Birthdate analysis and its application to the study of recruitment of the Atlanto-Iberian sardine *Sardina pilchardus*

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Abstract.–The ages of 217 juveniles from the Atlanto-Iberian sardine (*Sardina pilchardus*) stock were determined by means of counts of daily growth rings in otoliths. These juveniles were caught by the commercial purse-seine fleet off Galicia (NW Spain) between June and November 1992. The back-calculated hatching period was 13 December 1991 to 2 April 1992, with a mean date of 2 February and a standard deviation of ± 17 days. The original aim of the study was to relate the birthdate distribution of the recruits to environmental, biological, and physical data taken during a series of oceanographic cruises. Oceanographic cruises, carried out between March and July 1992, covered the spring-spawning area of the stock (Cantabrian Sea and coasts of Galicia, the supposed area of origin for the recruits) but such a relationship was not documented because the results of the study showed that most surviving juveniles were spawned before the period considered during the oceanographic cruises. However, the observed birthdate distribution of the recruits, together with hydrographic data, does suggest that a larval drift from the northern Portuguese coasts to the Galician coast took place. Thus, at least in 1992, there is evidence to suggest that the winter-spawning zone, located along the coast of northern Portugal, may have been the area of origin for recruits off Galicia, in contrast to the previous assumption that these fish were spawned in the Cantabrian Sea.

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The Atlanto-Iberian sardine *Sardina pilchardus* (also known as European pilchard [Robins et al., 1991]) is the dominant coastal pelagic fish species along the Atlantic coasts of the Iberian peninsula, as much for the biomass of the stock as for its importance in the pelagic fisheries of Spain and Portugal. Landings, carried out by purse seiners, reached a maximum value for the period 1975–92 of 214,000 metric tons (t) in 1981, and a minimum of 126,000 t in 1992. In the same period, the estimated biomass of the spawning stock varied between 160,000 t in 1976 and 510,000 t in 1985 (Anonymous[1]). An analysis of the abundance trend of the stock (Pestana, 1989) suggests that, in the short term, catches are dependent on recruitment, characteristic of short-lived pelagic species (Ulltang, 1980).

In recent years more intensive work has been done on documenting the oceanographic characteristics for the area of distribution of the Atlanto-Iberian sardine stock. Among these, the most noticeable is the seasonal upwelling that affects the west coast of the Iberian peninsula (Fiuza, 1984; Lavín et al., 1991; Cabanas et al., 1992). Numerous studies have also been carried out on the biological aspects of the species, such as areas and periods of reproduction (Ré et al., 1990; López-Jamar et al., in press; Cunha and Figueiredo[2]; García et al.[3]; Solá et al.[4]), frequency of spawning (Pérez et al., 1992a), batch fecundity (Pérez et al., 1992b), and larval growth (Ré, 1983; Alemany and Álvarez[5]), as well as the spatial distribution by age classes, of which the latter suggests a northward displacement of early age groups as they grow (Porteiro et al.[6]). In this area, the sardine has a protracted spawning season that can last prac-

[1] Anonymous. 1993. Report of the Working Group on the assessment of mackerel, horse mackerel, sardine and anchovy. ICES Council Meeting 1993/H:19, 274 p. (mimeo).

[2] Cunha, E., and I. Figueiredo. 1988. Reproductive cycle of *Sardina pilchardus* in the central region off the Portuguese coast (1970/1987). ICES Council Meeting 1988/H:61, 54 p. (mimeo).

[3] García, A., C. Franco, A. Solá, and M. Alonso. 1988. Distribution of sardine *Sardina pilchardus* egg and larval abundance off the Spanish North Atlantic coast (Galician and Cantabrian areas) in April 1987. ICES Council Meeting 1988/H:27, 8 p. (mimeo).

[4] Solá, A., L. Motos, C. Franco, and A. lago de Lanzós. 1990. Seasonal occurrence of pelagic fish egss and larvae in the Cantabrian sea (VIIIc) and Galicia (IXa), from 1987 to 1989. ICES Council Meeting 1990/H:25, 15 p. (mimeo).

