

The fate of eggs and larvae of three pelagic species, mackerel (*Scomber scombrus*), horse mackerel (*Trachurus trachurus*) and sardine (*Sardina pilchardus*) in relation to prevailing currents in the Bay of Biscay: Could they affect larval survival?

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SUMMARY: The spatial distribution of eggs and larvae of three pelagic species, mackerel, horse mackerel and sardine, in the Bay of Biscay was studied in 1998, 2001 and 2004. The spatial distribution was clearly different between the years studied and corresponds quite precisely to different water circulation regimes. Mackerel and horse mackerel larvae are more affected by the prevailing currents than sardine, as their spawning grounds are located offshore, far from the shelf break where the current velocities are higher. Survival rates for mackerel and horse mackerel were higher in 2001, when the offshore larval transport was stronger. However, for sardine, the mortality rate hardly varied between years. The abundance of 25-day-old larvae, considered as an index of the survival rate, appears to be a good recruitment indicator, at least for 1998, 2001 and 2004. Our results did not support the hypothesis of Bakun (1996), which states that dispersion of early life stages towards open ocean waters should cause high larval mortality. At least under the conditions observed for the years studied, the retention of larvae offshore appears to have a positive effect on larval growth and/or survival.

Keywords: ichthyoplankton, Bay of Biscay, survival rates, larval transport, recruitment.

RESUMEN: EL DESTINO DE HUEVOS Y LARVAS DE TRES ESPECIES PELÁGICAS CABALLA, (*SCOMBER SCOMBRUS*), JUREL (*TRACHURUS TRACHURUS*) Y SARDINA (*SARDINA PILCHARDUS*) EN RELACIÓN A LAS CORRIENTES PREVALENTES EN EL ÁREA DEL GOLFO DE VIZCAYA. ¿PODRÍAN AFECTAR A LA SUPERVIVENCIA LARVARIA? – La distribución espacial de los huevos y larvas de tres especies pelágicas, caballa, jurel y sardina en el Golfo de Vizcaya fue estudiada en 1998, 2001 y 2004. Esta distribución espacial fue claramente diferente entre los años estudiados y se ajustan, bastante bien a los diferentes regímenes de circulación. Las larvas de caballa y jurel resultaron más directamente afectadas por estas corrientes prevalentes que las larvas de sardina. Esto se explica porque las sardinias desovan en la plataforma, relativamente alejadas del cantil, donde las velocidades de las corrientes son más altas. Las tasas de supervivencia larvaria de caballa y jurel fueron superiores en 2001, cuando el transporte de larvas offshore era más importante. Para las larvas de sardina, sin embargo, la tasa de mortalidad apenas varió entre años. La abundancia de larvas mayores de 25 días, considerada aquí como un índice de la tasa de supervivencia larvaria, resultó ser un buen indicador del reclutamiento por lo menos para los años estudiados. Nuestros resultados contradicen la teoría de Bakun (1996), que afirma que la dispersión de las etapas de vida temprana hacia las aguas del océano abierto causa una alta mortalidad larvaria. Por lo menos bajo la condición que se observó durante estos años (temperatura y abundancia de alimento), la retención de larvas en mar abierto parece tener un efecto positivo en el crecimiento larvario y/o supervivencia.

Palabras clave: ictioplancton, Golfo de Vizcaya, tasa de supervivencia, transporte de larvas, reclutamiento.

INTRODUCTION

Mackerel (*Scomber scombrus*, L.), horse mackerel (*Trachurus trachurus*, L.) and sardine (*Sardine pilchardus*) populations represent the most important stocks of pelagic fisheries in southern European areas (Spain and Portugal). In the Bay of Biscay, these populations partially share spawning habitats, so their pelagic eggs and larvae compete for food and predators. Physical retention and food availability for eggs and larval fish have been proposed as two of the major factors that affect survival during early life history stages (Cushing 1975, Iles and Sinclair 1982). Physical and biological processes occurring at the shelf break appear to play an important role in the regulation of some fish populations, as their recruitment depends upon the dynamics during these early life stages (ELS). Understanding how eggs and larvae are influenced by oceanographic processes and exchanges between populations is fundamental for forecasting population dynamics (Knights *et al.* 2006).

Mackerel and horse mackerel show great similarities in their life cycles. These small pelagic species are distributed from the southern Norwegian coast to Mauritania. They are batch spawners, with a fairly extended spawning season. The peak of spawning for these species is late in the Bay of Biscay, where mackerel spawns from February to May, with the peak in March-April, while the highest incidence for horse mackerel occurs in May-June (D'Elbée *et al.* 2009). The spawning takes place at the shelf break or in the adjacent shelf region (Franco *et al.* 1993, Eaton 1989). In general, nurseries are located near coastal waters, zones where typically the food availability is sufficient to guarantee the survival of progenies. Within the region an important juvenile area of mackerel is located off the west coast of the Iberian Peninsula (Villamor *et al.* 1997). Sardine (*Sardina pilchardus*) spawning occurs along the northeast Atlantic margin from the Celtic Sea to southern Mauritania. In the Bay of Biscay sardine spawns in spring and autumn in the open sea, at temperatures ranging from 13°C to 16°C (Coombs *et al.* 2006). Juvenile areas (sardine at age 0) appear off the Iberian Peninsula in the northern and central parts of Portugal between summer and winter (Carrera *et al.* 2006).

For many fish populations, the spatial distributions of ELS and juveniles are less extended than the spatial range of the adult population. Additionally, these are usually consistent from year to year, over a long period of time. The entrainment of spawning products into juvenile nurseries is a prerequisite for the survival of the population. The ELS of fish species that spawn at the shelf edge are of particular interest, because these planktonic stages are especially vulnerable to advection to areas of unsuitable larval food supply and increased predation risk, or to subsequent inappropriate nursery grounds (Bartsch and Coombs, 2004). Transport of ichthyoplankton (both retention and/or dispersal) has an effect on the distribution and abundance of fishes (Boehlert and Mundy 1994). There-

fore, individuals that do not reach the nursery areas are unable to recruit and therefore play no further part in the dynamics of the parent populations. However, not reaching the nursery area does not imply that “adverse” dispersal will necessarily result in an increase in mortality rates but, following the “member/vagrant hypothesis” (Hjort 1926, Sinclair 1988), individuals stray from adult population dynamics, with varying consequences on the population. Numerous studies have indicated that much of the mortality-regulating future year-class strength takes place during these early developmental stages (Houde 1987).

Within the framework of the ICES Triennial surveys for mackerel and horse mackerel every three years, two surveys are carried out in the Bay of Biscay. The surveys occur during the peak of spawning for these species within the area. The aim of the cruises is to estimate the biomass of mackerel and horse mackerel using the annual egg production method (AEPM). In this paper, we analyse the eggs and larvae abundances obtained during the cruises undertaken in 1998, 2001 and 2004 for the target species mackerel and horse mackerel, and for sardine. The objective of this work is to assess the effects of environment and hydrodynamic regimes on the final fate and survival rate of ELS of these species in the Bay of Biscay. To this end, we used a Lagrangian particle tracking model to assess the eggs and larval dispersion and/or retention in the area during the three years studied. Finally, the influence on recruitment is also discussed.

MATERIALS AND METHODS

Sampling

The sampling was carried out in the Bay of Biscay during the ICES triennial surveys for mackerel and horse mackerel eggs, aboard the R/V *Investigador* (Fig. 1). Every three years the samplings are carried out in two periods: March-April and May-June. The dates of the samplings and the number of samples collected are listed in Table 1. Ichthyoplankton was collected using a 40-cm bongo net with a 330- μ m mesh, towed obliquely to a maximum depth of 200 m or to within 5 m of the bottom in shallower waters. The net was deployed at a rate of 50 m min^{-1} and recovered at a speed of 20 m min^{-1} . The speed of the ship during the tow was about 2 to 2.5 knots. The bongo nets were fitted with calibrated flowmeters in order to calculate the filtered volume. The net was lowered into the water at a 45° angle. Wire angle was measured with the use of a hand-held inclinometer and an angle of 35-55° was maintained for all the stations. For each station, the maximum sampling depth was provided by a Conductivity Temperature and Depth sensors system mounted on the bongo net.

