

Postflexion larvae and juvenile daily growth patterns of the Alborán Sea sardine (*Sardina pilchardus* Walb.): influence of wind

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SUMMARY: The Alborán Sea is a hydrographically complex and variable area in which wind-driven coastal upwelling occurs. Its most abundant small pelagic resource is the sardine (*Sardina pilchardus*), which is subject to major interannual oscillations. Postflexion stages of sardine larvae were sampled in their main nursery grounds in the north Alborán Sea, and sardine juveniles were sampled periodically throughout the recruitment season. Daily growth analysis was used to identify periods favourable for larval survival and to assess the evolution of daily increment widths during the first months of life. The results showed that juveniles born later in the spawning season grew relatively faster than those born earlier. Two main growth phases were observed in juveniles: an initial one in which daily increment widths increased progressively, and a second one in which widths fluctuated, showing a decreasing trend. The beginning of the second phase was almost synchronous among different sub-cohorts, suggesting that it was triggered by environmental factors. The estimated mean daily growth rates during the larval phase were higher in surviving juveniles than in postflexion larvae born in the same month, supporting the “bigger is better” hypothesis in relation to larval survival. The influence of the environmental regime on growth was explored, and the evolution of a growth-related index, derived from otolith increment width variability, was compared with a single environmental descriptor, a “wind index” based on wind stress and direction. This analysis suggested that larval survival and larval and juvenile growth rates showed a positive correlation with NW component winds, associated with upwelling events on the continental shelf and calm sea weather conditions in the inshore nursery grounds. Conversely, Levantine and southern wind periods, which interrupt the upwelling and create rough seas in the inshore bays, lead to a decrease in growth rates in juveniles and low larval survival.

Keywords: *Sardina pilchardus*, daily growth, wind stress, recruitment, Alborán Sea.

RESUMEN: CRECIMIENTO DIARIO EN LARVAS EN POSTFLEXION Y JUVENILES DE SARDINA (*SARDINA PILCHARDUS* WALB.) DEL MAR DE ALBORÁN: INFLUENCIA DEL VIENTO. – El mar de Alborán es una zona hidrográficamente compleja y variable, en la que se producen fenómenos de afloramiento costero inducidos por vientos. Su recurso más abundante entre los pequeños pelágicos es la sardina (*Sardina pilchardus*), que está sujeto a importantes fluctuaciones interanuales. Se muestrearon estadios larvarios avanzados (larvas en estadio de postflexión del urostilo), en sus principales áreas de reclutamiento del norte del mar de Alborán. Los juveniles de sardina fueron muestreados periódicamente a lo largo de la temporada de reclutamiento. Estudios de crecimiento diario permitieron identificar periodos de alta supervivencia larvaria, así como analizar la evolución de la anchura de los microincrementos durante los primeros meses de vida, revelando que los juveniles nacidos más tarde en la época de puesta crecieron relativamente más rápido que aquellos nacidos antes. Se observaron en los juveniles dos fases de crecimiento principales: una primera en la cual los incrementos diarios eran progresivamente más anchos y una segunda donde las anchuras de los incrementos fluctuaron, mostrando una tendencia negativa. El inicio de la segunda fase fue casi sincrónico entre las diferentes sub-cohortes, sugiriendo que fue determinado por factores ambientales. Las tasas de crecimiento diario medias estimadas durante el periodo larvario fueron mayores en los reclutas supervivientes que en las larvas

en postflexión nacidas en el mismo mes, dando apoyo a la hipótesis de “mayor es mejor” en relación con la supervivencia larvaria. La influencia de las condiciones ambientales sobre el crecimiento se estudió relacionando la evolución temporal de un índice de crecimiento basado en la variabilidad de las anchuras de los incrementos diarios con un sencillo descriptor ambiental, un “índice de viento” calculado teniendo en cuenta tanto la dirección como la intensidad de los mismos en el área. Este análisis indica una relación positiva tanto de la supervivencia larvaria como de la evolución de las tasas de crecimiento diarias en larvas y juveniles con periodos de viento de componente norte y oeste, que producen afloramiento en la plataforma continental y condiciones de mar calma en las bahías donde tiene lugar la cría. Al contrario, periodos de viento de levante y sur, que interrumpen el afloramiento e inducen condiciones de temporal en las zonas de las bahías, producen un descenso de las tasas de crecimiento de los juveniles y una menor supervivencia en las larvas.

Palabras clave: *Sardina pilchardus*, crecimiento diario, viento, reclutamiento, mar de Alborán.

