
	Mean	SD	Mean	SD	
	N = 115		N = 78		
<b><i>E. encrasicolus</i></b>					
3	110.79	203.47	147.96	289.23	0.074
4	78.12	152.51	106.54	124.10	<0.05
5	60.21	103.06	113.36	174.34	<0.05
6	46.63	88.37	91.47	140.10	<0.05
7	40.67	65.10	88.12	118.67	<0.05
8	28.70	50.09	66.55	78.80	<0.05
9	13.64	26.09	35.82	52.68	<0.05
10	6.53	13.05	22.22	37.22	<0.05
11	3.64	8.74	12.83	20.62	<0.05
12	2.65	7.25	8.30	14.41	<0.05
13	1.16	3.35	5.26	10.28	<0.05
14	0.58	1.65	3.46	8.80	<0.05
15	0.72	2.32	3.57	7.49	<0.05
16	0.41	2.34	4.00	11.29	<0.05
	N = 89		N = 64		
<b><i>S. aurita</i></b>					
3	11.87	50.44	6.33	32.12	0.325
4	105.49	291.33	85.90	280.30	0.727
5	100.61	189.06	147.73	403.06	0.343
6	33.51	65.69	69.94	150.25	<0.05
7	26.33	59.28	80.36	170.37	<0.05
8	16.27	43.10	41.09	85.21	<0.05
9	7.86	22.09	24.75	54.49	<0.05
10	5.32	14.25	19.57	42.85	<0.05
11	1.80	5.06	11.59	29.07	<0.05
12	1.28	5.12	5.97	15.47	<0.05
13	0.29	1.32	3.33	9.82	<0.05

### 3.3. Analysis of dispersion and retention areas through the BBM

To visually identify the mesoscale structures that retain/import or disperse/export larvae in each survey, balances are estimated for each single station and overlaid on the surface circulation maps (Fig. 5). This figure displays structures associated with areas of larval dispersion (negative balance), larval retention (positive balance), as well as some dipolar structures (i.e. zero balance, because one part of the structure exports larvae to the other part). Overall, these balance maps show that the coastal zone is a dispersion area for both species, and that there were more areas of negative balance for *S. aurita* than for *E. encrasicolus*. A detailed description of this first analysis in each survey is presented below.

Maps for the July 2003 survey (Fig. 5) show positive balance for anchovy larvae in the northern area, associated with the intrusion of the Northern Current. For round sardinella, the balance shown in this area is almost zero. Two eddies, A1 and B1, were present in the central area. Eddy A1 shows positive balance for both species, but the balance in eddy B1 was only positive for anchovy larvae. The southern area shows positive balance for both species.

Maps for the June 2004 survey (Fig. 5) also show positive balance for anchovy, associated with the Northern Current, but not as strong as in the previous survey. This is due to the presence of eddy A2 in the northern zone, with negative balance for this species. For *S. aurita*, however, this eddy had positive balance. Two more eddies were present in this sur-

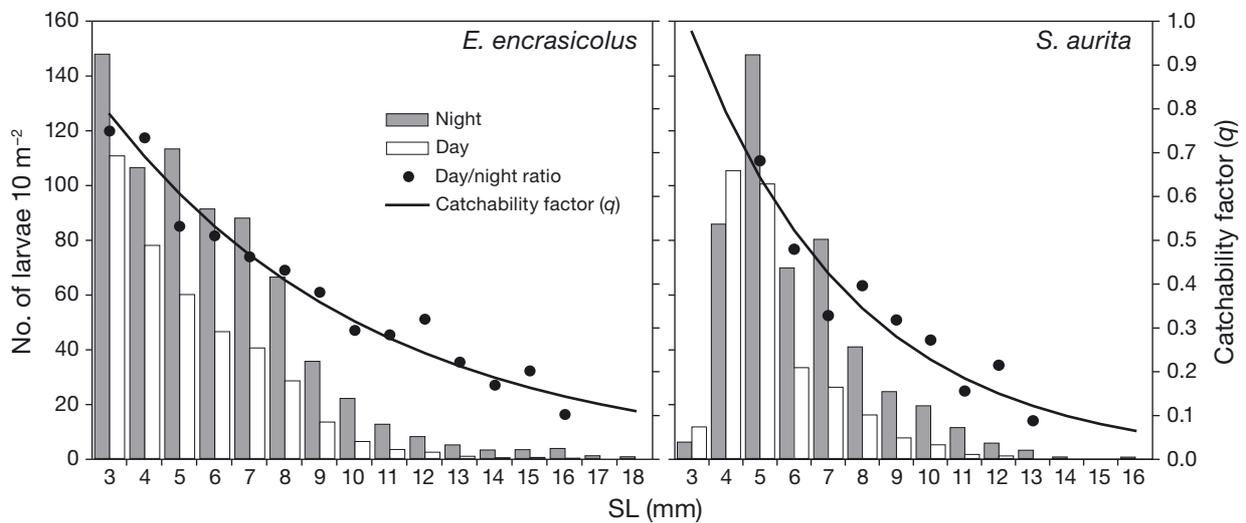


Fig. 3. Abundances at length for *Engraulis encrasicolus* and *Sardinella aurita* larvae (bars, left axis), showing day/night differences. Ratio of day/night (circles) for the adjustment of the curve to obtain the catchability factor ( $q$ , right axis) (see Section 2.4 for details)

Table 3. Linear regression analyses of larval log-abundances at age for the mortality estimation of *Sardinella aurita* and *Engraulis encrasicolus* by survey, specifying the age ranges (S, in days) used. SE: standard error of the estimate, CI: confidence interval. Comparisons among surveys are shown by the ANCOVA for both species