Once brought onboard, the nets were gently washed with a hose so that the specimens in the net could be collected in the cod-end. Samples were washed through a 150- μ m sieve and transferred into 500-mL

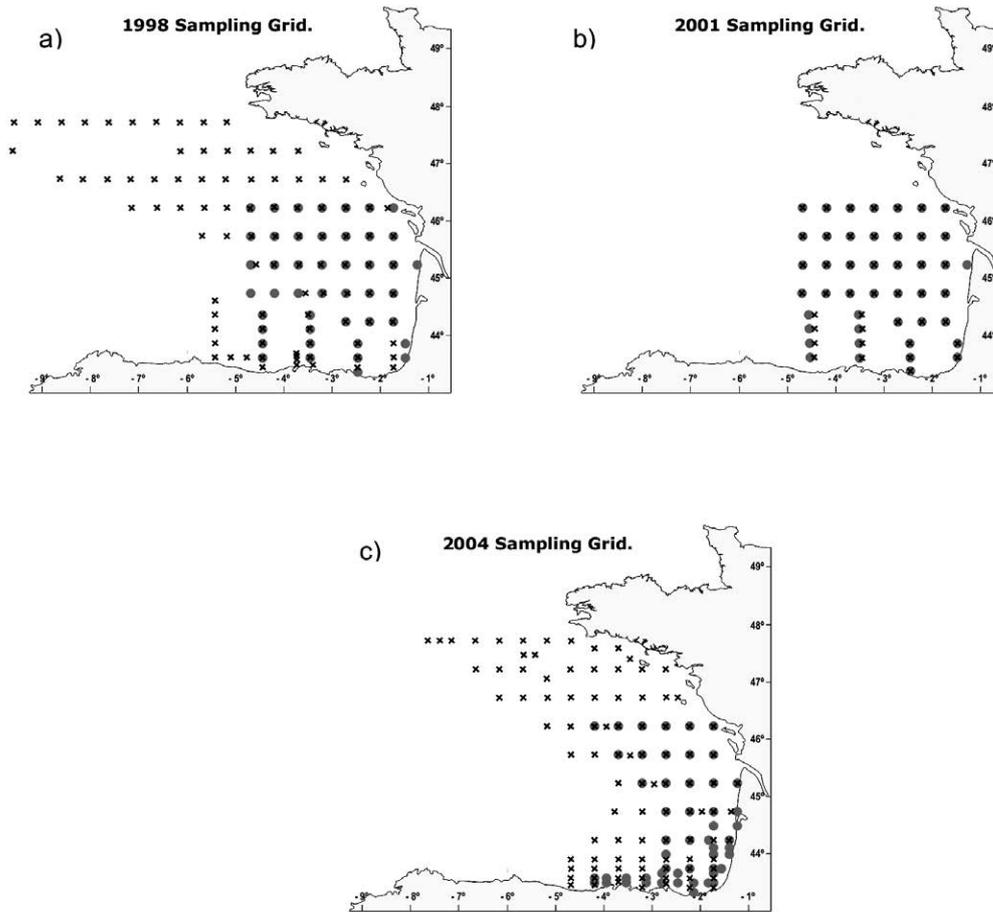


FIG. 1. – Distribution of the plankton stations used in the present study for (a) 1998; (b) 2001; and (c) 2004. Crosses and grey points indicate stations sampled during the first period (March–April) and the second period (May–June), respectively.

plastic jars with 4% formaldehyde with sodium borate buffer and seawater. The pH of the plankton samples was checked every 12 hours during the first two days after collection.

Eggs were sorted using the “spray method” (Eltink 2007). The eggs were identified then as sardine, mackerel and horse mackerel eggs, using a binocular microscope. Larvae were separated by hand, identified into species and standard length (SL), measured to the nearest lower 0.1 mm using a binocular microscope. No correction was made to allow for shrinkage of larvae due to fixation procedures. However, individual SL data were not available for horse mackerel and sardine in 1998.

Eggs and larval abundance were then converted to numbers per m², following standard procedures (Smith and Richardson 1977).

Age and mortality

The larval length data were converted to age using the linear regression age vs standard length (unpublished data) for each species, assuming no differences in growth rate between different months and years.

Mackerel:	$\alpha = 2.9409 \beta - 1.8199$ (n=78; R ² =80; P=0.001)
Horse mackerel:	$\alpha = 4.4625 \beta - 6.9828$ (n=47; R ² =88.5; P=0.001)
Sardine:	$\alpha = 1.2053 \beta - 3.0532$ (n=65; R ² =89.1; P=0.001)

where α is the age obtained for otolith readings (in days), β is the standard length (in mm), and n the number of data points.

Instantaneous daily mortality rates of larvae were estimated from an exponential model of decline in abundances (nb m⁻²), with respect to age as described by Ahlstrom (1954) and Smith and Richardson (1977):

$$N_{\alpha} \equiv N_0 e^{-z\alpha}$$

where N_{α} is the abundance at age α (nb m⁻²); N_0 is the estimated abundance at hatching (y-intercept of the regression; nb m⁻²); z is the instantaneous mortality coefficient (days⁻¹); and α is the age in days (estimated from age vs length regression, see above).

Daily mortality and cumulative mortality were expressed respectively as:

$$M = 1 - \exp(-z)$$

$$Mcum = [1 - \exp(-z\alpha)]$$

where α is the time interval (days).

Cumulative survival rate, as a percentage, was estimated as:

$$Scum = 100(1 - Mcum)$$

Quotient analyses

Quotient analyses techniques were used to characterize geographical preferences of fish ELS (Van der Lingen *et al.* 2001, Ibaibarriaga *et al.* 2007). In this method, the covariate of interest is divided into classes of bottom depths, the percentage of stations and the percentage of total abundance per class are compared using the quotient:

$$Q_i = \frac{A_i / \sum_i A_i}{N_i / \sum_i N_i}$$

where N_i and A_i denote, respectively, the number of stations and total abundance per class i .

Values greater than 1 ($Q_i \geq 1$) indicate an apparent prevalence of the species for particular depth classes.

Egg production and larval abundance

The egg production in eggs $m^{-2} day^{-1}$ was calculated for each sampled station. This production was based on the observed number of stage I eggs, the time it takes for an egg to pass through this stage at a temperature observed at 20 m depth, and the filtered water volume at the station. The time that the eggs spend in stage I was calculated from the formula given by Lockwood *et al.* (1981) and Pipe and Walter (1987). Productions in eggs $m^{-2} day^{-1}$ were extrapolated then to the area of the ICES rectangle that they represent (ICES, 1996).

The 25-day-old mackerel larvae abundance was calculated following the same methodology as for eggs. After establishing the larval abundance in larvae m^{-2} for each sampled station, the total abundance for cruise was determined as the sum of individual abundance per rectangle.

Sardine egg production in Spanish waters was provided from ICES WGMHSA (ICES, 2007). These data correspond to the years when the daily egg production method (DEPM) was carried out, namely, 1999, 2002, and 2005. As such, there is a mismatch with those for in which the mackerel and horse mackerel AEPM was executed.

Hydrological model and Lagrangian transport

The high-resolution 3D prognostic Regional Ocean Model System (ROMS, Shchepetkin and McWilliams 2003), driven by detailed atmospheric, hydrologic and

oceanic forcing, was used to simulate oceanic circulation and then evaluate its influence on egg and larvae distribution and survival. The model was also used to evaluate Lagrangian transport of passive particles assumed here to represent larvae. The model domain covers the whole of the Bay of Biscay, extending from the French and Spanish coasts (40.5°N) to the south of the United Kingdom (about 52.5°N) and to 13°W. The present model configuration of the whole of the Bay of Biscay is an extension of one limited to the south of the region developed by Ferrer *et al.* (2009). The bathymetry was obtained by interpolation, following optimisation analysis, of the two-minute digital Elevation TOPOgraphic model (ETOPO2, Smith and Sandwell 1997), General Bathymetric Chart of the Oceans (GEBCO), and International Bathymetric Chart of the Mediterranean (IBCM) data sets. ROMS for the Bay of Biscay computes the primitive equations on a 6.6-km grid in the horizontal and 32 non-equally distributed σ -levels grid in the vertical. The initial and boundary conditions for temperature and salinity were interpolated on the grid from the World Ocean Atlas 2005 (WOA05). The water level is specified for the initial condition, but also at each time-step along the open boundaries, using the OSU TOPEX/Poseidon Global Inverse Solution version 5.0 (TPXO.5, global model of ocean tides).

After a spin-up of 1 year, the simulation covers the period 1998-2009, with a constant time step of 15 min. The simulated results of currents were averaged for specific periods corresponding to the cruises (Table 1).

Moreover, a modelling experiment of particle tracking was achieved by following Lagrangian 3D trajectories, calculated on-line with ROMS. The depth of the simulated particles was fixed initially at 50 m as eggs and larvae of these pelagic species were predominately in the upper 50 m of the water column (Coombs *et al.* 2001). The simulated particles were released on four dates, identical for the three years: 20 April, 1 May, 10 May and 20 May. These dates correspond to periods prior to and during the May cruises. For the three simulations (1998, 2001 and 2004), the initial positions of the particles were similar. They were evaluated using all the observed egg positions during the three March-April cruises in 1998, 2001 and 2004. A total of 137 particles were released for each period.

For the three years, in each period the percentage of particles offshore (station depth >1000 m) was calculated for the initial positions and after 1 month of simulated transport: 20 April-20 May; 1 May-1 June; 10 May-10 June; and 20 May-20 June. Differences in percentages between initial positions and those after 1 month of transport were calculated, representing an "offshore transport index" for each of the periods:

$$T = P_{offshore}(t) - P_{offshore}(init)$$

where $P_{offshore}(init)$ and $P_{offshore}(t)$ are the percentage of offshore particles respectively initially (initial file of

TABLE 1. – Summary of main characteristic of sampling: date, number of samples analysed, temperature (°C) at 20 m depth, and total number of eggs and larvae sorted.

Survey	Date	N of samples	Mean temperature	Total eggs	Total larvae
Triennial 98	26 March-4 April	66	11.0	10701	1686
Triennial 98	19 May-7 June	46	14.2	3425	1165
Triennial 01	10-18 April	44	12.9	14130	5956
Triennial 01	14 May-8 June	45	14.7	14926	3856
Triennial 04	24 March-11 April	103	11.7	34114	12808
Triennial 04	2-22 May	54	12.9	36313	6792
Total		358		113609	32263

particle positions) and at a time t which corresponds here to 1 month.