INTRODUCTION

It is well-known that population size, especially in the case of small pelagic species, can exhibit large interannual fluctuations (Kawasaki, 1991; Wyatt and Larrañeta, 1988). These fluctuations are mainly attributable to variations in recruitment success, which in turn are mainly due to very high and extremely variable mortality (Peterson and Wroblewski, 1984; Bradford, 1992) during the planktonic stages (Hjort, 1914, 1926), which represent a critical period (May, 1974). Several authors have proposed hypotheses to explain the mechanisms controlling larval survival (Cushing, 1975, 1990; Lasker 1978), whose validity has been supported by field studies (Beaugrand *et al.*, 2003; Platt *et al.*, 2003; Fortier and Gagne, 1990; Parrish *et al.*, 1981; Lasker, 1985; Peterman and Bradford, 1987). In most cases it has been recognised that variance in recruitment can be explained through relatively simple atmosphere-ocean interaction models.

Following the SARP approach (Bakun *et al.*, 1991), daily growth studies of surviving juveniles were used to identify the periods when juveniles were born, and hence to determine the environmental conditions favourable for larval survival. This methodology was first applied in the CALCOFI area (Methot, 1983), and later in the SE Atlantic (Painting *et al.*, 1998; Van der Lingen, 2002), SW Atlantic (Anonymous, 1989) and NE Atlantic (López-Jamar *et al.*, 1995), in the latter case to analyse the recruitment process of European sardine (*Sardina pilchardus* Walbaum 1792). The present study was undertaken within the framework of a research project one of whose main objectives was to define the Optimal Environmental Windows (OEWs) (Cury and Roy, 1989; Guisande *et al.*, 2001) for Alborán Sea European sardine populations, which have showed major fluctuations in the last few decades (Abad *et al.*, 1998).

The sardine in the western Mediterranean has a protracted spawning season, from autumn to spring

(Alemany, 1997; Olivar *et al.*, 2003). In the Alborán Sea the presence of sardine eggs has been reported from September to May (Rodríguez, 1990). Along the narrow northern shelf of the Alborán Sea, several bays constitute important nursery grounds for small pelagic fishes, among which the Málaga bay is the most important (García *et al.*, 1988). Sardine is the most abundant small pelagic fish species in the Alborán Sea (Abad *et al.*, 1998) and, like anchovy, is one of the traditional target species of the Mediterranean Spanish purse seine fleet (Alemany and Álvarez, 1993).

The main objective of this work was to determine the birthdates of juvenile sardines of the Alborán Sea for the 2004 spawning season by means of daily growth analysis in order to define optimal environmental conditions of surviving sub-cohorts. We define juveniles as pre-reproductive individuals that have all the fin ray elements and scales and are morphologically similar to adults. In addition, a comparison was made between the daily growth patterns of the surviving juveniles from different periods of the spawning season, and between growth patterns of surviving juveniles and postflexion larvae born in the same period.

As the preliminary results showed that the daily growth rates of juveniles belonging to different sub-cohorts appeared to be synchronised, mainly from April onwards, suggesting that they were strongly influenced by some environmental factor, we explored the relationships between daily growth rates in juveniles and an environmental index based on wind direction and speed.

The study area

The Alborán Sea is a hydrographically complex region. It straddles the transition between the Mediterranean Sea and the Atlantic Ocean, and is mainly conditioned by the water masses flowing through the Straits of Gibraltar. However, the inflow of Atlantic waters only affects the slope

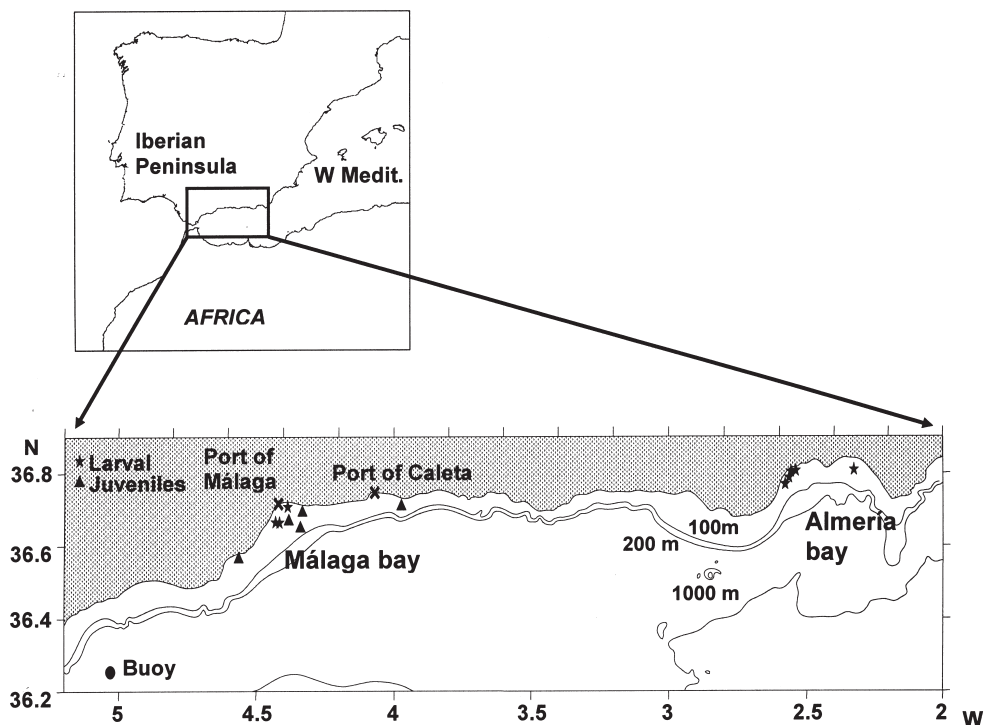


FIG. 1. – Map of study area, showing larvae and juvenile sampling sites and the location of the meteorological buoy