Survey	Regression							ANCOVA									
	Slope	95% CI	Intercept	95% CI	S	N	SE	R <sup>2</sup>	p	Source of variation	DF	SS	MS	F	p		
<b><i>E. encrasicolus</i></b>																	
July 2003	-0.326	-0.360	-0.292	9.709	9.399	10.019	3-14	12	0.181	0.979	<0.05	Survey	2	1.023	0.511	17.41	<0.05
June 2004	-0.342	-0.365	-0.319	10.671	10.389	10.953	7-17	11	0.108	0.992	<0.05	Age	1	51.504	51.504	1753.055	<0.05
July 2004	-0.322	-0.345	-0.299	9.374	9.154	9.594	1-16	16	0.196	0.985	<0.05	Interaction	2	0.0312	0.0156	0.531	0.593
												Residual	33	0.97	0.0294	-	-
												Total	38	65.271	1.718	-	-
<b><i>S. aurita</i></b>																	
July 2003	-0.478	-0.577	-0.379	8.930	8.398	9.462	2-8	7	0.203	0.969	<0.05	Survey	2	1.529	0.764	8.54	<0.05
June 2004	-0.599	-0.653	-0.545	10.355	10.033	10.677	2-9	8	0.148	0.991	<0.05	Age	1	39.728	39.728	443.862	<0.05
July 2004	-0.574	-0.659	-0.489	10.385	9.730	11.040	2-12	11	0.402	0.961	<0.05	Interaction	2	0.267	0.133	1.49	0.249
												Residual	20	1.79	0.0895	-	-
												Total	25	61.825	2.473	-	-

vey: eddy B2, east of Barcelona, that shows gains for *E. encrasicolus* and losses for *S. aurita* larvae, and eddy C2, north of the Ebro Delta, that shows a dipolar behaviour (negative balance on the coast and positive balance offshore). The southern area shows a negative balance for both species.

Maps for the July 2004 survey in the northern area (Fig. 5) show positive balance of anchovy larvae over the Northern Current, as observed in 2003, and almost zero balance for *S. aurita*. Two eddies were detected: eddy A3, east of Barcelona, with positive balance for both species, and eddy B3 that shows positive balance for anchovy larvae but negative for round sardinella. In this case, in the southern area, balances were negative for round sardinella but not for anchovy.

After this quick look, the BBM was applied to some selected boxes, related to the oceanographic structures mentioned above, to assess their behaviour and quantify the corresponding balances. The behaviour of these structures analysed by means of the BBM supported the results provided by the maps.

The northern area always had a relevant role as an import area of *E. encrasicolus* larvae of all ages, which were advected by the Northern Current (Fig. 6). This transport was especially important in July 2004 with an input of +3324 larvae. In July 2003, the balance was lower (+1127), but still relevant. The import behaviour in this area is not reflected in the *S. aurita* larvae balances, which are even slightly negative (-36 in July 2004 and -4 in July 2003). Among the other import areas clearly identified, such as intrusions following the south edge of some eddies, the most relevant was related to eddy C2, in June 2004, that imported larvae of both species from offshore with larval balances of +359 and +117 for *E. encrasicolus* and *S. aurita*, respectively.

The anticyclonic eddies in each survey presented interesting results in terms of balances. Some of them acted as retention mechanisms. The best example was found in July 2004, in the central area, where eddy A3 retained both anchovy and round sardinella larvae from its neighbourhood, with respective balances of +488 and +1038 (Fig. 7). When balances are calculated in the area surrounding eddy A3, the values are -333 for anchovy and +896 for round sardinella. Finally, the overall balance in the whole central area indicates a slightly net gain of anchovy larvae (+85) but an important gain of round sardinella (+1928). These values give the area a dipolar character for anchovy but a retention behaviour for round sardinella. Another interesting result concerning eddies was found in June 2004 in the southern area,

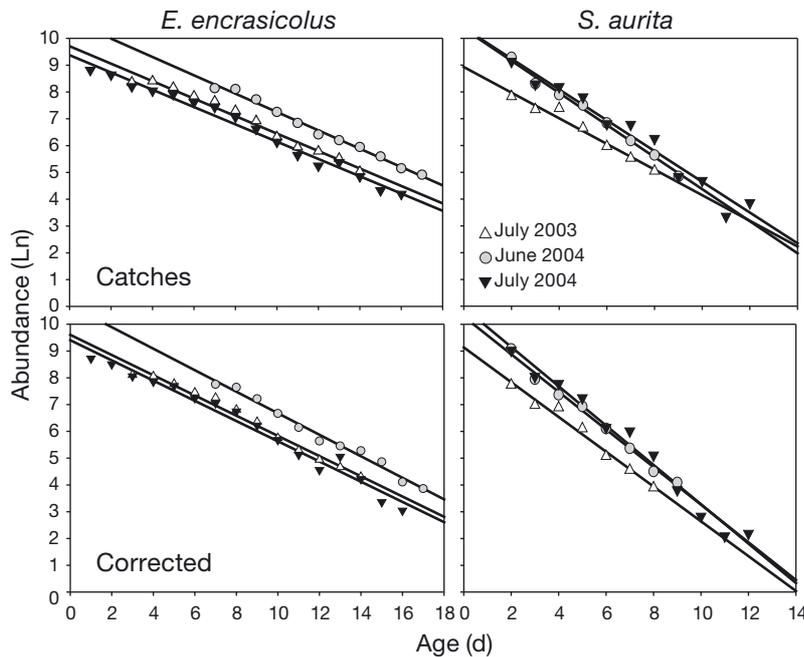


Fig. 4. Larval mortality rates for *Engraulis encrasicolus* and *Sardinella aurita* in each survey, estimated from log-abundances at age, without applying the day/night correction (upper panels), and applying the correction (lower panels) used in the box-balance model

where eddy C2 showed a dipolar behaviour for *E. encrasicolus* larvae, with a nearly zero balance (−11) (Fig. 8). In this case, the abundances at age show a loss of young anchovy larvae (7–12 d old) compensated by a gain of older larvae (13–18 d old), indicating that young larvae from one side of the dipole are transported to the other side. This mechanism, however, was not evident for *S. aurita*, since the balance shows a net loss of larvae (−292) mainly due to younger larvae (3–4 d old) not compensated by gains of older larvae.

Finally, 2 examples of larval export are presented, both south of the Ebro Delta where the shelf is wider. In June 2004, the balances were −214 for *E. encrasi-*

*colus* and −967 for *S. aurita* and, in July 2004, the balances were −549 and −326, respectively (Fig. 9).

#### 4. DISCUSSION

##### 4.1. Analysis of larval survival based on growth and mortality rates

The results of the present study provide new basic information on larval growth and mortality rates of 2 species, and contribute to the understanding of their survival strategies under particular environmental conditions.