Chlorophyll a and recruitment data

Chlorophyll a (chl a) values were abstracted from the “Daily Mapped SEAWIFS chlorophyll a concentration” (NASA ocean-colour, with a resolution of 9 km). Each chl a concentration data point was calculated as the mean value of a 45×45 km window around the stations where larvae were present. Afterwards, for each year and period a mean and standard deviation was derived.

Indices of recruitment for each species were compiled from the ICES group (ICES, 2008a,b). This information was obtained by the FLICA assessment method for mackerel, the SAD08 assessment model for horse mackerel and Assessment model Combining Information (AMCI) for sardine. These data correspond to the complete stock of these species, which cover the whole area of the Northeast Atlantic waters for mackerel and horse mackerel and Iberian Peninsula waters for sardine.

Correlation indices between egg production, abundance of larvae older than 25 days and recruitment were calculated.

RESULTS

Egg and larva distribution

A total of 113609 eggs and 32263 larvae were removed from 358 Bongo plankton samples (Table 1). The species *Scomber scombrus* (mackerel), *Trachurus trachurus* (horse mackerel) and *Sardina pilchardus* (sardine) represented a high percentage of the ichthyoplankton collected during this study in March and April (>80% of eggs and 50% of larvae). In May, this percentage decreased dramatically for eggs (37.5%), but was similar for larvae (56%). In March and April, the predominant eggs were those of sardine in 1998 and mackerel in 2001 and 2004. In May 1998, horse mackerel eggs were predominant (55%). For 2001 and 2004, the most abundant were sardine eggs, representing 12% and 26% of the total eggs, respectively. For all of the periods the larvae of sardine were the most abundant, with a maximum of 76% of all of the larvae in May 1998.

The original data of eggs and larvae abundances are mapped in Supplementary material Appendix 1. For a synthesized view, the quotient analyses of each species of eggs and larvae with respect to water depth are plotted in Figure 2a. These quotient analyses revealed inter-annual differences. In 1998, most of the eggs and larvae were found on the continental shelf, except for mackerel larvae which were found on the shelf break. Horse mackerel eggs showed the most coastal distribution. In 2001 and 2004, eggs of mackerel and horse mackerel were found on the shelf break while sardine eggs were distributed mainly at water depths of less than 200 m. Mackerel and horse mackerel larvae distribution were very different in 2001 than in 1998 and 2004. In 2001, the larvae showed an offshore distribution, while in 1998 and 2004 they were found mainly close to the spawning ground on the shelf break. For sardine larvae no distinctive inter-annual variability in spatial distribution was observed. Large and small larvae were found primarily on the continental shelf.

In order to assess any preferential transport of larvae, larval abundances were grouped into two size ranges. The ranges were different for each of the species, in order to represent the species-specific morphological development. Quotient analyses in relation to water depth for different size ranges and species are shown in Figure 2b. For mackerel and horse mackerel, both small and large larvae were located close to the spawning grounds, except in 2001; here, the larger larvae were found mainly within oceanic waters. For sardine, the distribution pattern was similar for the three study years: both small and large larvae were distributed on the continental shelf

Larval survival rates

Table 2 presents the instantaneous mortality (Z), daily mortality rates (M , %) and cumulative survival rates (Scum), with the latter two calculated for: (i) the total range of estimated age which varied from 22 to 40 days, depending upon the survey (upper panel of the table); and (ii) a similar age (20 days) for each species, year and period (lower panel of the table). For comparison, only the latter case is analysed. Larval cumulative survival rates (Scum, %) were very variable among species and between years. The highest and lowest Scum values were estimated for mackerel in

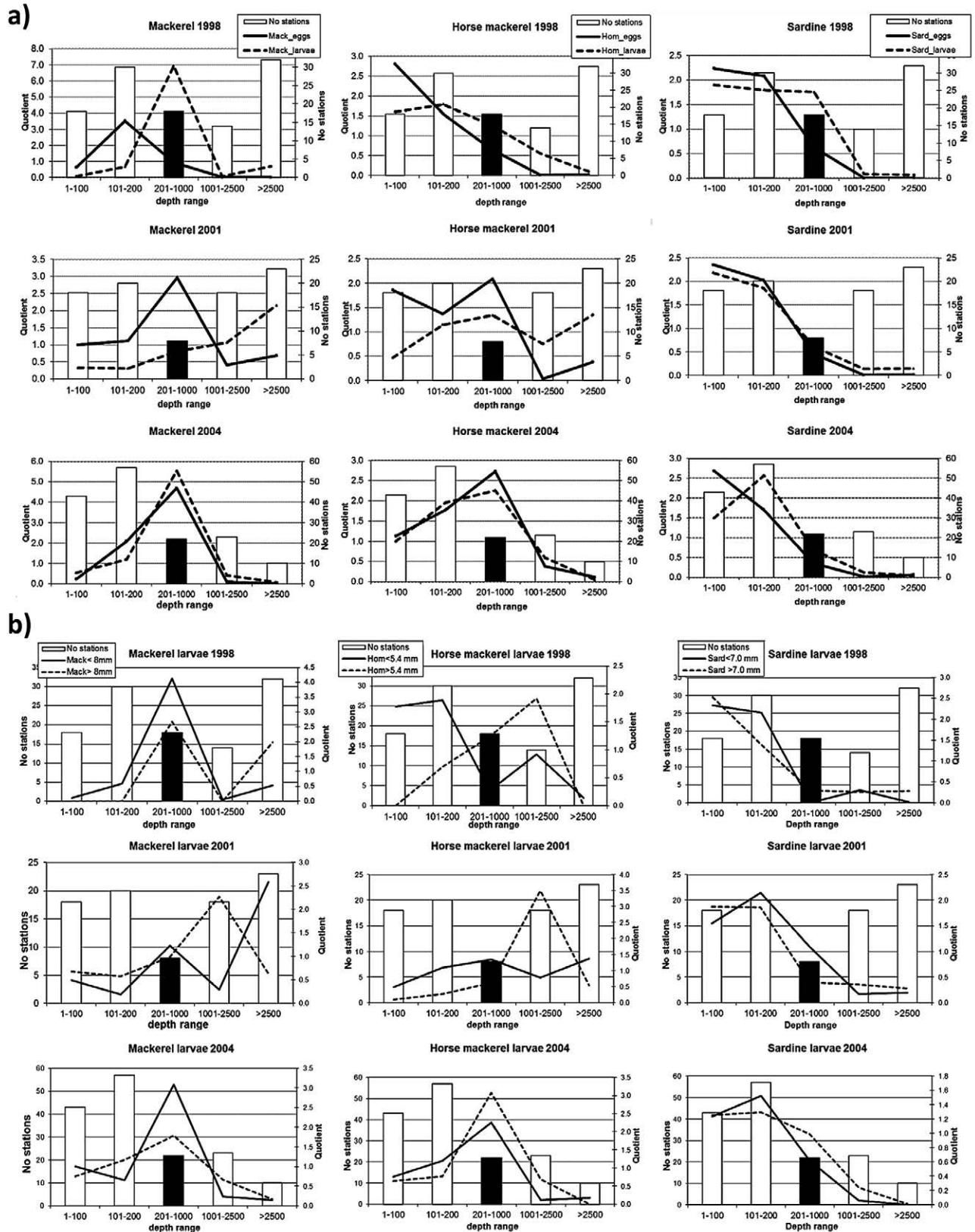


Fig. 2. – Quotient lines of: (a) each species egg and larval abundance and (b) each species larval size abundance with respect to water depth (solid and dashed lines, respectively). The vertical bars indicate the number of samples collected within each water depth class. Black bar represents the shelf break.