area, since on the shelf local surface currents are wind-driven (Cano and Lafuente, 1991). In the NW sector, between Gibraltar and Málaga bay, where sardine larvae and juveniles are mainly found, upwelling processes are caused by both northern and western winds (Bakun and Agostini, 2001; Cano, 1978; Sarhan *et al.*, 2000; García-Gorritz and Carr, 2001).

MATERIAL AND METHODS

Postflexion larvae and juvenile sampling

Sardine larvae were sampled off the Alborán Sea coast during the acoustic-ichthyoplanktonic survey carried out on board the R/V “Cornide de Saavedra” in November-December 2003. Selection of optimal sites for sampling postflexion larval stages of sardine was based on zooplankton samples from night oblique standard bongo 60 tows, carried out along a set of transects quasi-parallel to the coastline off the northern Alborán Sea, which were briefly examined on board for the presence of postflexion sardine larvae. All selected postflexion sardine larvae sites were located in the bays of Málaga and Almería (Fig. 1). Surface night hauls were carried out between 14 and 18 December 2003 using a quadrangular bongo net

with black tinted 1 mm mesh. In order to prevent larval damage, 10 minute hauls were carried out at two knots, and sardine postflexion larvae were immediately sorted and frozen in liquid N₂ for storage. In the laboratory, sardine postflexion larvae were thawed at ambient temperature and then measured to standard length using an image analysis program (NIH Image). A representative sample of postflexion larvae from each sample site was selected: 64 from Almería, ranging between 16.04 and 22.92 mm, and 55 from Málaga, ranging between 16.14 and 22.70 mm. The otoliths were then extracted using fine needles, dropped onto a slide and cleansed with a drop of distilled water. After drying, the sagitta were fixed with nail lacquer.

Juvenile sardines, belonging to age class 0 were sampled from the commercial purse seine fleet landings at the Alborán Sea ports of Málaga and Caleta de Vélez (Fig. 1). But, as the fishery does not target juveniles, they were only occasionally found in commercial landings (Table 1). Seven samplings were carried out between May and September 2004, with a total of 311 individuals sampled. Standard length was measured to the nearest mm and both sagittal otoliths were removed. After cleaning and drying, the otoliths were mounted separately on glass slides with the *sulcus acusticus* on the glass side and embedded in Eukitt.

TABLE 1. – Juveniles sampling scheme.

Sampling	Date	Place	Total ind.	Read ind.	Size rank (mm)
1	13/05/04	Málaga	67	39	69-96
2	25/05/04	Caleta de Vélez	60	40	75-96
3	22/06/04	Caleta de Vélez	45	25	75-120
4	24/06/04	Málaga	46	25	52-110
5	06/07/04	Caleta de Vélez	39	17	90-129
6	27/08/04	Caleta de Vélez	28	rejected	76-122
7	28/09/04	Caleta de Vélez	23	10	125-144

Reading otoliths

The daily nature of microincrements in sardine larvae otoliths was validated by Ré (1984), and the location of hatch ring was defined by Alemany and Álvarez (1994). Taking into account these references, the larval sagitta—one per individual—were read by one reader using the OTO program for McIntosh (Andersen and Moksness, 1988), as described in García *et al.* (2003). Daily microincrements were counted and their width measured for every individual. All the final sagitta measurements for the numerical analysis (counts, widths, radius) were done at 1000 x magnification.

Juvenile otoliths were analysed with the first MS-DOS version of the OTO program, using the methodology proposed by Methot (1981), as described in Álvarez and Alemany (1997). For each individual, a preliminary examination of each pair of otoliths was carried out in order to select those showing the clearest rings and the most complete readable transects (without breaks), from the focus to the posterior margin of the otolith. Increment widths were measured from live images using a video-coordinated digitiser interfaced with a microcomputer. In each case, the optimal focus was chosen. Several readings at different magnifications (160 x, 630 x and 1000 x) were made along a transect located at $\pm 5^\circ$ of the longest radius, from the focus to the posterior margin of the otolith. Groups of homogeneous daily increments were sequentially counted and measured. Otoliths were progressively polished on one side between readings to reveal increments, using 30.9 and 0.3 μm lapping film. All otoliths were read independently by two readers. Data from different readings were finally combined to calculate the age of each individual. Whenever discrepancies in age estimations exceeded four days, a joint reading session was carried out and discussed, and subsequently the otolith was again independently examined by the two readers. When discrepancies remained—only 7% of cases—the data

were rejected. Interpolation procedures were not applied, since in all the otoliths the whole reading transect, from the hatching ring (Alemany and Álvarez, 1994) to the border, was analysed in at least one of the subsessions. All otoliths in which some part of the transect was unreadable, or subdaily increments were not clearly distinguishable from true daily microincrements, as well as all otoliths that got broken during the polishing procedure before complete readings, were also rejected. All 40 pairs of otoliths from the August sample were rejected because, for unknown reasons, they appeared to be degraded and did not show a clear enough internal structure. Therefore, out of 311 pair of otoliths available, only the data from 156 individuals were finally considered.