The growth rate estimated in the present work for *Engraulis encrasicolus* larvae, 0.66 mm d<sup>−1</sup>, lies within the range reported for this species in the NW Mediterranean, i.e. between 0.49 and 0.89 mm d<sup>−1</sup> (Palomera et al. 1988, García et al. 1998, Sabatés et al. 2007). In other Mediterranean areas, such as the Adriatic, growth rates ranged between 0.54 and 0.90 mm d<sup>−1</sup> (Dulčić 1996, McFadzen & Franceschini 1997), and in the Aegean Sea, between 0.41 and 0.75 mm d<sup>−1</sup> (Somarakis & Nikolioudakis 2007, Catalán et al. 2010). This variability in anchovy daily growth rates has been linked to temperature differences, but also to the productivity of the regions (García & Palomera 1996, Peck et al. 2013).

The estimated growth rate for *Sardinella aurita* larvae, 1.10 mm d<sup>−1</sup>, is significantly higher than that obtained for anchovy. Although information on the growth rate for round sardinella larvae is very scarce, similar values have been reported off the coast of Senegal (0.96 mm d<sup>−1</sup>; Conand 1977) and in Caribbean waters (1.10 mm d<sup>−1</sup>, Ramírez & Marín 2006),

Table 4. Linear regression of corrected larval log-abundances at age for the mortality estimations, as applied to the box-balance model for *Sardinella aurita* and *Engraulis encrasicolus*, specifying the age ranges used for each survey (S, in days). SE: standard error of the estimate; CI: confidence interval

Survey	Slope	95% CI		Intercept	95% CI		S	N	SE	R <sup>2</sup>	p
<b><i>E. encrasicolus</i></b>											
July 2003	−0.377	−0.413	−0.341	9.606	9.278	9.934	3–14	12	0.191	0.982	<0.05
June 2004	−0.401	−0.436	−0.366	10.691	10.266	11.116	7–17	11	0.163	0.987	<0.05
July 2004	−0.377	−0.410	−0.344	9.406	9.086	9.726	1–16	16	0.287	0.977	<0.05
<b><i>S. aurita</i></b>											
July 2003	−0.650	−0.759	−0.541	9.137	8.551	9.723	2–8	7	0.224	0.979	<0.05
June 2004	−0.702	−0.764	−0.640	10.286	9.915	10.657	2–9	8	0.170	0.992	<0.05
July 2004	−0.734	−0.814	−0.654	10.623	10.012	11.234	2–12	11	0.375	0.979	<0.05

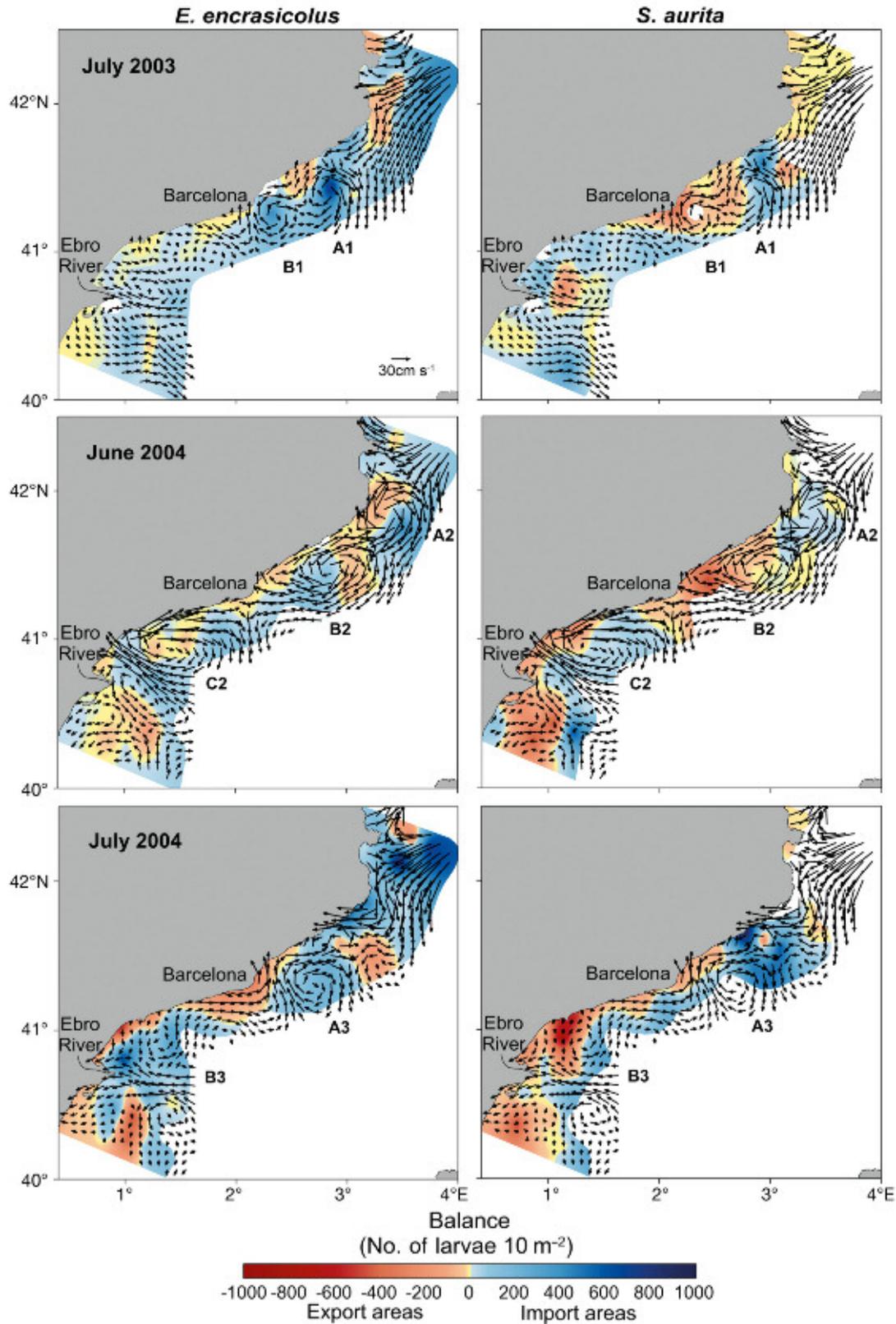


Fig. 5. Maps of the surface circulation overlaid on the balances (see Section 2) estimated at each sampling station, showing the structures of larval import/retention and export/dispersion areas in each survey, for *Engraulis encrasicolus* (left column) and *Sardinella aurita* (right column). Eddies observed by Sabatés et al. (2013) are identified. The white areas indicate the sampling stations where balance determination was not possible