[5] Alemany, F., and F. Álvarez. 1992. Regional growth differences in sardine *Sardina pilchardus* larvae from Cantabrian and Galician coasts. ICES Council meeting, 22 p. (mimeo).

[6] Porteiro, C., F. Alvarez, and J. A. Pereiro. 1986. Sardine (*Sardina pilchardus* Walb.) stock differential distribution by age class in Divisions VIIIc and Ixa. ICES Council Meeting 1986/H:20, 13 p. (mimeo).

tically all year. The main spawning periods, however, are in the spring (April–May) along the northern coast of Spain (Cantabrian Sea) (Solá et al.[4]) and in winter (December–January) off the northern Portuguese coast (Ré et al., 1990). Thus, in a given year, a wide range of likely birthdates exist. Depending on the particular biotic and abiotic conditions that affect survival during the prerecruitment period, the abundance and the age composition (birthdate distribution) of recruits will be restricted, however, to a relatively short period.

An important part of the present study was initiated through Spanish-USA collaboration (Anonymous, 1990) within the framework of the Sardine Anchovy Recruitment Project (SARP). The work carried out in this program continued for the next 3 years under the auspices of a European program that also sponsored research on the sprat *Sprattus sprattus* in the German Bight and the anchovy *Engraulis encrasicolus* within Portuguese estuaries. The original aim of this project was to identify the biological and environmental factors affecting interseasonal larval mortality of short-lived coastal pelagic fish. Birthdate analysis is one of the more relevant tools for the study of recruitment processes (Campana and Jones, 1992). Birthdates of juvenile fishes were first calculated by Methot (1983) who showed that the data can be used to determine periods of high survival. This technique is a key element in the work of SARP, i.e. to test the critical survival-period hypothesis (Hjort, 1914 and 1926) and its later variants (Cushing, 1975; Lasker, 1981; Parrish et al., 1981). Only one paper, in which this technique was applied, is available for the area studied (Alvarez and Butler, 1992). It shows that birthdates of surviving fish occurred at the beginning of a period of calm weather in May and is consistent with Lasker's (1981) stable-ocean hypothesis.

The aims of the present work were 1) to calculate the birthdate distribution of recruits in the stock of the Atlanto-Iberian sardine in 1992, as inferred from daily otolith growth increment analysis; 2) to relate the birthdate distribution of recruits to environmental conditions during earlier development stages; and 3) to verify the previous hypothesis that sardine recruits in the Galician area originate in the Cantabrian Sea.

Material and methods

Age determination

Juvenile sardines were sampled fortnightly, 30 June–19 November 1992, from landings of the commercial purse-seine fleet at the ports of Vigo and La Coruña (Fig. 1), providing a total of 22 samples, each of 50 specimens. These ports are located in the area of recruitment of the Atlanto-Iberian sardine (age-0 fish) (Anonymous[1]). A subsample of ten individuals was taken at random from each sample for birthdate analysis from counts of the daily growth-ring incre-