As a first step to evaluate the reliability of juvenile otolith readings, length at age data were analysed using the Fishfarm software package to obtain Von Bertalanffy growth parameters. Furthermore, to detect sub-cohorts and to explore general growth patterns and compare them with those obtained from otolith readings, a modal progression analysis of the standard length distributions was carried out using Battacharya's method, again using the Fishfarm software.

Otolith data post-processing

To calculate the birthdate of each individual, the age in days was directly subtracted from the sampling date, since all the counts started in the recognisable hatching day ring (Alemany and Álvarez, 1994). Rough data of otolith readings from postflexion larvae were processed using the OTO program (Andersen and Moksness, 1988) to obtain the width of each daily microincrement per specimen. Daily increment widths were later averaged to estimate the mean otolith growth. Rough data of juvenile otoliths were processed using Matlab software to calculate the width of each daily growth microincrement,

since the OTO software version used did not provide these data directly. Then, five temporal series of these microincrement widths were calculated by averaging, for each calendar day, daily increment width data corresponding to such calendar day from individuals born within the same month. It must be highlighted that the individual series of microincrement widths were similar to the averaged values, with small standard deviations that remained more or less constant throughout the whole time periods. After that, considering the close relationship between otolith and somatic growth (see Results section) as an indicator of daily growth performance, a growth index was calculated for each of the five averaged series, by subtracting from the width of each microincrement the width of the previous one. Finally, a global series was obtained by averaging the data for each calendar day from the five series considered.

The mean growth in length of each of the five groups of juveniles was back-calculated from otolith microincrement width data. This was done by applying the equations obtained from linear regressions between otolith and somatic growth, calculated from both larva and juvenile otolith radius *vs.* standard length pairs of data (see Figs. 5A and 5B). Although using simple linear relationships is not the most accurate method for back-calculation (Francis, 1990), we considered the results reliable enough for our purposes. This was because regression values were obtained from individuals sampled within a short period and back-calculation was only applied to a limited range of lengths of the same individuals. Regression coefficients obtained from postflexion larvae analysis were applied for the larval period up to 26 mm in length, whereas for the juvenile phase, from 36 mm onwards, regression values estimated from juveniles were used. The growth in length during metamorphosis was not back-calculated, because due to the important morphological changes that take place during this phase, the available linear relationships are not valid to obtain reliable estimations.

Wind index

To explore the possible relationships between daily growth rates and environmental factors, a wind index based on the wind induced upwelling index proposed by Bakun and Parrish (1990) was developed. Basic wind data coming from a “Seawatch”

meteorological buoy located off Algeciras, which can be considered representative of the whole study area, were obtained from the “Puertos del Estado” web site (www.puertos.es). Hourly records of wind stress and direction from November 7 onwards were averaged to calculate a mean daily wind intensity and direction vectors. Northern and western winds produce upwelling in the Alborán Sea area (Bakun and Agostini, 2001; Sarhan *et al.*, 2000) and calm sea surface conditions in the inshore areas of the northern Alborán Sea, where the nursery areas of sardine are located (Ramírez *et al.*, 2004). Thus, each wind vector was decomposed and added up, considering N-S and W-E components as positive and S-N and E-W ones as negative, and the result were multiplied by the wind intensity, using the resulting value in m/s as a “wind index”. The formulae used were:

$$\text{-1}^{\text{st}} \text{ quadrant: } (V * |\cos a|) - (V * |\sin a|)$$

$$\text{-2}^{\text{nd}} \text{ quadrant: } (V * |\cos a|) + (V * |\sin a|)$$

$$\text{-3}^{\text{rd}} \text{ quadrant: } (V * |\sin a|) - (V * |\cos a|)$$

$$\text{-4}^{\text{th}} \text{ quadrant: } -(V * |\sin a|) - (V * |\cos a|)$$

where V=wind velocity in m/s and a=wind direction.

Finally, the daily data series was smoothed by means of running average over 3.

Regression between wind and growth indices

To analyse the relationship between sardine growth and wind, linear regression analysis between temporal series of growth and wind indices were applied. Two regressions analyses were performed, the first considering the whole series of data and the second only the period comprised between November and April, coinciding with the first growth phase of juveniles characterised by a progressive increasing in daily increment width.