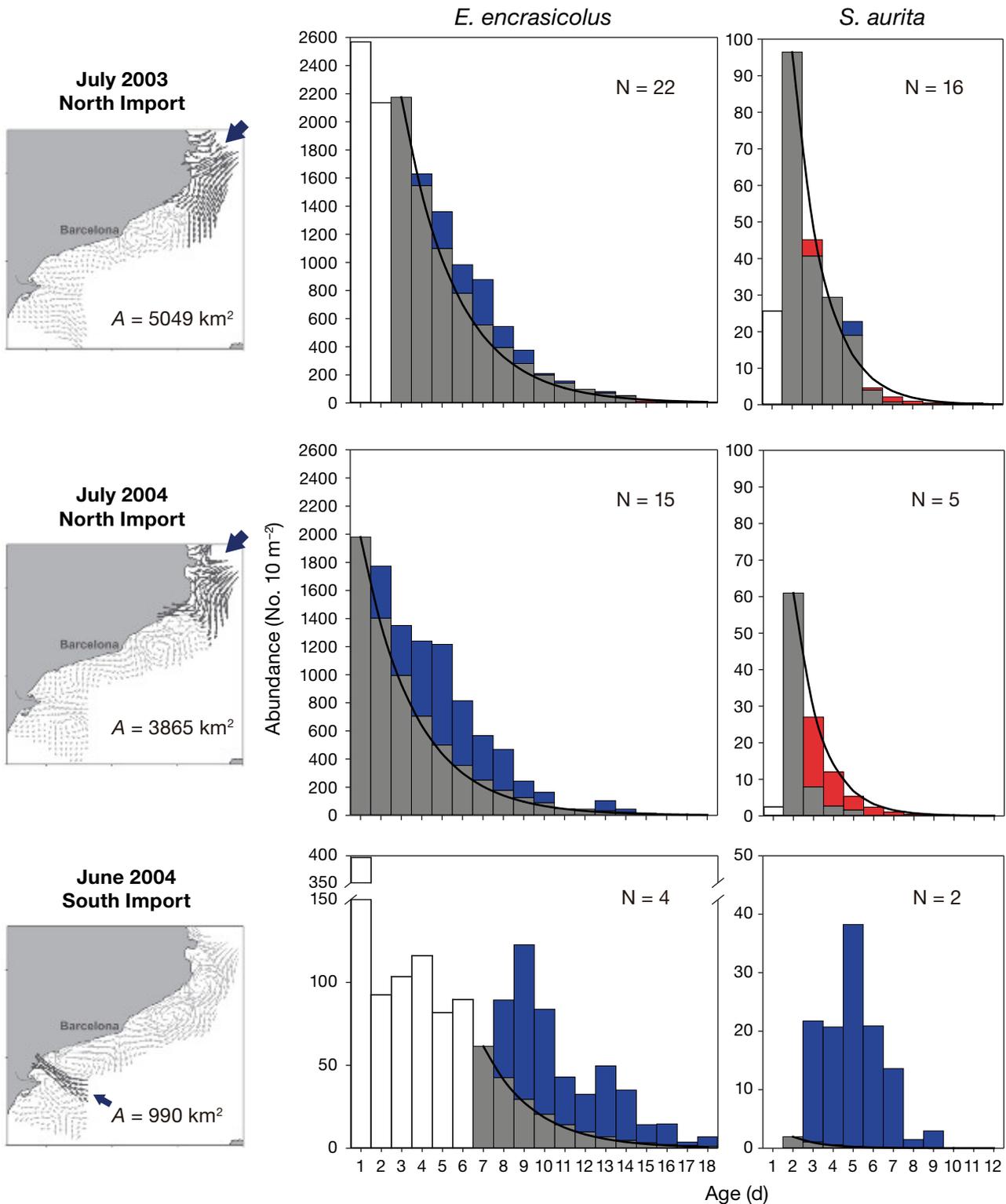


Fig. 6. Box-balances in areas of net larval import: the north import area (July 2003 and July 2004; upper rows) and the south import area (June 2004; bottom row) for *Engraulis encrasicolus* and *Sardinella aurita*. The reference maps (left column) indicate their respective position in the region; *A* is the area analysed (indicated by dark arrows). *N* indicates the number of sampling stations pooled. Solid line in bar graphs indicates the larval abundance at age predicted by the mortality estimate. The bars indicate the abundances at age—white: those that do not contribute to the mortality estimates, blue: the portion that exceeds the predicted value (gain), red: the abundance that would be required to reach the predicted value (loss)