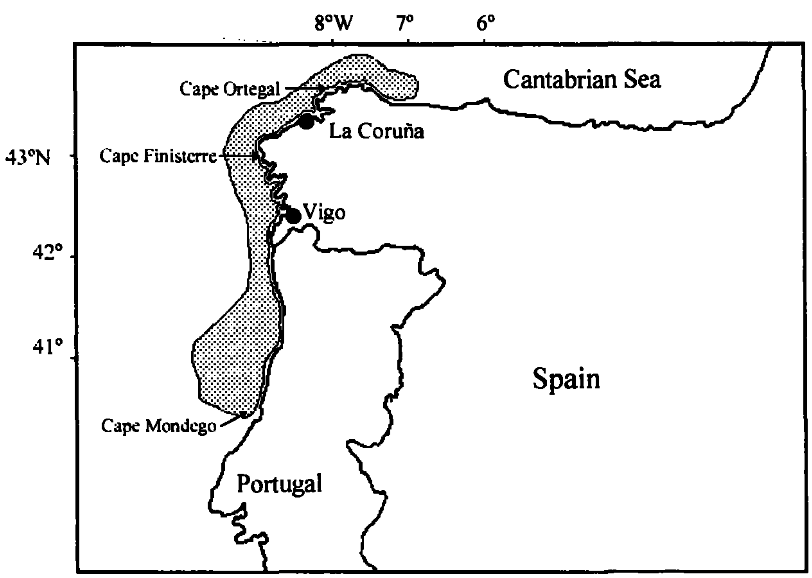

Figure 1
Map of the northwestern Iberian peninsula showing sampling ports (dots) and area of distribution of age-0 sardines, *Sardina pilchardus* (shadowed), during the 3rd and 4th quarters in 1992 (redrawn from Anonymous, 1993).

ments (Methot, 1981). The length ranges by sample of the analyzed specimens (n=220) are given in Table 1. Fish were measured (standard length and total length by 1-mm size classes), weighed (0.1 g), and their otoliths were removed and mounted on microscope slides with Eukitt mounting medium. It is possible to determine the ages of juveniles and their daily growth rates because the daily deposition of growth increments has been validated for sardine (Ré, 1984), the time of formation of the first daily growth ring is known (Alemany and Álvarez, 1994), and because it is possible to distinguish false or subdaily increments from true daily growth rings. It should be pointed out that no gaps were observed in the daily growth rings in the sagittal otoliths of the analyzed specimens. Each daily ring was counted and its width was measured, along a transect located at ± 5° of the longest radius from the focus to the posterior margin of the otolith, with a video coordinated digitizer connected to a microcomputer (Methot, 1981). To reveal increments, the otoliths were progressively polished between readings by using 30-, 9-, and 0.3-micron lapping film. Magnifications of ×60, ×640, and ×1,000 were used. Data from several replicate transects per otolith, at different magnifications, were combined to estimate age. Occasionally, daily increments were difficult to resolve within short (<60 microns) segments of the otoliths. In these cases, widths of rings, and hence their number, were interpolated by using linear approximation based on the widths of previous and later clearly visible daily rings. Data from an otolith reading were rejected as unreliable if the interpolation process affected more than 5% of the readings.

Environmental conditions

During the main sardine spawning season off the northern and northwestern coasts of the Iberian peninsula, 5 cruises were conducted between March and July 1992 (López-Jamar et al., in press). The protocols established during a pilot cruise carried out in April 1991 (López-Jamar et al.[7]) were followed. The

[7] López-Jamar, E., S. Coombs, F. Alemany, J. Alonso, F. Álvarez, C. Barrett, J. M. Cabanas, B. Casas, G. Díaz del Río, M. L. Fernández de Puelles, C. Franco, A. García, N. C. Halliday, A. Lago de Lanzós, A. Lavín, A. Miranda, D. Robins, L. Valdes, and L. M. Varela. 1991. A SARP pilot study for sardine *Sardina pilchardus* off north and northwest Spain in April/May 1991. ICES Council Meeting 1991/L:69, 36 p. (mimeo).

Table 1

Summary statistics for the Atlanto-Iberian sardine *Sardina pilchardus* by port and sampling date in 1992. TL=total length (mm), SD=standard deviation, BD=birthdate, Age=days.