TABLE 2. – Values of instantaneous mortality (Z , day^{-1}), daily mortality rates (M , %), percentage of survival for each period and species (Scum), calculated for the maximum interval time recorded in the study. In the lower panel, these calculations were repeated for a standard interval time of 20 days. The last column shows the annual mean value of cumulative survival rate (ScumR), as an average of period 1 and period 2. R^2 , Correlation coefficient and N , number of data points for the equation $N\alpha = N_0 * e^{-\alpha}$; NA, not available

Specie-year	March-April survey (period 1)					May survey (period 2)				
	α (days)	Z (day^{-1})	R^2 ; N	M (%)	Scum (%)	α (days)	Z (day^{-1})	R^2 ; N	M (%)	Scum (%)
MACK-98	22	0.3006	0.57; 5	25.96	0.13	45	0.048	0.48; 9	4.69	11.53%
MACK-01	40	0.0820	0.65; 22	7.87	3.76	46	0.102	0.73; 21	9.70	0.92%
MACK-04	27	0.4190	0.97; 13	34.23	0.00	35	0.167	0.81; 13	15.38	0.29%
HOM-98	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
HOM-01	39	0.1911	0.82; 20	17.40	0.06	54	0.0825	0.72; 28	7.92	1.16%
HOM-04	32	0.1823	0.66; 16	16.66	0.29	30	0.2012	0.92; 19	18.23	0.24%
SARD-98	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
SARD-01	27	0.2696	0.92; 23	23.63	0.07	22	0.2279	0.90; 20	20.38	0.66%
SARD-04	33	0.2163	0.97; 23	19.45	0.08	32	0.2632	0.96; 27	23.14	0.02%
	α (days)	Z (day^{-1})	R^2 ; N	M (%)	Scum (%)	Z (day^{-1})	R^2 ; N	M (%)	Scum (%)	Annual mean ScumR
MACK-98	20	0.1778	0.47; 4	16.29	2.86	-0.146	0.89; 5	13.58	5.39	4.12%
MACK-01	20	0.113	0.42; 9	10.68	10.44	-0.142	0.68; 18	13.24	5.84	8.14%
MACK-04	20	0.409	0.97; 9	33.57	0.03	-0.148	0.82; 6	13.76	5.18	2.60%
HOM-98	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
HOM-01	20	0.263	0.87; 17	23.13	0.52	-0.189	0.86; 16	17.22	2.28	1.40%
HOM-04	20	0.393	0.93; 13	32.50	0.04	-0.191	0.83; 12	17.39	2.19	1.12%
SARD-98	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
SARD-01	20	0.274	0.85; 18	23.97	0.42	-0.212	0.88; 19	19.10	1.44	0.93%
SARD-04	20	0.218	0.96; 18	19.59	1.28	-0.231	0.96; 16	19.18	0.99	1.13%

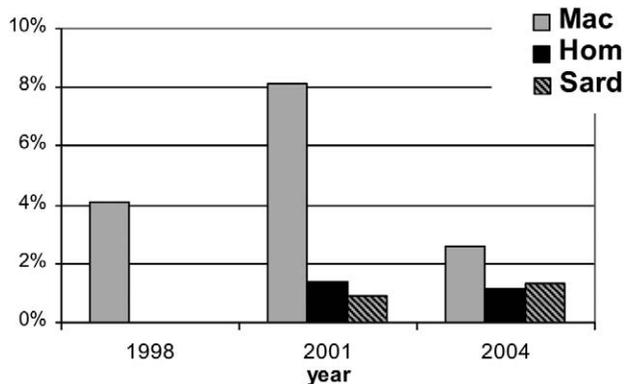


FIG. 3. – Histogram of mean survival rates (%) in the Bay of Biscay for each species of larvae calculated as an annual average (including period 1 together with period 2).

March 2001 ($S=10.4\%$) and in March 2004 ($S=0.03\%$) respectively.

Analysis of variance was applied to test whether there are any significant differences among the annual means of cumulative survival rate (ScumR) for the species (Fig. 3). The results of the ANOVA indicated significant differences between the mean of ScumR, at the 95% confidence level ($F=4.31$; $P=0.0414$). The mean of mackerel larvae, ScumR (4.95%), was statistically higher than those for horse mackerel (1.25%) and sardine (1.02%). These differences were investigated in detail, including in the ANOVA two factor levels: years and periods. Neither years nor periods were found to have any statistically significant effect on the ScumR, even when the ScumR for mackerel and horse mackerel were higher in 2001 than in 1998 and 2004.

Egg production, larval abundance and recruitment

Figure 4 shows daily egg production (DEP), estimated by year for mackerel and horse mackerel (Fig. 4a). For mackerel, the maximum DEP was in 1998 ($6.39 \cdot 10^{12}$ eggs) and the minimum was in 2001 ($5.11 \cdot 10^{11}$ eggs). For horse mackerel, the DEP was similar in 1998 and 2001 ($2.3 \cdot 10^{12}$ eggs) and lower in 2004 ($1.51 \cdot 10^{12}$ eggs).

The annual evolution of abundance of larvae of mackerel and horse mackerel older than 25 days old and estimated for each year is shown in Figure 4c. For mackerel, the peak of abundance was in 2001 ($1.42 \cdot 10^{11}$ larvae). This abundance reached a mid-level ($5.6 \cdot 10^{10}$ larvae) in 2004 and a minimum in 1998 ($1.25 \cdot 10^{10}$ larvae). For horse mackerel, the differences between the years were lower than those for mackerel. The highest larval abundance was estimated for 2001 ($3.6 \cdot 10^{10}$ larvae) and the lowest in 2004 ($3.79 \cdot 10^9$ larvae).

Sardine egg production in Spanish waters was similar in 1999 and 2005, reaching a minimum in 2002 (Fig. 4b). With respect to old larvae, abundance was much higher in 2004 (Fig. 4d). No data of old sardine larvae could be determined for 1998, because data on the individual standard length of larvae were not available.

Recruitment estimates for these three pelagic species are shown in Figure 4e,f. The abundance of mackerel and horse mackerel recruits (Fig. 4e) had a dome-shape: a maximum value in 2001 and lower values for 1998 and 2004. For sardine, a continued increase in recruit abundance was estimated from 1998 to 2004 (Fig. 4f).

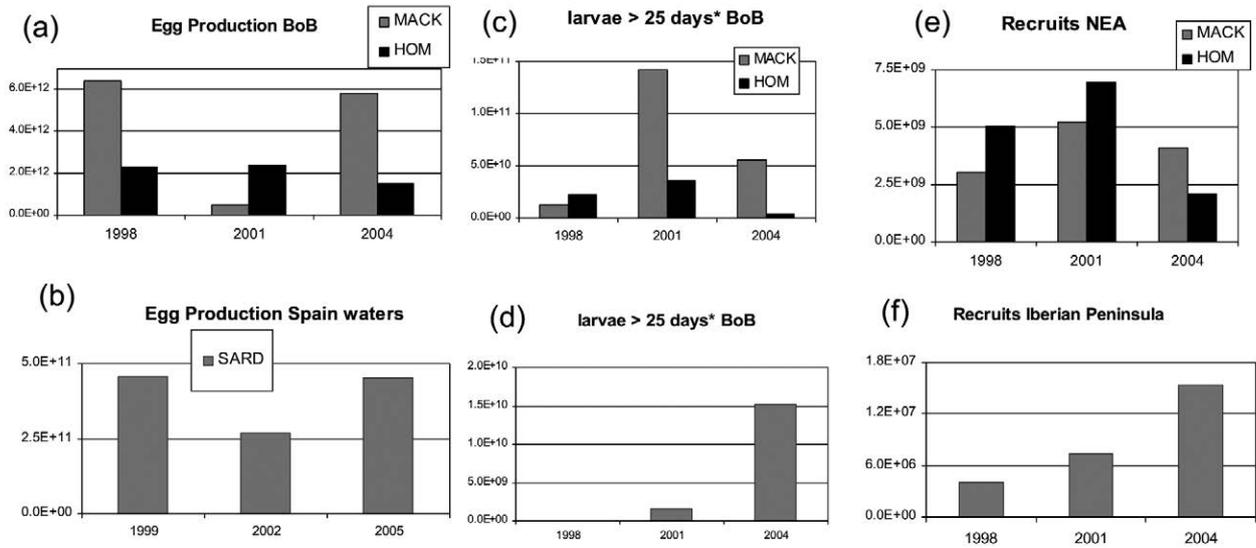


FIG. 4. – (a) and (b) estimates of egg production, (c) and (d) abundance of larvae older than 25 days in the Bay of Biscay, and (e) and (f) recruits in the whole area of population distribution for each species. BoB, Bay of Biscay; NEA, northeast Atlantic.

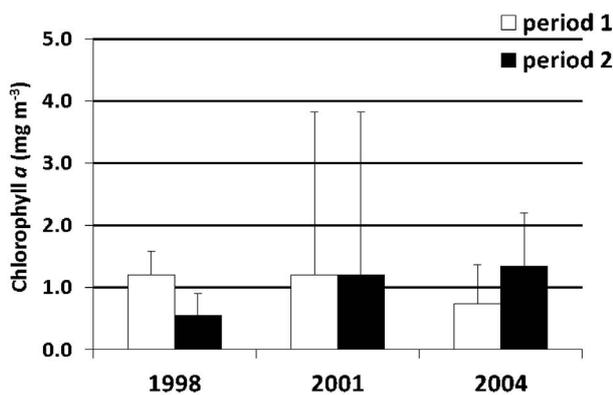


FIG. 5. – Histogram of mean chlorophyll *a* abundance (mg m^{-3}) for the three years and two periods (see text for more details).

Abundance of Chlorophyll *a*

Annual variability in the mean value of chl *a* and its standard deviation (SD), by periods and years, is shown in Figure 5. Small variations were observed between years or periods, although the tendency between periods was somewhat different. In 1998, the mean chl *a* was highest in period 1 (March–April), whereas in 2004 it was highest in period 2 (May). In 2001, similar values of mean chl *a* concentration were calculated for periods 1 and 2; however, the SD within the periods was very high.

Circulation and transport

Figure 6 shows the 40–60 m layer simulated circulation in the Bay of Biscay, averaged every 15 days in April and May for three years (1998, 2001 and 2004). At the beginning of April, the sub-surface circulation was fairly similar in 2001 and 2004; it was stronger

in 1998. From mid-April until the end of May 2001, the slope current was almost absent, while it was much stronger in the same period in 1998 and 2004. This characteristic of the water circulation in 2001 also appears unusual when compared with the same period in 2002 and 2003 (simulated results not shown). In April 1998, the simulated sub-surface current was strong in the southeastern corner of the Bay of Biscay, in an eastward direction along the northern Spanish coast and a northward direction over the shelf along the Aquitaine coast. In 2001 and 2004 this circulation was not so strong.