RESULTS

Birthdate distribution and standard length modal progression in juveniles

Postflexion larvae sampled in Málaga bay were born between 7 and 27 November, with 61% of birthdates concentrated between 15 and 23 and peaking on 20 November (Fig. 2a). Postflexion larvae from Almería bay were born in general a little earlier, between 1 and 22 November, with 64% of

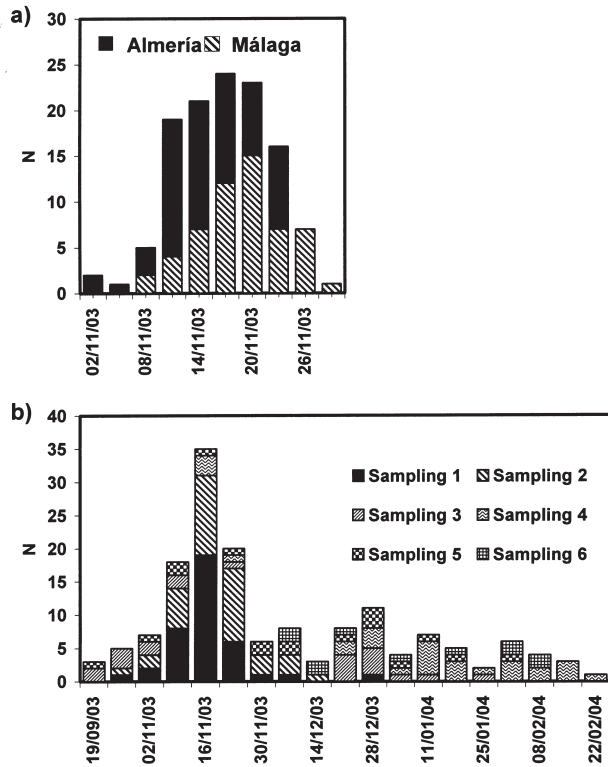


FIG. 2. – a) Birthdate distribution of sardine postflexion larvae sampled in December 2003 in the bays of Málaga and Almería; b) Birthdate distribution of sardine juveniles from Alborán Sea population sampled throughout 2004. N: number of individuals.

birthdates between 9 and 17 November, with the mode on 20 November (Fig. 2b).

The birthdate distribution, estimated from daily microincrement counts in otoliths from juvenile sardine (Fig. 2b), showed three main modal groups, with birthdates centred in mid-November, late December and early February, respectively. The best represented sub-cohort, including almost 2/3 of individuals, was that formed by specimens born in November. Modal progression analysis in standard length distributions also revealed at least three well-defined sub-cohorts (Fig. 3). Fitting the modal standard lengths of the respective sub-cohorts to linear functions, daily growth rates were approximately 0.4 mm day⁻¹ and the mean birthdates were between mid-November and early March.

General growth pattern

Length at age data from postflexion larvae otolith readings are shown in Figure 4a. The best fit ($R^2=0.8044$) was obtained with a logarithmic function. According to these results, the mean daily growth rate between 20 and 40 days (postflexion lar-

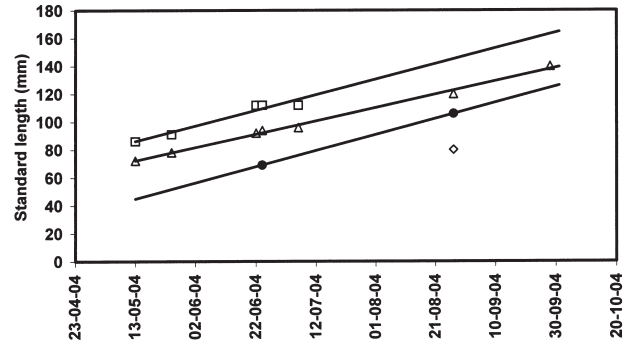


FIG. 3. – Standard lengths modal progression of sardine juveniles from Alborán Sea population sampled throughout 2004. Different symbols represent the modal length detected for each one of the proposed subcohorts. Solid lines, representing a proxy of modal lengths progression, were obtained by linear fitting.