Port and sampling date	Mean TL	SD	Min. TL	Max. TL	Mean BD	Mean age	SD	Min. age	Max. age
La Coruña									
7 Jul	90	6	82	103	18 Jan	173	11	156	193
24 Jul	113	7	105	127	13 Jan	194	13	172	215
9 Sep	116	3	111	122	23 Jan	231	8	216	246
17 Sep	130	3	125	133	21 Jan	243	13	225	265
1 Oct	128	9	121	155	20 Jan	256	19	231	294
6 Oct	126	6	118	135	1 Feb	249	19	228	295
13 Oct	118	11	105	139	1 Feb	254	22	215	298
28 Oct	133	6	121	140	30 Jan	273	13	241	291
4 Nov	115	2	112	120	14 Feb	265	22	217	293
13 Nov	109	3	105	113	13 Feb	275	21	256	290
Vigo									
30 Jun	83	3	77	87	26 Jan	157	5	151	169
8 Jul	89	5	80	97	25 Jan	165	5	154	173
16 Jul	97	3	94	105	22 Jan	177	13	162	207
8 Sep	104	3	92	102	9 Feb	212	11	193	224
22 Sep	112	6	107	127	3 Feb	235	13	218	254
1 Oct	104	5	93	111	11 Feb	234	10	220	247
9 Oct	107	6	99	122	10 Feb	243	7	238	260
14 Oct	113	5	103	120	30 Jan	259	11	240	279
22 Oct	131	6	121	141	8 Feb	259	9	249	273
27 Oct	138	13	101	145	1 Feb	270	14	254	292
11 Nov	122	4	117	132	1 Mar	258	17	231	280
19 Nov	121	8	112	137	23 Feb	271	11	247	287

seasonal production and distribution of sardine larvae and their nutritional condition were determined during these cruises as were the spatial and temporal distributional patterns of larvae in relation to hydrographic and biological parameters. During the first 3 cruises, additional transects were located in French waters to estimate the extension of spawning in the northeastern area of the Cantabrian Sea. In the western area, spawning during these months is very low from Cape Finisterre southwards (García et al., 1992); therefore sampling was curtailed at the Portuguese border. The sampling design for the present study did not cover, either spatially or temporally, spawning along the entire Iberian peninsula, because sampling on the Portuguese shelf during winter was not possible owing to logistical reasons. Sampling of this area was not considered important because other studies (Robles et al., 1992; Cabanas et al.[8]; Roy et al.[9]) have suggested that recruitment of the Atlanto-Iberian sardine stock depends mainly on spring spawning in the Cantabrian Sea, as well as on upwelling features along the west coast of the Iberian peninsula.

[8] Cabanas, J. M., C. Porteiro, and M. Varela. 1989. A possible relation between sardine fisheries and oceanographic conditions in NW Spanish coastal waters. ICES Council Meeting 1989/H:18, 12 p. (mimeo).

[9] Roy, P., C. Porteiro, and J. M. Cabanas. 1993. The optimal environmental window hypothesis in the ICES area: the example of the Iberian sardine. ICES Council Meeting 1993/L:76, 13 p. (mimeo).

Results

The length distribution of a subsample of 220 juveniles used for the birthdate analysis was not significantly different from that of the entire sample of 1,100 juveniles (Kolmogorov-Smirnov test, $P>0.2$). Of these 220 juveniles, 3 were rejected because daily rings were not visible in more than 5% of the transect readings. The age of the remaining 217 fishes ranged from 151 to 298 days, with birthdates from 13 December 1991 to 2 April 1992 (Fig. 2). Data by sample date are shown in Table 1. The average birthdate of juveniles from La Coruña was 28 January 1992 (n=98, SD=19 d, birthdate range: 13 December 1991 to 2 April 1992), and the average birthdate of juveniles from Vigo was 6 February 1992 (n=119, SD=16 d, birthdate range: 23 December 1991 to 26 March 1992). The observed differences between the two birthdate distributions (Fig. 2) were significant (Kolmogorov-Smirnov test, $P<0.001$). Specimens younger than 5 months were not caught by the fish-