The simulated westward transport and the mesoscale activity in the open sea were more intense in April and May 2001 than in the same periods in other years. In particular, we observed a strong simulated westward current located approximately along the latitude of 45°N, from the slope through to the open sea, where mackerel and horse mackerel larvae were observed. These water circulation characteristics induced an unusual cross-slope transport in 2001, whereas the transport was along the slope and over the shelf in 1998 and 2004. This pattern could then allow the eggs and larvae to reach the open sea region.

In order to analyse the above hypothesis, a numerical Lagrangian experiment was performed. The Lagrangian trajectories of particles released in the model are shown for one month in Figure 7. In the simulations for 2001 (centre panels), we observe a stronger westward transport between 44°N and 46°N than in the two other years. Moreover, in 1998 and 2004, the tendency was a strong poleward transport along the slope (Fig. 7b, on the right and left panels); retention and low transport predominated on the slope and shelf in 2001. For the three years, a strong retention zone was simulated in the southeastern part of the Bay of Biscay, with the presence of particles encapsulated within ed-

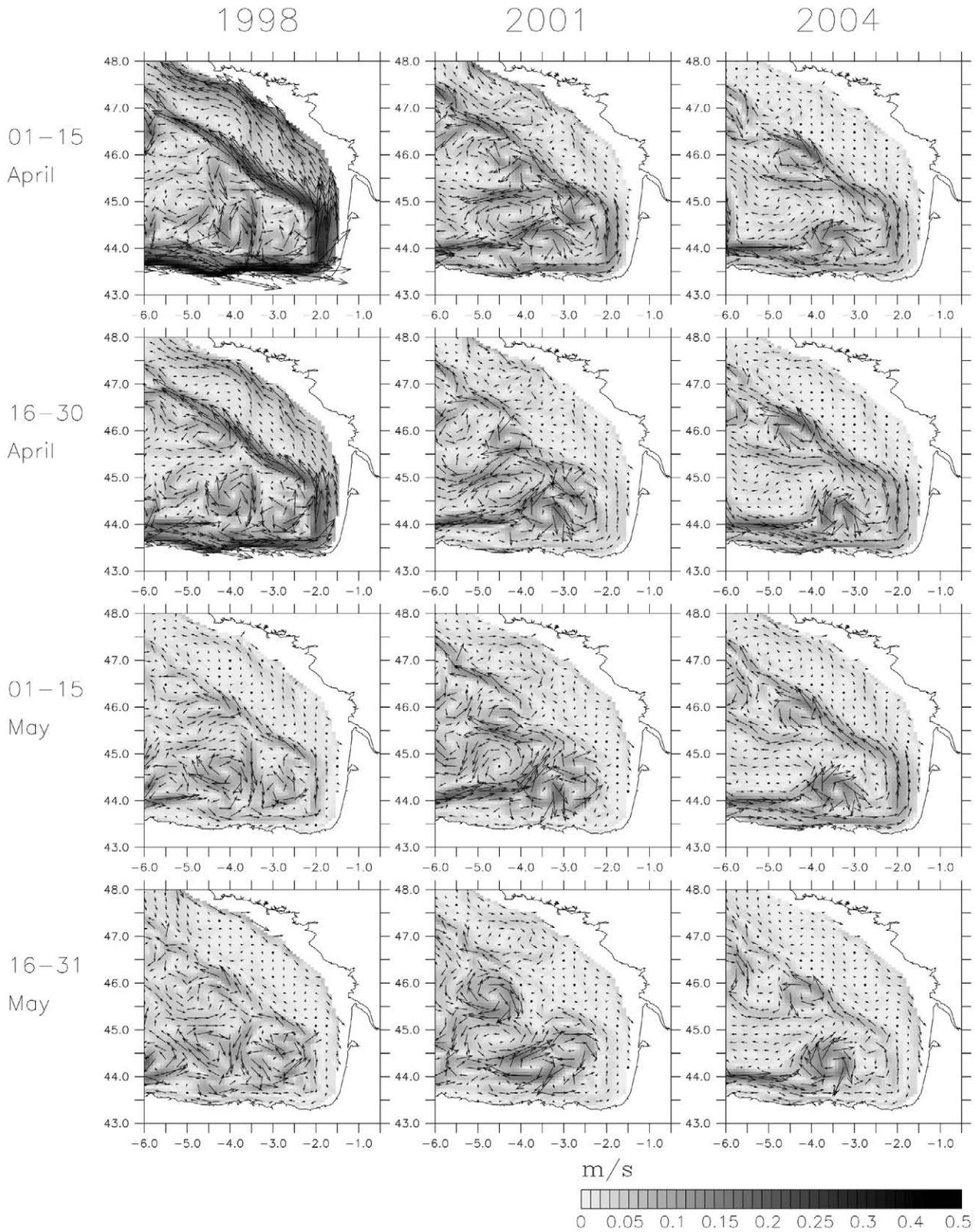


FIG. 6. – Simulated circulation at 40-60 m depth in the Bay of Biscay for 1998, 2001 and 2004. Data are averaged every 15 days (for more details, see text).

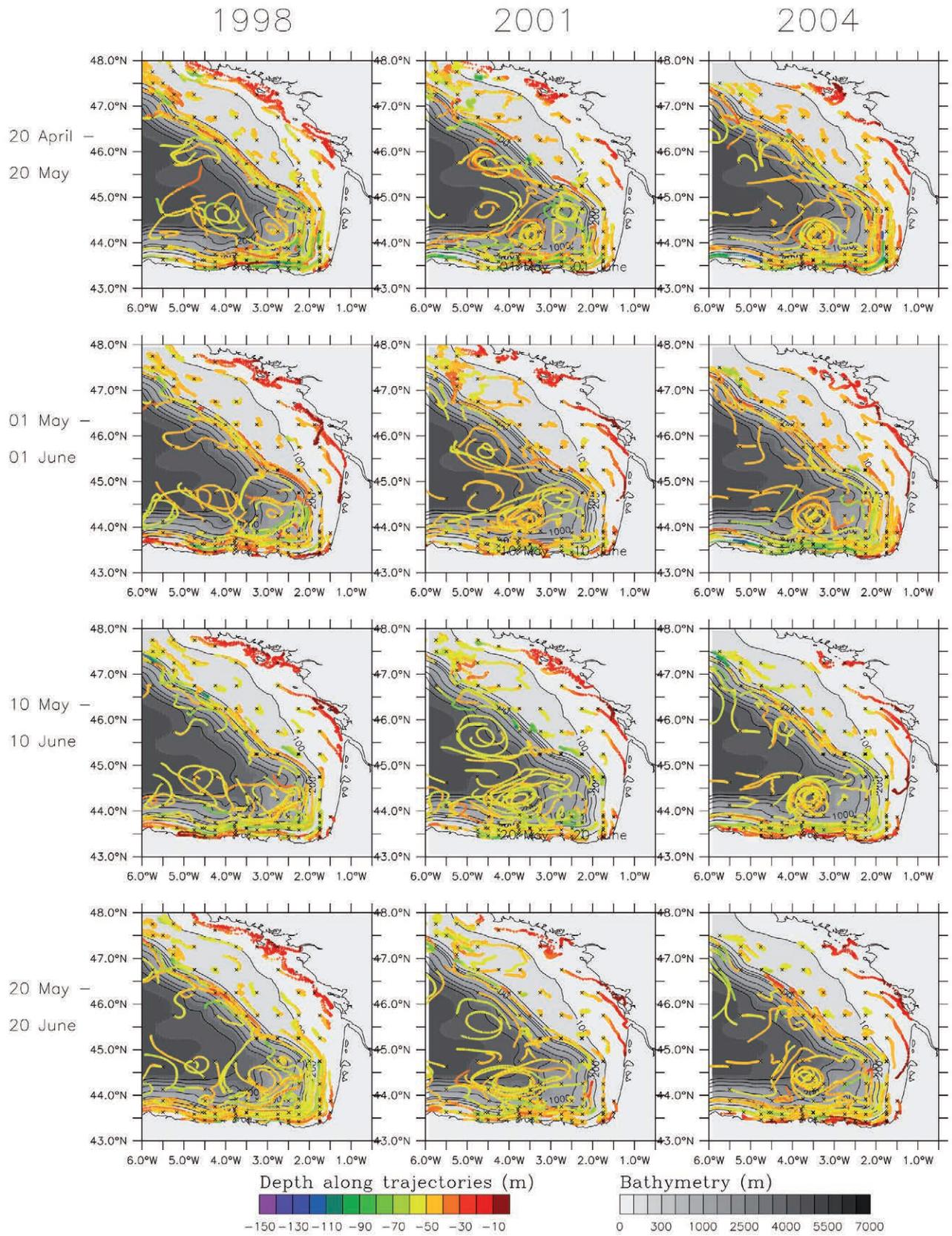


FIG. 7. – One-month Lagrangian trajectories of particles released in the ROMS-model. The depth of simulation is 50 m. Crosses on the upper chart indicate initial positions of particles in the simulation.