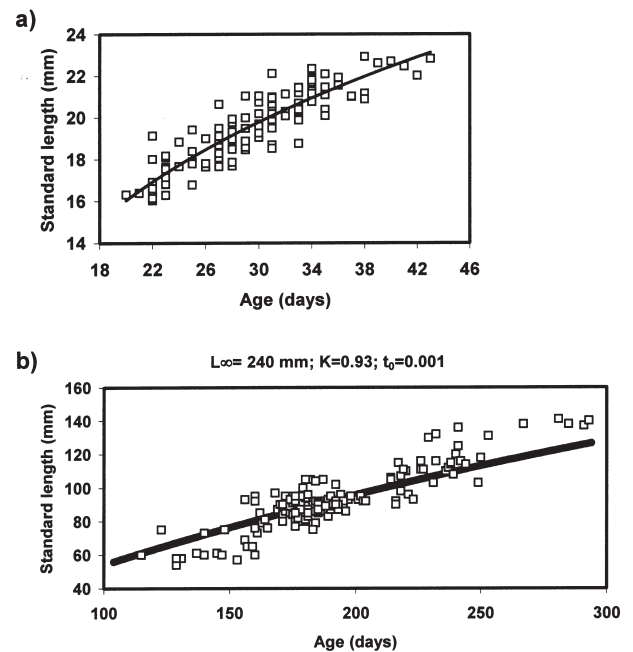


FIG. 4 – a) General growth pattern of the postflexion larvae sampled in December 2003 in the bays of Málaga and Almería; b) von Bertalanffy growth parameters for Alborán Sea sardine population based on daily length at age data from juveniles sampled throughout 2004.

vae) was 0.32 mm day⁻¹. Regarding juveniles, despite the limited range of ages considered, between 116 and 294 days, sardine standard length at age data fitted well to a von Bertalanffy growth model (Fig. 4b), giving the following growth parameters: $L_{\infty}=240$ mm; $K=0.93$ and $t_0=0.001$. This implies a mean growth in this range of ages of 0.4 mm day⁻¹.

Somatic and otolith growth relationship

Otolith and somatic growth showed a close relationship in both postflexion larvae and juveniles.

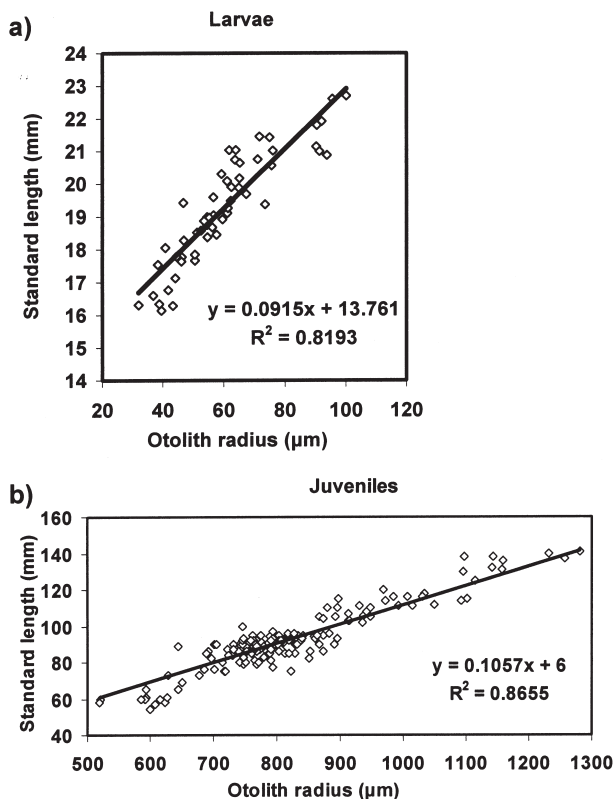


FIG. 5. Linear regressions between a) otolith radius and fish length in sardine postflexion larvae sampled in December 2003 in Málaga and Almería bays, and b) otolith radius and fish length in sardine juveniles sampled from Alborán Sea population throughout 2004.

Linear regressions between otolith radius and standard lengths for larvae and juveniles (Figs. 5a and b) presented R values higher than 0.9, with $p < 0.001$.

Daily increment width evolution: postflexion larvae/juveniles and among-subcohort comparisons

Postflexion larvae from both Málaga and Almería bays showed an initial period of continuous increase in increment widths, from around $1 \mu\text{m}$ in the first days of life, during the yolk sac reabsorption, to $>2 \mu\text{m}$ in 18-day-old larvae (Fig. 6). From day 18 to 28, microincrement widths remained stabilised around the same values. Maximum values, between 2.5 and $3 \mu\text{m}$, were reached by day 34. Finally, they follow a decreasing trend from day 34 onwards, reaching values $<2.5 \mu\text{m}$ in the last daily microincrements of post larvae more than 40 days old.

The evolution of average daily increment widths in the five groups of juveniles considered (Fig. 7) revealed two main phases. In the first phase microincrement widths increased almost continuously, from 1 to $5-7 \mu\text{m}$, whereas in the second