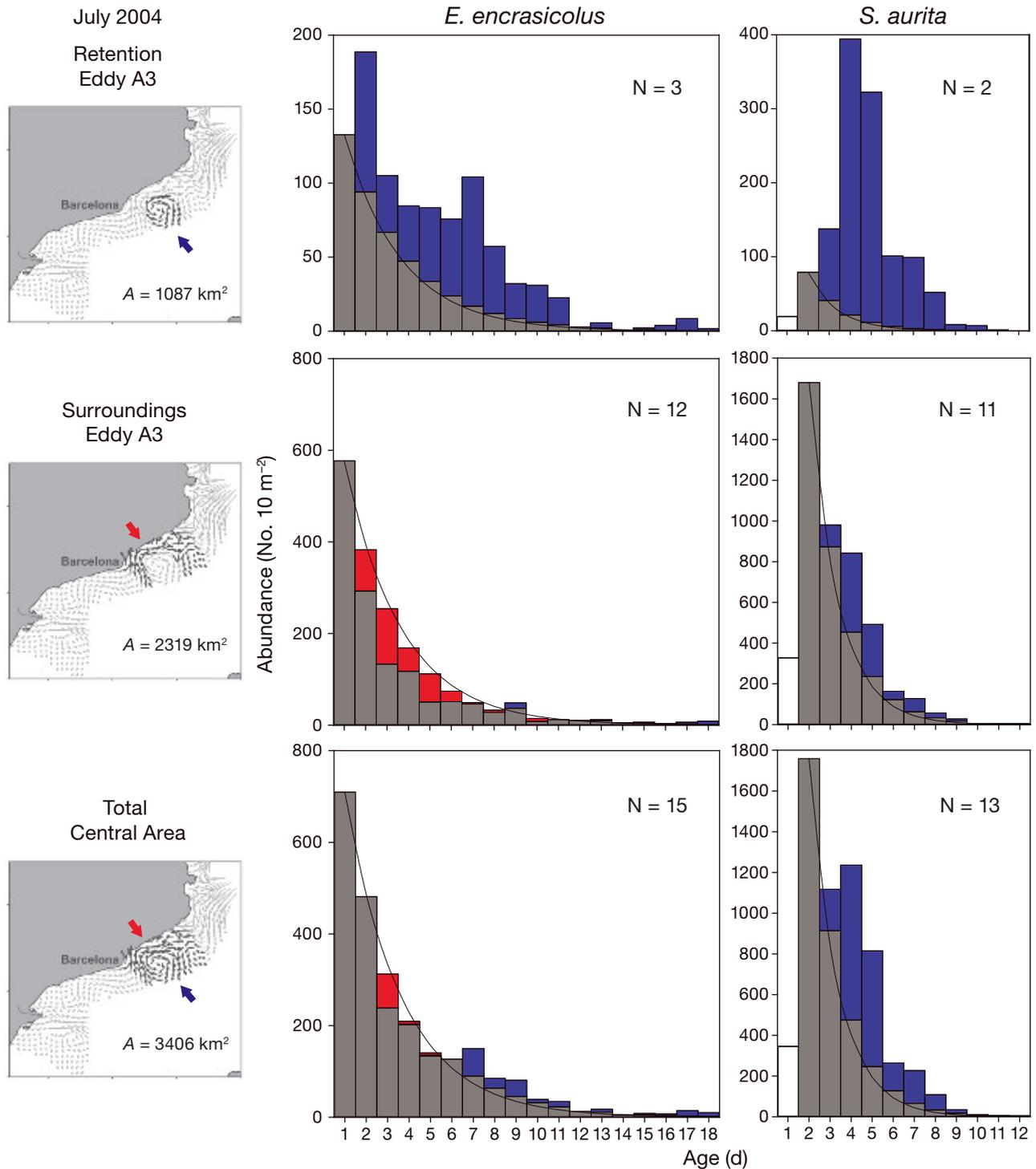


Fig. 7. Box-balances in one of the retention areas, eddy A3, in July 2004 (upper panels), its neighbourhood (central panels) and the total central area (eddy A3 and its neighbourhood) (bottom panels). Descriptions of panels as in Fig. 6

while lower growth rates have been estimated in the Eastern Mediterranean (0.60 mm d<sup>-1</sup>; Walline 1987).

In the present study, the instantaneous mortality rate estimated for *E. encrasicolus* larvae, 0.33, lies in the wide range between 0.12 and 0.58 previously re-

ported for this species in the Mediterranean and in the European Atlantic (Palomera & Lleonart 1989, Coombs et al. 2003, Somarakis & Nikolioudakis 2007, Cotano et al. 2008). The mortality rate estimated for *S. aurita* larvae, 0.56, is higher than that obtained for

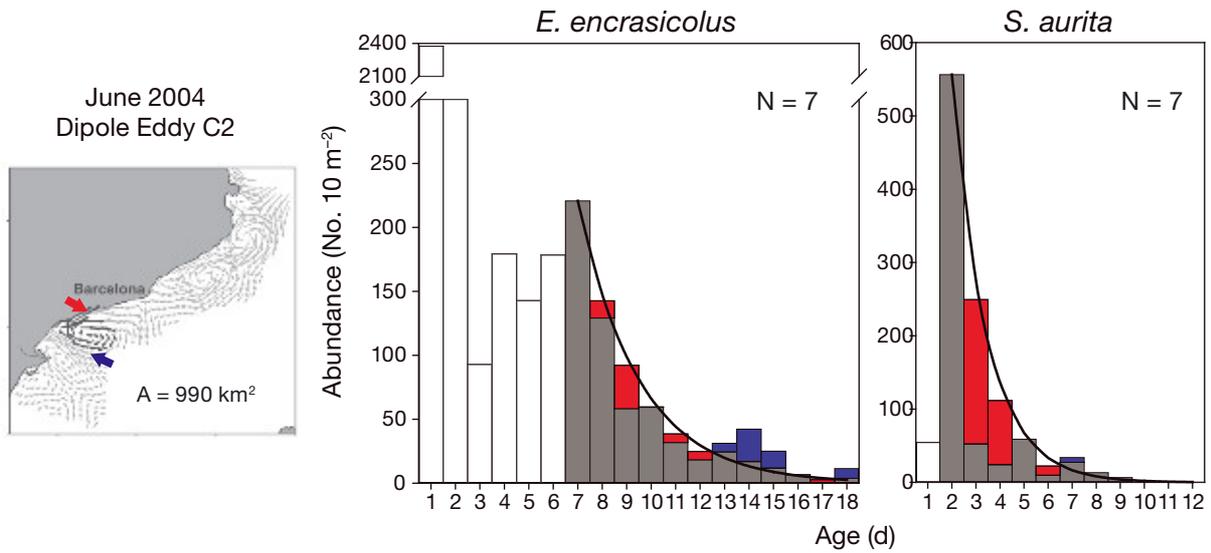


Fig. 8. Box-balances in one of the dipolar structures, eddy C2, in June 2004. Descriptions of panels as in Fig. 6