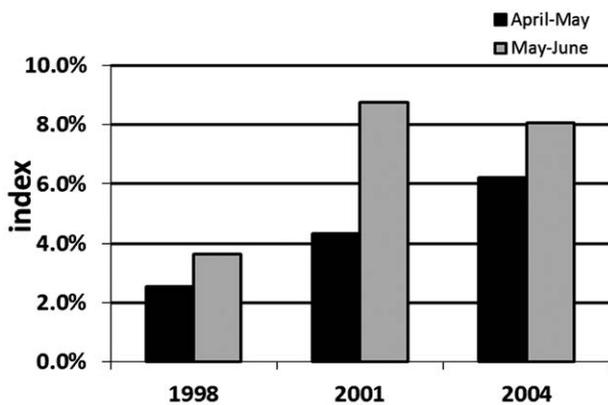


FIG. 8. – Offshore transport index (as %) of particles across the 1000 m isobath for the three years and two periods (see text for more details).

dies. The offshore transport index for each period and each year is shown in Figure 8. The period April-May corresponds to a mean transport of the 1st and 2nd simulations (20 April-20 May and 1 May-31 May), whereas the period May-June corresponds to the mean transport of the 3rd and 4th simulations (10 May-10 June and 20 May-20 June). The offshore transport across the 1000 m isobath was at its lowest in 1998. In 2001, the transport across the 1000 m isobath was offshore for both of the periods, reaching a value of 4.3% in April-May, while the highest value of the three years was 8.7%, in May-June. In 2004, the transport was always offshore, with absolute values of 6.2% and 8.0%, respectively, for both periods.

DISCUSSION

Ichthyoplankton studies provide important information on the localisation of spawning habitats. The spawning grounds depend, first, on initial spawning positions (the release of eggs by the parental stock) and, second, on the hydrographical features acting upon this initial distribution. Climatic and hydrological variations in the ocean are known to control a large fraction of the spatial and temporal variability in marine populations, from primary production to top predators. Hydrodynamic models are a tool for integrating these variables and exploring interaction mechanisms related to recruitment processes. Several studies had been made for cod, sprat and haddock (Hinrichsen *et al.* 2002, Baumann *et al.* 2006, Lough *et al.* 2006) in the Baltic sea and the George Bank. In the area of the Bay of Biscay, Allain *et al.* (2007a,b) and Irigoien *et al.* (2007 and 2008) focused these studies on anchovy. Contradictory conclusions on the effect of offshore drift on anchovy recruitment are a matter of discussion. Recently, Huret *et al.* (2010), applying a Lagrangian model, concluded that spawning location had a dominant effect on the ending positions of particles. Thus, spatial variability of the dispersal is more important than seasonal variability.

Over large scales, changes in ocean circulation patterns are known to alter the geographical distribution of plankton and fish (Beaugrand *et al.* 2002). Although the mackerel and horse mackerel egg distributions appear to be linked to the presence of a shelf break (ICES 2005, 2008a), yearly and monthly differences were observed in these distributions in 1998, 2001 and 2004. Spawning grounds for sardine are related to the shelf and, in contrast to what was observed for mackerel and horse mackerel, the sardine egg distribution remained invariable throughout the three years. Larval spatial distributions are more influenced by the hydrological conditions than eggs because larval stages stayed in the water column for longer than egg stages (weeks vs. days). We observed that small larvae generally showed a similar preferential distribution to eggs, but large larvae did not. This fact was especially significant in 2001, when neither small larvae nor large ones appeared to have a typical planktonic distribution: the exclusive presence of larvae offshore suggested a strong influence of regional events on ELS fate. At a regional scale, a number of processes such as upwelling, tidal fronts, eddies, jet currents and river discharges are also known to modulate the regimes of production and distribution of marine species (Mann and Lazier 1991, Bakun 1996). Thus, these features of the marine environment are responsible, at least partially, and through complex webs, for year-to-year fluctuations in abundance and spatial distribution of marine fish populations. As can be seen in Figure 6, the water circulation characteristics in 2001 appeared unusual in comparison to other years; they were characterized by an intense cross-slope transport and high mesoscale activity in the open sea waters. The offshore transport index calculated for the three years highlights this particular feature: the offshore transport was especially high in May-June 2001. These specific features were ultimately responsible for the inter-annual differences in spatial distribution, as the Lagrangian experiments predicted (Figs. 7 and 8). The immediate consequences of this inter-annual variability in sub-surface circulation are that larvae located on the shelf break were transported offshore; likewise, this transport was especially intense in 2001. This pattern would suggest that the future of larvae could be intricate. The circulation in 2004 was intermediate, with an offshore transport index in April-May and an inshore one in May-June. Hence, special circulation in spring 2001 explains, at least partially, the unusual location of mackerel and horse mackerel eggs and larvae observed during this year.

Can these differences in distribution affect larval mortality/survival? Instantaneous mortality rates were relatively low (Table 2), except for mackerel in March-April 2004. Houde and Zastrow (1993) estimated some 21.3% of mortality for marine fish larvae. For mackerel mortality rates of 10-60% have been reported by Kendall and Gordon (1981), Ware and Lambert (1985) and Morse (1989). Despite these relatively low mortality rates per day (11% for mackerel in 2001 to 34% for

mackerel in 2004), the percentage of survivors calculated for a standard interval time period (20 days, see Table 2) shows the extremely high loss of larval biomass that occurs during this period of the life cycle. In the best circumstances, the survival rate reached 10.4% for mackerel in April 2001; nevertheless survival rates lower than 1% appear to be more common.

Statistically significant differences in survival rates were found between species ($P < 0.05$); this means that, during this period of the life cycle, the environmental conditions have different impacts according to the species.

In relation to food availability, the impact of starvation on larval mortality is a difficult variable to measure because poorly nourished larvae become highly vulnerable to predation. Starving or poorly developed larvae are therefore rarely found. Although no direct measures of food availability have been recorded, food conditions are indirectly available using surface chl *a* biomass obtained from SeaWiFS data. Except for sardine, the spatial distributions of larvae do not appear to be especially linked to coastal zones but occur on the shelf break or offshore, where the values of surface chl *a* are commonly assumed to be low or medium during the periods considered. The mean chl *a* (mg m^{-3}) calculated for the area of presence of larvae for each year and period does not show great inter-annual differences (Fig. 5). However, even if the mean chl *a* estimated for the two periods in 2001 were similar, a high standard deviation was calculated; this means that the surface chl *a* biomass showed high variability at the larvae positions in 2001. The presence of larvae in the open sea in May 2001 seems to suggest that this area was not as deficient in food as was expected. Bearing in mind the limitation of the information on food availability, the indirect observations suggest that food was not a limiting factor for the larvae transported offshore in our study.

The abundance of larvae older than 25 days was calculated and considered as a survival rate index (Fig. 4c,d). Larvae older than 25 days were more abundant in 2001 for mackerel and horse mackerel but not for sardine. This result is in agreement with the survival rates estimated for each year and species, which for mackerel in 2001 was twice and three times the values of 1998 and 2004, respectively; for horse mackerel, it was 25% higher in 2001 than in 2004. However, similar rates were estimated for sardine for the two years (Table 2). The recruitment indices estimated by ICES assessment groups (ICES, 2008a,b) for 1998, 2001 and 2004 are shown in Figure 4e,f. The partitioning between egg production, 25-day-old larvae and recruitment data (early fish stage) allows us to examine how each life history stage interacts with the environment and contributes to the variability between recruits and spawners (Paulik 1973, Rothschild 2000). Correlation between these different parameters is shown in Figure 9. The best correlation was obtained between old larval abundance and recruits. Absence of correlation between egg production and recruits has classically

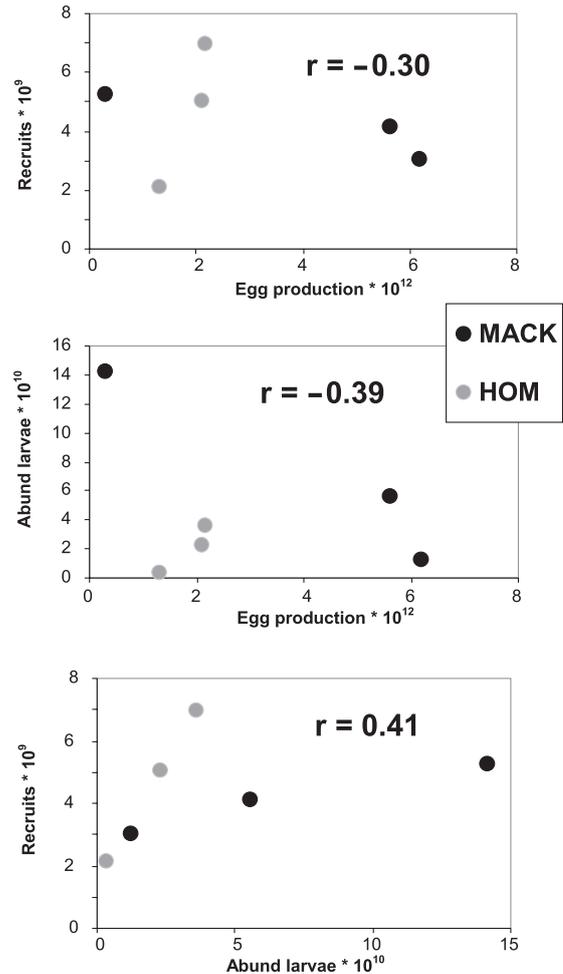


FIG. 9. – Graphs showing the correlations between: (a) recruit and egg production; (b) abundance of larvae more than 25 days old, and (c) egg production and recruits and abundance of larvae more than 25 days old.

been reported for several species, showing high mortality rates affecting the fish population, from ELS to juveniles. However, as we are able to measure more advanced development stages of ELS, the correlation with recruitment improves. Additionally, higher old larval abundance does not result from high egg production rates, supporting the non-functional relationship between stock size and recruitment; however, it matches the higher survival rates during the first 20 days of life (Fig. 3).