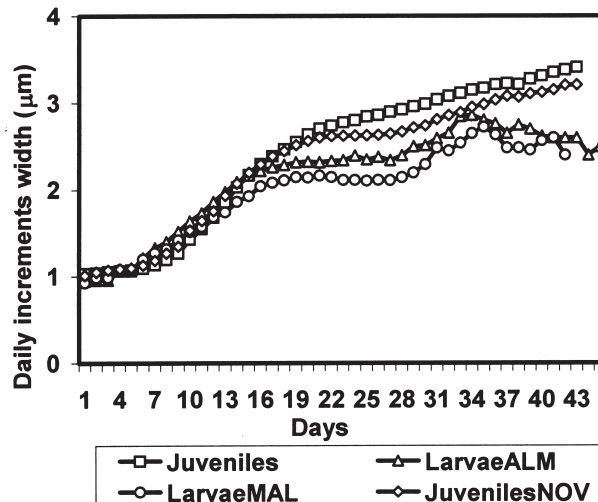


FIG. 6. – Daily increment widths during larval stages in 2004 sardine juveniles from Alborán Sea population and postflexion larvae sampled during December 2003 in Málaga and Almería bays

phase microincrement widths fluctuated, showing a general decreasing trend. The length of the first phase was variable, and progressively shorter in the individuals born later. For example, it was about 5.5 months in specimens born in October and only 3.5 months in those born in February. Within this phase, in all groups, an initial inflexion in otolith growth rates was observed when increment widths reached about $2.5 \mu\text{m}$. At this moment the larvae were around 20 days old and their standard length was about 20 mm. Later, also in all the groups, a period of stabilisation in the increment widths was observed, around $3.5 \mu\text{m}$ in the October-December groups and between 4 and $5 \mu\text{m}$ in the January-February groups. This stabilisation in daily increment widths started when individuals were about 50 days old. This period of stabilisation was progressively shorter in the five considered groups. Besides

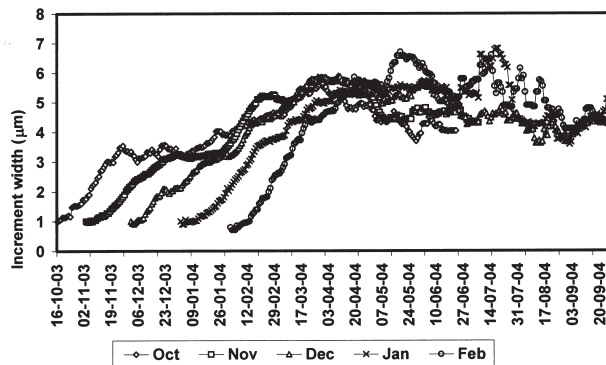


FIG. 7. – Evolution of daily increment widths in 2004 sardine juveniles from Alborán Sea population. Each series represents the average value for all the individuals born within the same month, from October to February.

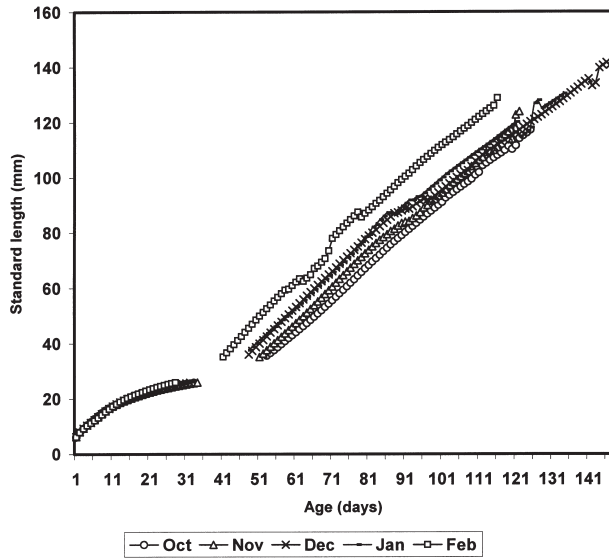


FIG. 8. – Mean back-calculated growth of 2004 sardine juveniles from Alborán Sea population born in the different spawning season months. The regression values presented in Figure 5a were used for larval period and for juveniles those showed in Figure 5b.

these inflexion points that occur in all groups irrespective of the date, other periods of relative increase or decrease in microincrement widths seem to have been synchronised among groups. As for comparisons among increment widths from larval or juvenile otoliths (Fig. 6), the latter always showed wider increments. The differences became evident from the 18th day of life, when in postflexion larvae the daily microincrement widths remained stable,

whereas in the surviving juveniles the daily microincrements continued being progressively wider. This difference was greater from day 34 onwards, when daily microincrements in juveniles continued increasing their width, whereas the last microincrements of the analysed postlarvae showed a decreasing trend.

Back-calculated lengths

Evolution of mean back-calculated standard lengths of the five groups of juveniles studied is shown in Figure 8. As expected, growth in length revealed two different phases. According to these back-calculated growths, specimens born later grew faster than those born at the beginning of the spawning season. These differences became more evident in the juvenile stage. For example, individuals born in February took less than five months to reach a standard length of 80 mm, whereas those born in October needed more than six months to attain the same length.