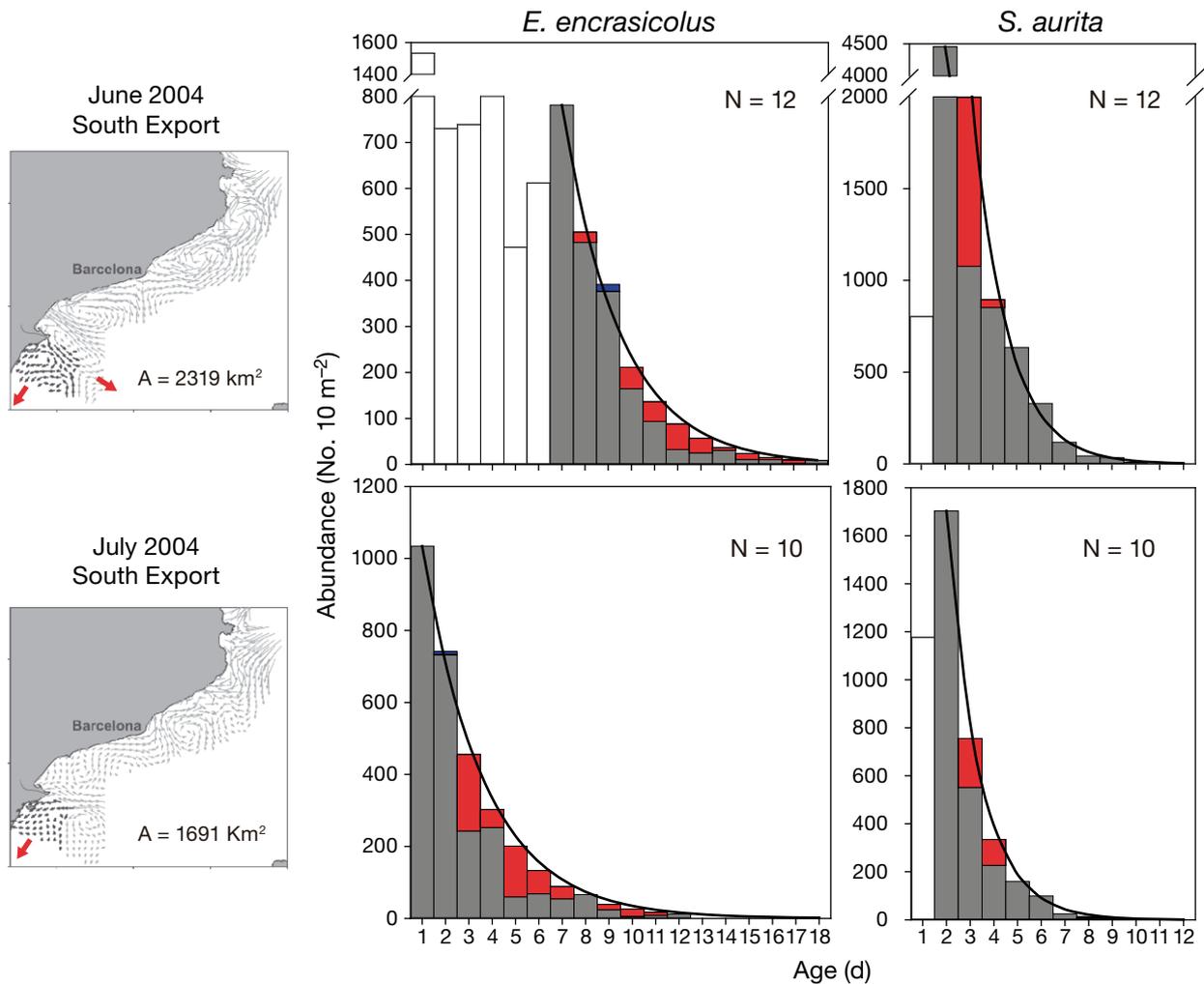


Fig. 9. Box-balances in the south area of net larval export in June 2004 (top panels) and July 2004 (bottom panels). Descriptions of panels as in Fig. 6

anchovy, and lies in the range between 0.20 and 0.65 reported by Conand (1977) in Senegal waters, that, to our knowledge, is the only available study on larval mortality of *S. aurita*.

Anchovy larvae have both lower growth and lower instantaneous mortality rates than round sardinella. Such a direct growth–mortality relationship was previously found in many species (Morse 1989, Pepin 1991, 2016b). Temperature and food availability are 2 crucial environmental factors that determine larval growth rates (Peck et al. 2013) with specific requirements for each species. In the NW Mediterranean, Morote et al. (2008) observed that round sardinella larvae were more voracious than anchovy, thus requiring higher prey availability. This behaviour would explain both the higher growth and mortality rates we found for round sardinella larvae. Houde (1989) suggested that mortality due to starvation would be more probable in species with high growth rates unless larval food abundance is high.

The direct positive relationship between growth and mortality rates at early stages has its counterpart in the long term. According to the ‘growth–predation’ hypothesis (Anderson 1988), larger and faster-growing larvae are less vulnerable to predation and will have a higher probability of survival. This hypothesis has been supported by different field studies for individuals within the same species or among different species (Pepin 1991, Campana 1996, Allain et al. 2003, Baumann et al. 2003). However, other studies showed an opposite trend, that is, higher probability of mortality of larger individuals (Pepin et al. 1992, 2003, Takasuka et al. 2004b). To elucidate these differences, other factors determining fish larval survival must be considered, such as the ability of larvae to escape from predators, larval conspicuousness (Folkvord & Hunter 1986, Litvak & Leggett 1992) or predator characteristics (Pepin et al. 1992, Paradis et al. 1996, Takasuka et al. 2004b).

The positive relationship between growth and mortality rate mentioned above leads to a paradoxical situation, since the fast growth is penalised by high mortality but allows an individual to reach a size large enough to be less vulnerable within a shorter period of time. In our case, according to their respective growth rates, the periods required to reach a ‘relatively safe’ size of 20 mm are 30 d for anchovy vs. 20 d for round sardinella. Applying the corresponding mortality rates to these periods in Eq. (2), the survival of larvae per million is 50.2 and 13.7 for anchovy and round sardinella, respectively. In other words, the surviving population of *E. encrasicolus* larvae is almost 4 times higher than that of *S. aurita*

larvae. This would mean that the slow growth strategy of larval anchovy is better for survival in the environmental conditions of the NW Mediterranean than the fast growth of the round sardinella.

In subtropical areas of the NE Atlantic, high growth and mortality rates of round sardinella are compensated by protracted spawning that would favour offspring survival (Conand & Fagetti 1971, Moyano & Hernández-León 2009, Mbaye et al. 2015). In addition, upwelling contributes to provide food availability for larvae. In our region, close to the northern edge of the distribution area of the round sardinella (Lloret et al. 2015), its reproductive period stretches over the warmest, and more oligotrophic, period of the year (Sabatés et al. 2006, Palomera et al. 2007), in accordance with its tropical origin. While anchovy show a more extended spawning period and their larvae are widely distributed all over the shelf, round sardinella larvae are restricted to coastal areas where production pulses are highly variable (Estrada et al. 1985). Furthermore, recent studies have documented a decrease in biological productivity, likely due to a decrease in riverine runoff waters (Colella et al. 2016, Cozzi et al. 2019). Overall, these conditions would not be suitable for the development of *S. aurita* larvae (Maynou et al. 2020).