In conclusion, we believe that the transport of larvae offshore does not necessarily have a negative effect on recruitment, as long as nutritional factors do not become limiting for larval growth. We found that higher larval survival rates were related to higher old larval abundance and to higher recruitment. Surprisingly, the maximum survival rates were estimated when hydrological conditions appeared not to be favourable, i.e. intense offshore transport. The Bakun (1996) hypothesis was developed within the context of upwelling ecosystems. Indeed, in areas with intense upwelling on

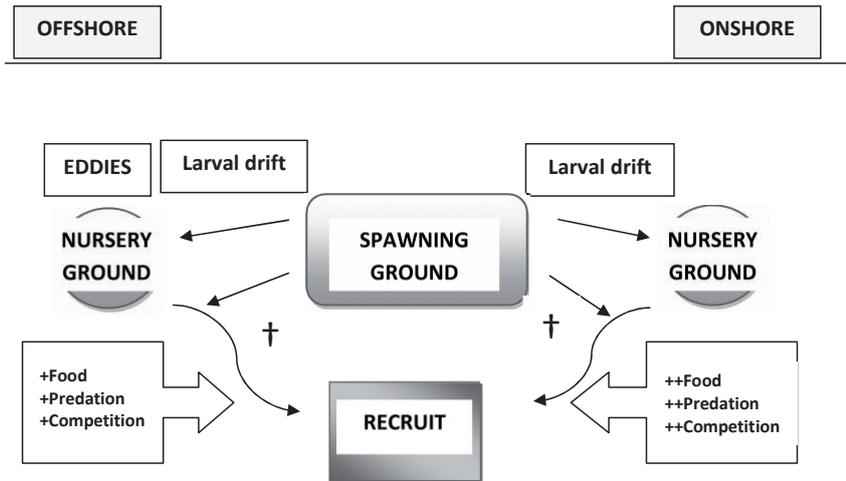


FIG. 10. – Schematic representation of ELS dynamics from the spawning ground to nursery ground derived from this study. Persistence of eddies offshore seems to contribute positively to larval survival.

the continental shelf and coastal margins, fish larvae will benefit from increased productivity associated with upwelling. However, this is not the case for the Bay of Biscay, where the upwelling phenomenon is relatively poor or very localised. Hence, it would appear that the advantage of being transported offshore is not always so evident. At least in early spring, no significant differences in surface chl *a* concentration were observed between inshore and offshore areas. In these conditions, being transported offshore can certainly be beneficial for larval growth: (i) temperatures tend to be warmer than in coastal areas, which are influenced by large rivers; and (ii) zooplankton size and abundance gradient distribution have been observed from highly productive coastal waters close to the mouth of Gironde River, up to the shelf edge waters (Albaina and Irigoien 2004), smaller individuals and higher concentrations being associated with coastal waters. Moreover, as larvae reach the offshore areas at a relatively high length size and therefore a larger mouth size, the capture of large zooplankton is unlikely to be a limitation. All these factors can help to explain the beneficial effect of being transported offshore on the survival rates of larvae.

Finally, Figure 10 shows a schematic representation of mechanisms affecting the fate of fish eggs and larvae, derived from this study. For both mackerel and horse mackerel, spawning areas are isolated from nursery areas. Advective and retention pathways to nurseries and dispersal/advective losses occur throughout the spawning season. Basically, our results support the conceptual model of Harden-Jones (1968), the “Triangle of Migration”, in which successful denatant drift of larvae from spawning grounds to nurseries is hypothesized to lead to high survival. The denatant drift is dependent on behaviour of adults in selecting spawning areas and prevailing water circulation patterns. However, a major contribution of our study is that a deviation of the average circulation pattern that favours offshore transport

can, when the circumstances are suitable, contribute positively to recruitment. These conditions appear to have occurred in 2001, when the oceanographic features and/or physical processes seemed to produce safe sites for larvae in offshore areas (a good level of food and, theoretically, lower levels of predation and competition than in onshore nurseries), resulting in an additional contribution to the recruitment.

ACKNOWLEDGEMENTS

We wish to thank the AZTI-Tecnalia laboratory staff for their assistance in the identification of ichthyoplankton and Yolanda Sagarminaga (AZTI-Tecnalia) for providing chl *a* data from satellite images. This research was supported by the Department of Agriculture, Fisheries and Food of the Basque Country Government. This paper is contribution n° 550 from AZTI-TECNALIA (Marine Research Unit). We thank Michael Collins for revising the English of this paper.

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Scient. ed.: J. Salat.

Received November 10, 2011. Accepted January 26, 2012.

Published online May 7, 2012.

SUPPLEMENTARY MATERIAL

The following Appendix is available through the web page <http://www.icm.csic.es/scimar/supplm/sm03298SMA.pdf>

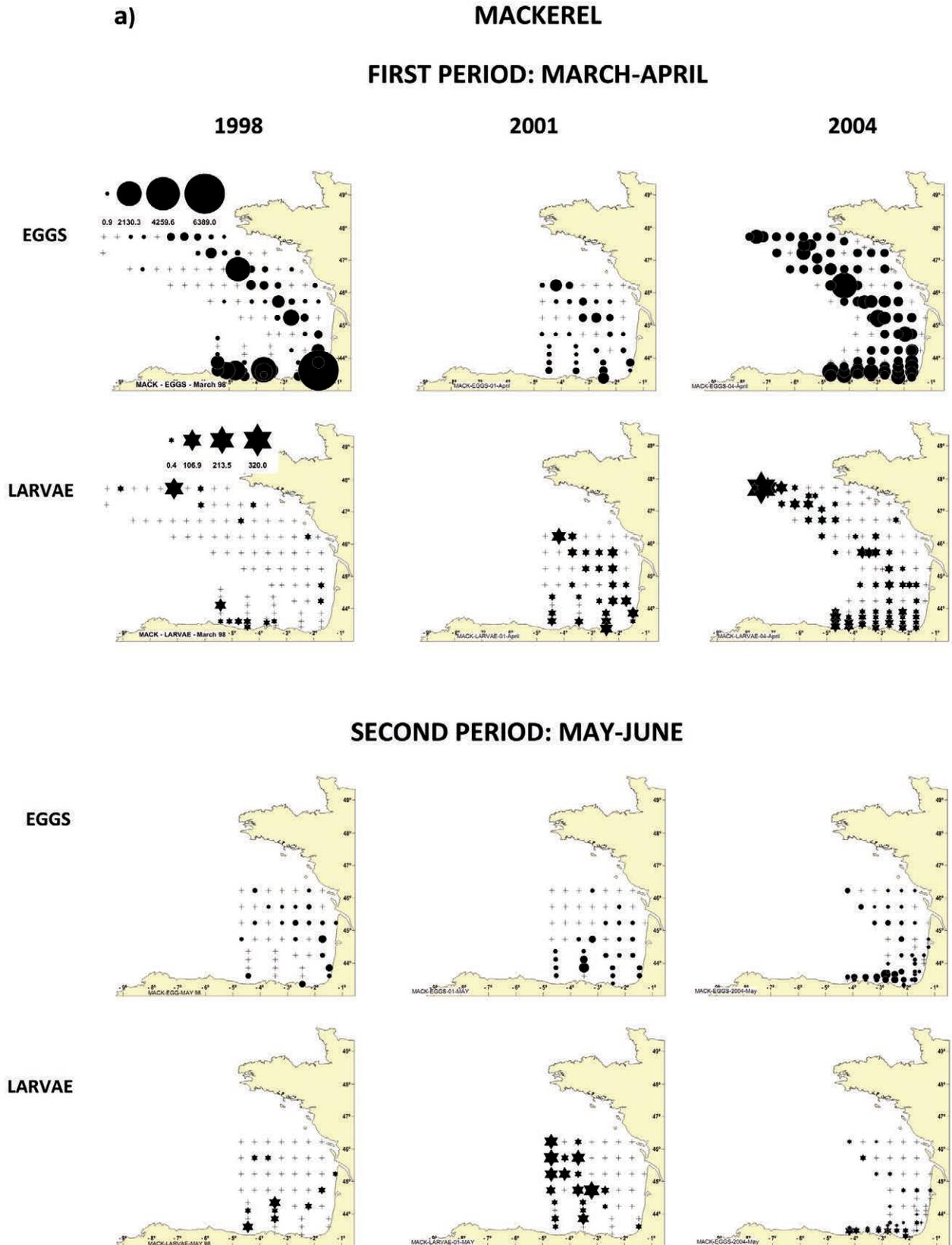
APPENDIX 1. – Maps showing the abundance (number m⁻²) of mackerel (a), horse mackerel (b), and sardine (c) eggs and larvae for each period and year. Crosses indicate stations where neither eggs nor larvae were found.