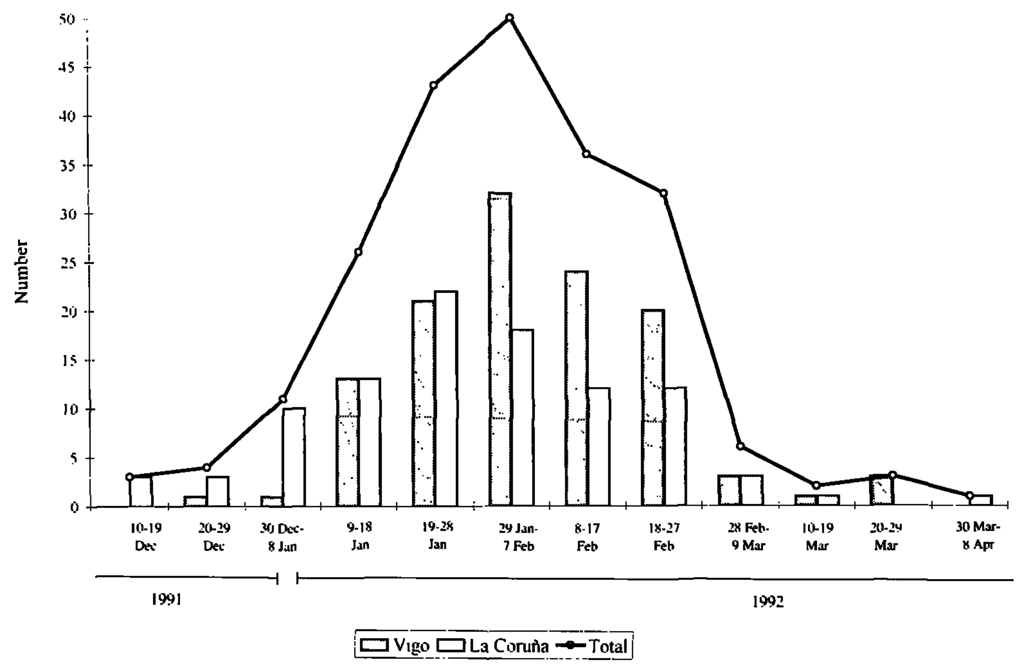

Figure 2
Birthdate frequency distributions for juveniles of the Atlanto-Iberian sardine *Sardina pilchardus*, by sampling port and total number of specimens caught.

ery (see Table 1; Robles et al., 1992). Thus, no corrections for cumulative mortality were made because the corrected birthdate distribution would be quite similar to the uncorrected distribution (Methot, 1983). The most significant aspect of these results is that they indicate a period of birthdates outside the main period of larval production in the Cantabrian Sea.

The relationship between the estimated age and length of the sampled recruits from Vigo and La Coruña are shown in Figure 3. In both cases, the relationship was linear, and significant (ANOVA, $P<0.000$). The slopes ($t=1.26$, $P>0.10$, df=213) and the intercepts ($t=0.96$, $P>0.20$, df=214) were not significantly different. Thus, a regression from pooled data was fitted (ANOVA, $P<0.000$).

The precision of ageing within each sample and within each 1-cm length range was assessed with the calculated coefficient of variation, CV (standard deviation divided by the the mean estimated age). The precision was good (CV<20%), stabilizing at a level of about 5–10% as fish grew in length (Fig. 4). The within-sample CV did not show any trend and remained at values less than 10% across all ages (Fig. 5). These results suggest that the intrinsic variability that may exist between otoliths of different fish of the same length range is low and that the precision of the age estimates is not affected by age.

To assess seasonal changes in the estimated birthdate distribution, we performed a test to compare birthdate distribution from early samples (June–September, $n=89$) with a distribution calculated from late samples (October–November, $n=128$). There was no significant difference (Kolmogorov-Smirnov test, $P>0.05$), which indicated that the samples came from the same cohort and that mortality during the period was not age selective.

Discussion

The juvenile birthdate distribution, which shows that the 1992 recruits were winter spawned, does not support the hypothesis that sardine recruits in the Galician area are mainly spawned during spring in the Cantabrian Sea, as was suggested by a previous study on the birthdate distribution of juveniles in this area (Álvarez and Butler, 1992). In fact, the surviving juveniles observed in our study were spawned earlier than the time when the sampling cruises were carried out in 1992. Thus, it was not possible to draw any detailed conclusions on the relationship between larval survival and environmental factors from otolith data. This was a significant obstacle for the achievement of the objectives of SARP because the "within year" exercise relies on a comparison of the birthdate distribution of juveniles with environmental conditions that occur during their larval development (Bakun et al.[10]).