After considering the different characteristics of each species and the quantitative results obtained, it appears that round sardinella has not yet developed a survival strategy as successful as that of anchovy in the NW Mediterranean.

#### 4.2. Mesoscale analysis of larval survival based on the BBM

Larval abundances at the local scale can be affected by import or export due to advection. An import (export) of larvae to a particular area can lead to an underestimate (overestimate) of mortality. Helbig & Pepin (1998b) found that even very modest currents can significantly bias the overall mortality estimate, equivalent to the contribution of any other biological component. In this line, Cotano et al. (2008) reported differences in anchovy mortality rates for different areas in the NE Atlantic that were attributed to the advection processes.

In our region, oceanographic structures play an important role in the local survival of these species. The structures associated with larval advection, retention and dispersion, previously identified by Sabatés et al. (2013) are: (1) the trace of the intrusion of the slope current in the northern region, (2) some

anticyclonic eddies over the shelf and (3) some other intrusions of the slope current in the southern area.

In a mesoscale structure, *a priori*, a negative balance (higher mortality) could be due to the export/dispersion of larvae or to conditions in the structure that are not favourable for larval survival. Reciprocally, a positive balance (lower mortality) may be either due to the import/retention of larvae or to favourable conditions. The structures that we identified as being associated with areas of positive (negative) balances in the maps (Fig. 5) allow us to identify whether local mortality anomalies are due to physical or biological processes. The maps also highlight the differences between the 2 species, which become more evident in the detailed analyses when the BBM is applied to particular areas.

A well known phenomenon in the northernmost area is the import of anchovy larvae advected by the Northern Current from the spawning areas of the Gulf of Lions (Sabatés et al. 2007, 2013, Ospina-Alvarez et al. 2015). The results of the present study showed that there was a gain in anchovy larvae of all ages, suggesting a continuous supply of larvae (Fig. 6). In this import area, an estimate of mortality based on the local abundance would lead to an underestimation of larval mortality, as evidenced by Palomera & Lleonart (1989). This is an example of the bias in mortality estimates due to the import of larvae, since the low anchovy larval mortality (0.12) reported by these authors was attributed to the high productivity of the waters. For *S. aurita*, the low abundance and the negative balance in that area, with higher losses than gains, confirm that this northern area is not favourable for round sardinella survival, as previously stated by Sabatés et al. (2009).

The southern area has been identified as dispersive, according to the negative balances for both species, with larval losses at all ages by advection. This export behaviour would be compatible with a spawning area as reported by different authors (Palomera 1992, García & Palomera 1996, Palomera et al. 2007).

The balances observed in eddies A1, B2 and A3 showed import/retention of larvae of both species of all ages, suggesting that these structures offer suitable conditions for larval survival (Fig. 5). In different geographic regions, mesoscale eddies have been identified as important habitat for fish larvae because they increase their survival by enhancing retention, concentration and feeding (e.g. Logerwell & Smith 2001, Bakun 2006, Govoni et al. 2010). It should be expected that larvae retained by these eddies would come from their surroundings, which would involve a negative balance around the eddy and an almost zero balance when considering the whole eddy-

influenced area (i.e. the eddy and its surroundings). However, in the case of eddy A3, balances show important differences between the 2 species (Fig. 7). While the results for anchovy are as expected, round sardinella shows a positive balance, i.e. a net gain in larvae over the whole eddy-influenced area, that must necessarily have come from outer regions. Sabatés et al. (2009) suggested that round sardinella larvae found in this central coastal area would be advected from the south of Barcelona by a northwards coastal current. This area was also characterized by high levels of primary productivity (Atienza et al. 2016) offering suitable conditions for *S. aurita* larvae survival.

The BBM also provides complementary information to larval drift estimates based on particle dispersion models (e.g. Werner et al. 1993, 2001, Ospina-Alvarez et al. 2015, Patti et al. 2018). For instance, based on the dynamic characteristics of eddy A3, Sabatés et al. (2013) suggested that fish larvae would stay inside the eddy for at least 10 d. However, according to the BBM, this would be true for anchovy but not for round sardinella, which could not remain there more than 8 d.

Other eddies, such as A2 or B1, showed different behaviour among species (Fig. 5). B1 only retained anchovy since it received waters from the open sea, where anchovy larvae, but not round sardinella, are found (Palomera et al. 2007). A2 acted as a retention structure for round sardinella while it was dipolar for anchovy. In this case, the eddy received coastal waters, with a much higher content of round sardinella than anchovy.

The case of eddy C2 (June 2004) is especially interesting because the box-balance showed its dipolar behaviour for anchovy and dispersive behaviour for round sardinella (Figs. 5 & 8). This eddy received waters from the open sea side and is linked to a coastal current towards the NE. The coastal current would export both anchovy and round sardinella larvae, but only anchovy would be compensated by an import of larvae from open sea water. In addition, local distributions of the 2 species within the eddy are not coincident, and round sardinella appears to be more exposed to the coastal current, especially the youngest larvae (3–4 d old). However, from our point of view, these explanations are likely, but incomplete, so we should seek additional biological factors to explain the differences in balances between these 2 species.

Pepin et al. (2015) suggested that the existence of a 'critical period' (Hjort 1914) in the early developmental stages, with high mortality due to starvation, likely occurs in fast-growing species, and could be detrimental to round sardinella. Although this could be a possibility, waters on the coastal side of the

eddy, influenced by runoff from the Ebro River, historically had high concentrations of food in shallow waters (Arin et al. 2005). Another possibility is related to the 'offshore transport' hypothesis (Hjort 1914); that is, once larvae are dispersed from productive surface waters, they do not find suitable conditions for survival. However, it should be noted that anchovy larvae can perform diel vertical migrations out of these surface productive waters to feed at the deep chlorophyll maximum, whereas round sardinella could not reach these deep levels, remaining at the surface (Olivar et al. 2001, Sabatés et al. 2008, Tiedemann & Brehmer 2017). In addition, the high concentration of round sardinella at the surface is likely to make them more vulnerable to predation (Bailey & Houde 1989).