The fate of eggs and larvae of three pelagic species, mackerel (*Scomber scombrus*), horse mackerel (*Trachurus trachurus*) and sardine (*Sardina pilchardus*) in relation to prevailing currents in the Bay of Biscay: Could they affect larval survival?

PAULA ALVAREZ and MARINA CHIFFLET

Supplementary material

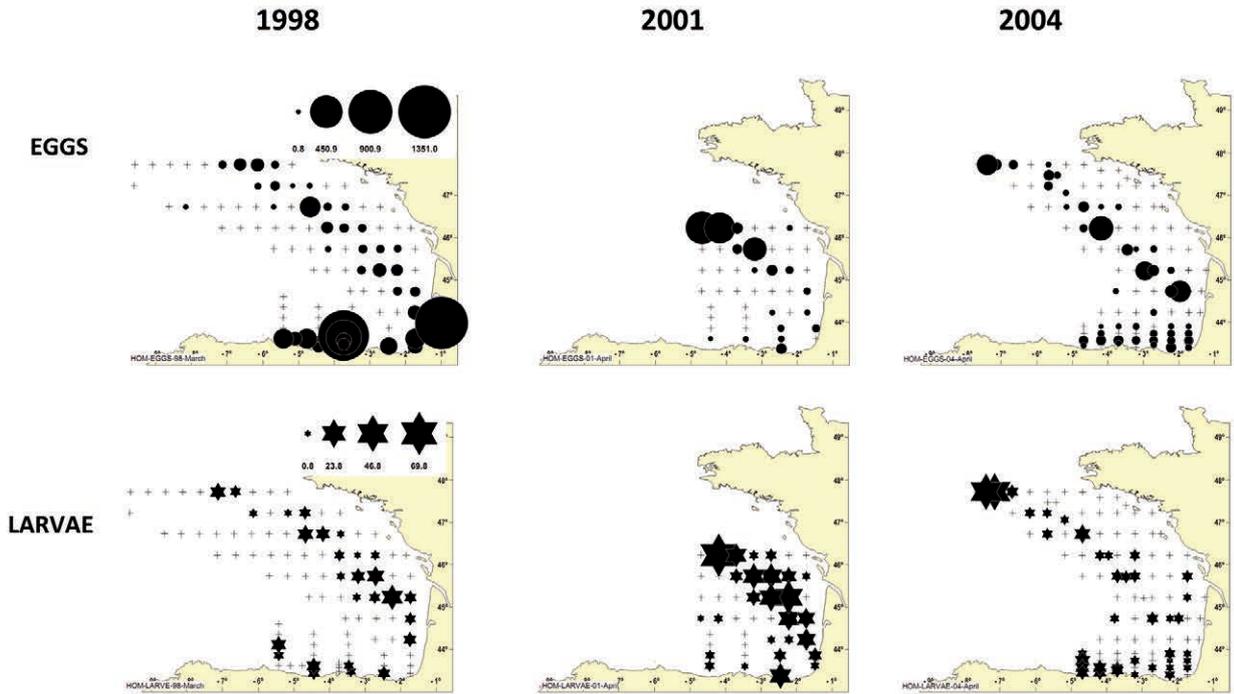
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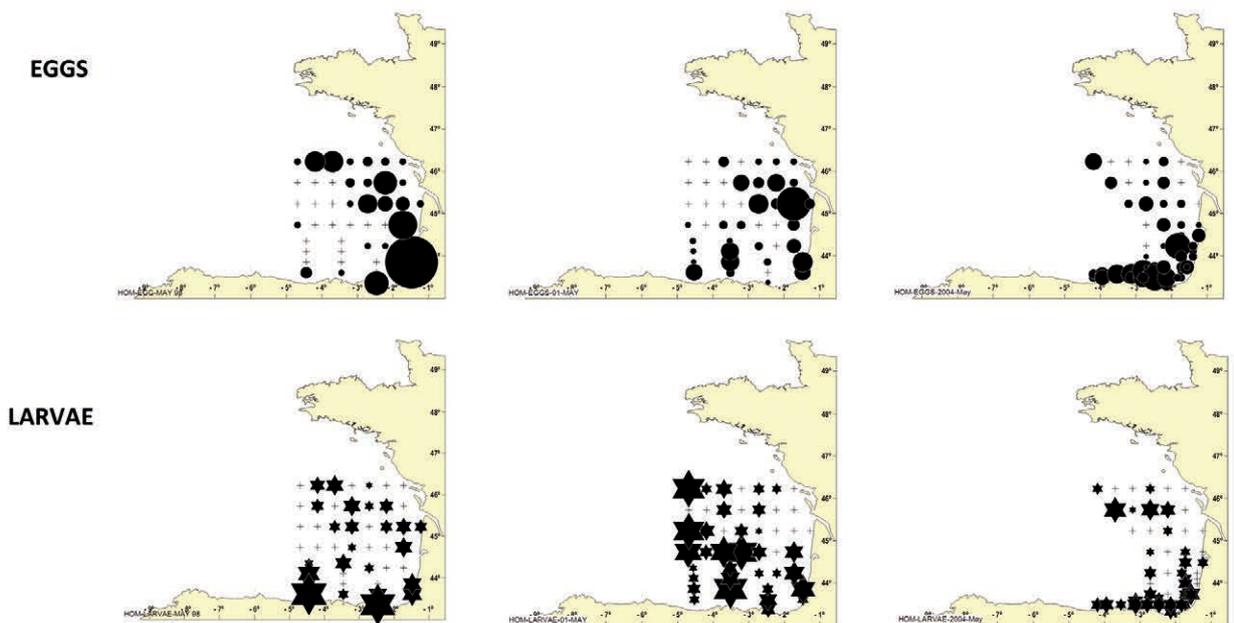
b)

HORSE MACKEREL

FIRST PERIOD: MARCH-APRIL



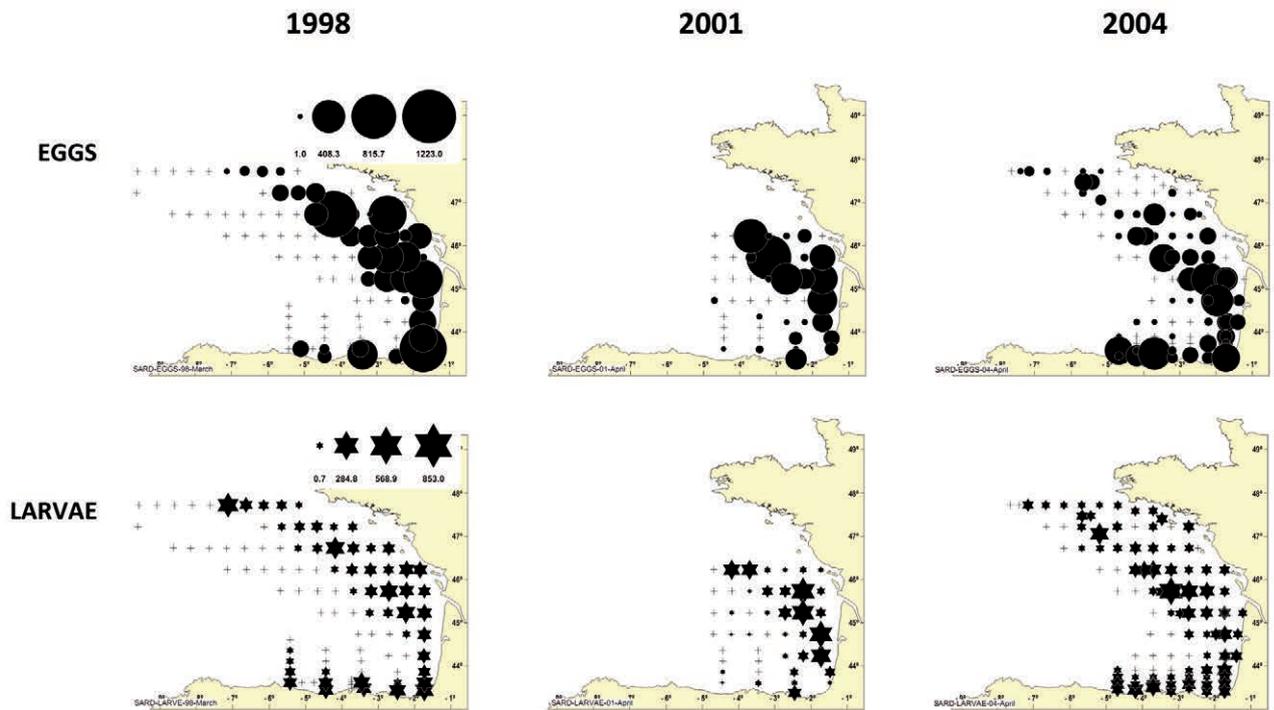
SECOND PERIOD: MAY-JUNE



c)

SARDINE

FIRST PERIOD: MARCH-APRIL



SECOND PERIOD: MAY-JUNE