[10] Bakun, A., J. Alheit, and G. Kullenberg. 1991. The sardine-anchovy recruitment project (SARP): rationale, design and development. ICES Council Meeting 1991/L:43, 17 p. (mimeo).

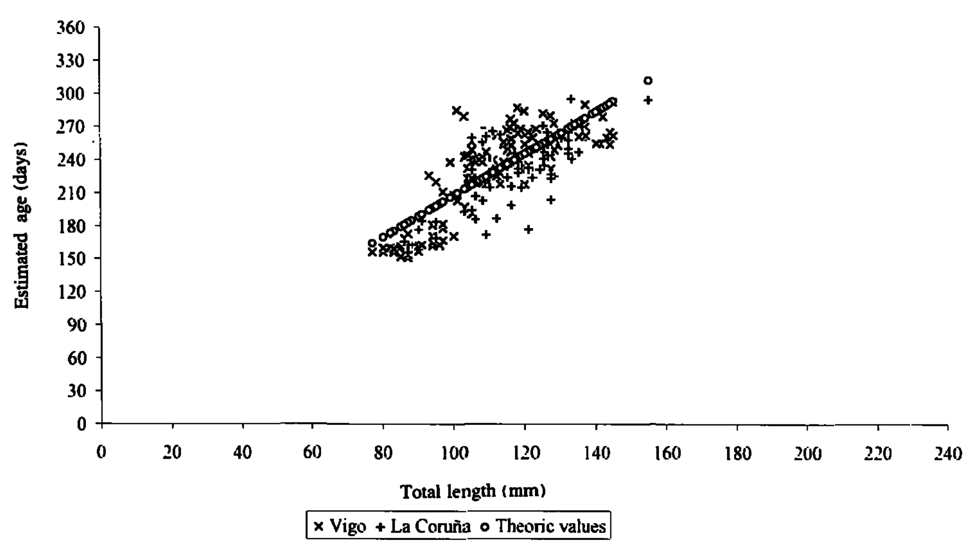

Figure 3
Age-length relationship and fitted regression for juveniles of the Atlanto-Iberian sardine *Sardina pilchardus*. Data are indicated by sampling port.

However, if the spatial-temporal features of spawning of this species in this area are taken into account, the results of Álvarez and Butler (1992), cited above, cannot be considered to be based on an unbiased sampling of the 1988 recruitment because they were derived from two samples only.