Differences in larval vertical distribution patterns between the species could contribute to the specific dispersal trajectories, and hence to their survival (Paris & Cowen 2004, Ospina-Alvarez et al. 2012). This effect in eddy C2 could also be applied to complement the above explanations for the differences in balances observed in other eddies such as A2 and B1. In summary, all of the mesoscale structures analysed by means of the BBM favour anchovy larvae.

### 4.3. Strengths and weaknesses of the BBM

The BBM developed in this work has been designed to clearly separate the impact of fish larval transport from natural mortality in shaping the population age structure. In a multispecies analysis under common environmental conditions, the method allows us to assess the role of larval transport vs. other processes, when age structures among species show significant differences. It only requires a good circulation scheme as well as growth and natural mortality parameters for each species.

To exclude the larval advection effect on the natural mortality estimates, the method can be applied in a straightforward way in ichthyoplankton routine surveys. The water circulation map overlaid on the balances at the sampling stations provides comprehensive information on retention and dispersion areas where the BBM can be applied. However, the survey must have a good coverage of the larval population to allow a good estimate of its natural mortality in the whole region, and be as unbiased as possible. Therefore, it is not suitable if the survey only covers small areas in relation to the mesoscale, or for unidimensional surveys such as a section. By design, the method cannot be applied to discriminate among

other factors, such as starvation and predation, involved in natural mortality estimates.

In the present study, this model has been successfully applied to identify larval concentration and dispersion areas for 2 coexisting species. In contrast to other analyses based on particle dispersion, the BBM has the advantage that the age structure of the real population is taken into account.

## 5. CONCLUSIONS

The BBM allows us to clearly separate the effect of physical from biological factors in fish larval survival estimates, and it can be applied to highlight differences among species that would remain hidden by other methods. For the first time, the present study quantitatively compared the survival chances for larvae of *E. encrasicolus* and *S. aurita*. Our results evidenced that, although the increasing temperature trend would favour the expansion of a fast-growing species like *S. aurita*, the latter has not yet developed an adaptation strategy as successful as that of *E. encrasicolus*, a well established species in the NW Mediterranean.

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### APPENDIX. Applying the box-balance model (BBM) to field data

The original field data consist of a set of samples of fish larvae of one or several species in a region,  $R$ . At every station (Stn), larval abundances,  $D_k$ , of each species,  $k$ , are classified in length intervals,  $l$ . For  $\Omega$  stations and  $\Gamma$  species, we have (Section 2.1 of the main text):

Stn 1: position, time,  $\{D_1(l)\}, \{D_2(l)\}, \dots, \{D_\Gamma(l)\}$

Stn 2: position, time,  $\{D_1(l)\}, \{D_2(l)\}, \dots, \{D_\Gamma(l)\}$

.....

Stn  $\Omega$ : position, time,  $\{D_1(l)\}, \{D_2(l)\}, \dots, \{D_\Gamma(l)\}$

**A.** Convert length,  $l$ , to age,  $t$ , using the age-length relationship parameters  $a_k$  and  $b_k$  (Section 2.2). For each species,  $k$ :

$$t_k(l) = a_k \times l + b_k$$

The converted data consist on a set of abundances at age  $t$ :

Stn 1: position, time,  $\{D_1(t)\}, \{D_2(t)\}, \dots, \{D_\Gamma(t)\}$

Stn 2: position, time,  $\{D_1(t)\}, \{D_2(t)\}, \dots, \{D_\Gamma(t)\}$

.....

Stn  $\Omega$ : position, time,  $\{D_1(t)\}, \{D_2(t)\}, \dots, \{D_\Gamma(t)\}$

**B.** Parameters for the BBM, for each species,  $k$  (Section 2.4):

B.1. Determine the age interval,  $S_k$ , where its mortality rate  $M_k$  is expected to be constant (Section 2.4)

B.2. Determine the catchability factors at age,  $\{q_k(t)\}$ , to correct day/night effect to homogenise abundances (Section 2.4). For each Stn  $i$ :

$$d_k(t) = D_k(t) q_k(t), t \in S$$

B.3. Calculate the pool of homogenised abundances at age  $\{\Sigma d_k(t)\}$ ,  $t \in S$ , extended for all  $\Omega$  Stations in  $R$  (Section 2.4).

B.4. Estimate the mortality rate,  $M_k$ , for the region,  $R$ , valid to apply the BBM, by linear regression on the log-abundances at age calculated in step B.3. (Section 2.4).

B.5. Estimate the confidence intervals ( $\alpha = 0.05$ ) for  $M_k$  (Section 2.4).

**C.** Box balances for each species,  $k$  (Section 2.5):

C.1. Select a box,  $A$ , in  $R$ . Let  $\mathfrak{R}$  be the set of all the stations whose position lies in  $A$  (Section 2.5).

Then, for each species,  $k$  (note that subscript  $k$  will be omitted hereafter because the same procedure has to be applied to each species):

C.2. Estimate the abundances at age  $\{N(t)\}$  in the box (Section 2.5),

$$N(t) = \Sigma_{\mathfrak{R}} d(t).$$

C.3. Estimate the projected values at age  $\{P_{\min}(t)\}$  in the box (Section 2.5), and the projected minimum (maximum) values:

$$P(t) = N(m) e^{-M(t-m)}, \text{ where } m \text{ is the lowest } t \text{ in } S, \text{ and}$$

$$P_{\min}(t) = N(m) e^{-M_{\min}(t-m)}, \text{ where } M_{\min} \text{ is the lowest bound of the confidence interval for } M.$$

C.4. Estimate the local anomalies  $X(t)$  at age in the box (Section 2.5),

$$\text{if } N(t) > P_{\max}(t), \text{ then } X(t) = N(t) - P_{\max}(t),$$

$$\text{if } N(t) < P_{\min}(t), \text{ then } X(t) = N(t) - P_{\min}(t), \text{ and}$$

$$X(t) = 0, \text{ otherwise.}$$

C.5. Estimate the balance,  $B$ , in the box (the box-balance) using Eq. (4) in Section 2.5 (i.e. summing all of the  $X(t)$  obtained in  $\mathfrak{R}$ )

**D.** Map of the balance values of single stations using an adequate (e.g. kriging) interpolation method (as in Fig. 5).

**E.** Analysis of the gains and losses by age of fish larvae at selected areas using bar graphs representing the abundances at age and the projected abundances (as in Figs. 6–8).