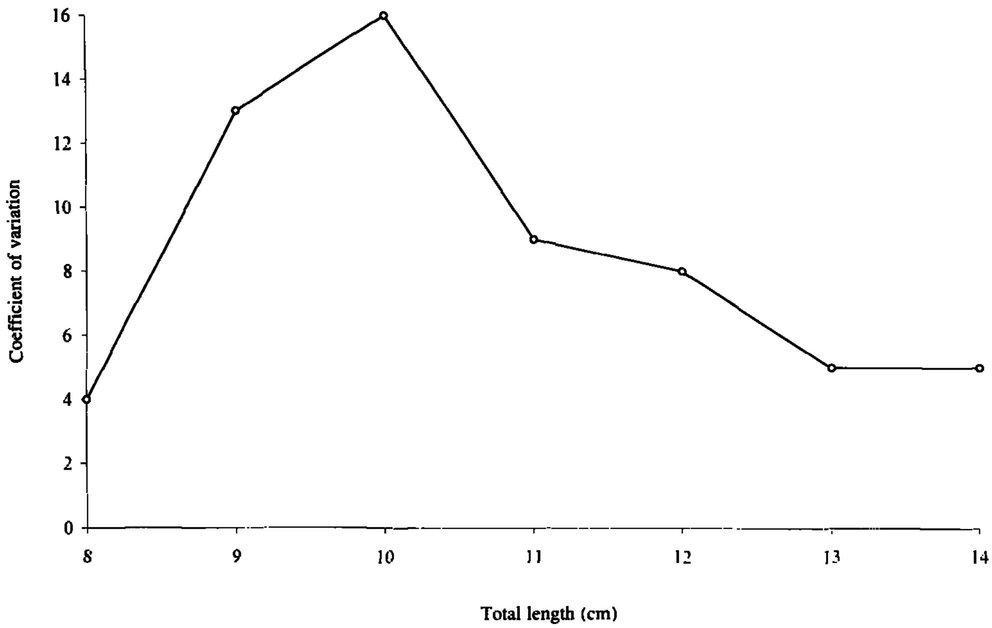

Figure 4

Ageing precision for juveniles of the Atlanto-Iberian sardine *Sardina pilchardus* within 1-cm length ranges. Precision is defined as the standard deviation divided by the mean (CV).

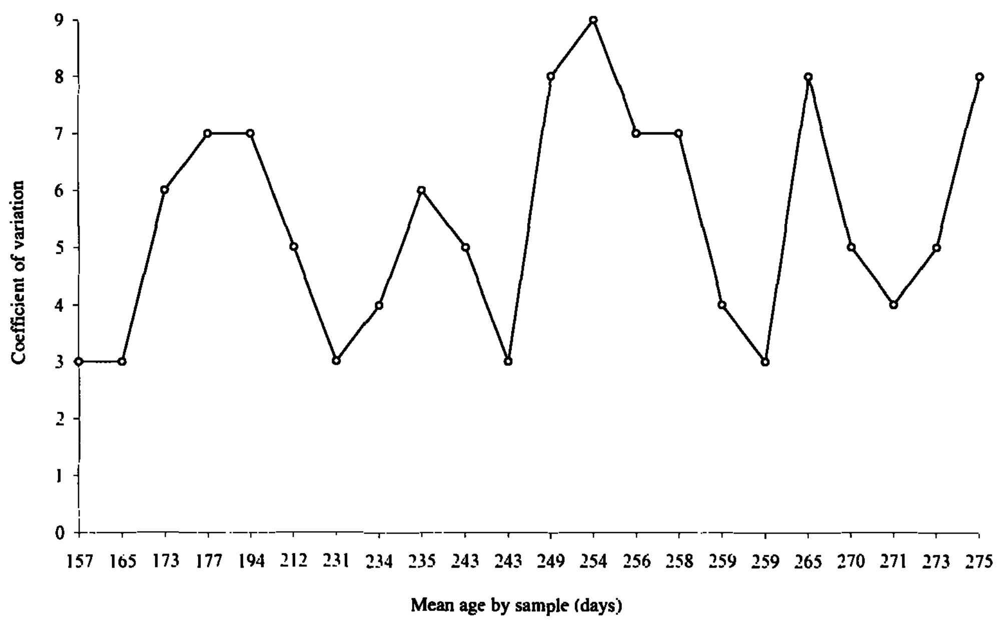

Figure 5

Ageing precision for juveniles of the Atlanto-Iberian sardine *Sardina pilchardus* within each sample. Precision is defined as the standard deviation divided by the mean (CV).

An alternative area of origin for the 1992 recruits is the coastal waters off northern Portugal, where eggs are presumably spawned during the winter. Relatively large larvae were found in March–April in southern and western Galicia. These larvae may not have been locally spawned, because spawning is low in this area (García et al., 1992; López-Jamar et al., in press), but rather spawned during the winter off the coasts of north Portugal where high winter spawning has been observed (Ré et al., 1990). Supporting evidence for such an area of spawning was deduced by López-Jamar et al. (in press) from the results of a 1992 sampling, where the progressive northwards and westwards displacement (around Galicia) of a group of larger larvae (mean length >13 mm) was documented. Using a larval growth-rate estimate of 0.59 mm/day in March off Galicia (Alemany and Álvarez[5]), we found that the length range of this group of larvae is in accordance with a February birthdate. Moreover, such a spawning area is consistent with the poleward flow of winter circulation in the coastal ocean off southwest Europe (Frouin et al., 1990).

The significant differences between the mean birthdates of recruits sampled at Vigo and those sampled at La Coruña are also consistent with the hypothesis of a larval drift from the south. The larvae that were produced at the beginning of the period, when the displacement northwards took place, would reach areas farthest from the spawning zone. Thus, the mean birthdate of specimens at La Coruña would be earlier than that of specimens at Vigo, as was observed. It is suggested from the evidence of the overall distribution pattern of sardine larvae in the Cantabrian Sea that, during the 1992 spawning season, most larvae drifted westwards and were dispersed offshore in northern Galicia (López-Jamar et al., in press). This pattern could be explained by the hydrographically dynamic area observed off northwestern Galicia in spring (López-Jamar et al., in press; Chesney and Alonso-Noval[11]). On the other hand, several studies have also suggested that recruitment of the Atlanto-Iberian sardine stock depends mainly on spring spawning in the Cantabrian Sea and on upwelling features along the west coast of the Iberian peninsula. These studies have been based on empirical relationships (Dickson et al., 1988; Cabanas et al.[8]) and a qualitative approach (Robles et al., 1992; Roy et al.[9]). Possible mechanisms associated with physical factors that could influence early life-stage larvae from spring spawning in the Cantabrian Sea are suggested in these works. However, the present study is a process-oriented approach, which accounts for intraseasonal effects of the biotic and physical environment on the survival of a fish cohort.

There is a possibility that spring-spawned recruits could exist off Galicia, but owing to their later incorporation into the juvenile fishery, they may not have been present before the sampling of recruits was finished in November 1992, when the March–June larvae may not have yet recruited to the fishery. However, on the basis of the age range given in Table 1, these spring-spawned recruits would be caught by the fishery from August and should be distinguishable in birthdate distribution. Moreover, the routine sampling of sardine length-frequency distributions carried out for stock assessments at the same area from January 1993 onwards has not revealed the presence of smaller sizes,[12] which would be an indication of recruitment from spring-spawned larvae in the Cantabrian Sea.

In summary, our results reinforce the suggestion of an alternative origin for the Atlanto-Iberian sardine recruits of the Galician area, at least in some years. The particular hydrological conditions along the northern coast of Portugal would favor either spring- or winter-spawned recruits, as outlined by López-Jamar et al., (in press). If upwelling in spring is weak, larvae spawned at this time in the Cantabrian Sea could be transported to the Galician area. On the other hand, if upwelling is intense, they may drift offshore at Cape Ortegal, as was postulated by López-Jamar et al. (in press) for the 1992 spawning in the Cantabrian Sea. In this latter case, the recruits in the Galician area would come from winter-spawned larvae in northern Portugal, which could reach the Galician area by northward-flowing surface currents during the winter. The influence of these mechanisms on year-class abundance remains to be investigated.

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[11] Chesney, E. J., and M. Alonso-Noval. 1989. Coastal upwelling and the early life history of sardine *Sardina pilchardus* along the Galician coast of Spain. ICES Council Meeting 1988/H:61, 54 p. (mimeo).

[12] Porteiro, C. 1994. Instituto Español de Oceanografía, P.O. Box 1552, 36280 Vigo, Spain. Personal commun.

Fischereiwissenschaft) and involved in the larval sampling cruises, especially to E. López-Jamar, S. H. Coombs, A. García, R. Knust, and W. Nellen. We are also grateful for the contribution and the support of J. M. Cabanas and C. Porteiro, and we would like to thank E. Moksness and two anonymous reviewers who offered useful suggestions for improvement of the manuscript. This work was carried out with partial funding from the Consejo Interministerial de Ciencia y Tecnología (CICYT) of Spain, contract 91.0089, and from the Fisheries Aquaculture Research (FAR) programme of the European Union, contract MA196.

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