Influence of environmental factors on juvenile sardines growth

A similar evolution pattern was observed for the environmental (wind) and biological (growth) indices from November 2003 to September 2004

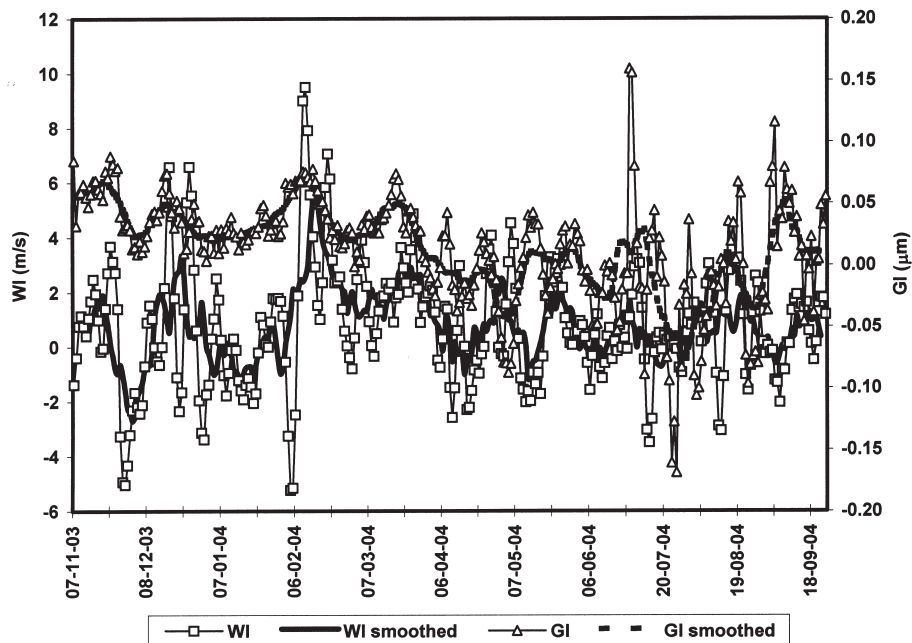


FIG. 9. – Temporal evolution of wind index (WI) and growth index (GI) (see Material and Methods section for details on the calculations). Solid lines represent smoothed values of both series by means of running average over 13.

(Fig. 9). The match seems especially strong from late autumn to early spring, whereas from May onwards the relationship is less clear. It must be pointed out that, despite the visual correspondence in the temporal evolution of the two variables, regression analysis including the whole series of data showed a weak but significant relationship ($R=0.12$; $P=0.036$). Considering only the period from November to April, when visually the concordance between the two series is higher, the R value was 0.24, with $P=0.0017$.

DISCUSSION

The length at age data obtained for postflexion larvae match those presented in previous studies on sardine postflexion larvae growth in the Alborán Sea (Ramírez *et al.*, 2001; Ramírez *et al.*, 2004). For juvenile growth, our mean length at age values are very similar to those reported by Álvarez and Morales-Nin (1992) and Álvarez (2002) for autumn and winter spawned juvenile sardines in the Balearic Sea, and also to those found by Álvarez and Alemany (1997) for winter spawned juvenile sardines from Atlantic Iberian stock. Furthermore, despite the narrow range of length-at-age data considered, the parameters of the fitted von Bertalanffy growth equation are coherent, with a L_{∞} value (240 mm) close to the maximum-recorded lengths in the Alborán populations and t_0 close to 0. This growth pattern was similar to those obtained previously from annual ring readings in the area (Alemany and Álvarez, 1993). The growth rates estimated from modal progression analysis, around 0.4 mm day⁻¹, also coincided with the growth rates estimated from daily increment readings during the juvenile stage. The coherence of results suggests that the microincrement count was reliable, reflecting the true age of analysed individuals with a low deviation. However, some bias cannot be discarded, mainly in the oldest specimens sampled in September. In this species, the microincrements are usually easily readable during the first growth phase, from the nucleus to the moment in which increments reach their maximum width. At this stage, in some cases it is rather difficult to distinguish true daily rings from subdaily increments. In older juveniles, the increments laid down during late summer are also difficult to count, since they are much more irregular and less defined than those formed in spring.

Estimated postflexion larvae and juvenile birthdates were within the spawning period of the species in the area. Curiously, the birthdates of the best-represented sub-cohort of juveniles (November) matched the birthdates of the postflexion larvae sampled in December. This confirms that survival rates were high in the larvae born in November. However, since the juvenile sampling scheme was not strictly random, and could not be extrapolated to total catch, this does not necessarily mean that this sub-cohort is the one which most contributed to 2004 recruitment. The other two sub-cohorts detected, those born in December and February, could have been less abundant in the first juvenile samples because in the first samplings they would be not fully recruited to the fishing areas. Furthermore, other sub-cohorts born in spring could have finally been fully incorporated into the fishery once the sampling programme finished, as suggested by the presence of some small isolated specimens around 80 mm in the August sampling. Therefore, these later sub-cohorts would be not properly represented in our sampling scheme.

The comparison between the growth rates during the first weeks of life of postflexion larvae and that of surviving juveniles born in the same month showed that the postflexion larvae that survived to juveniles were those that had a faster growth during larval stages and were therefore bigger at a specific age. This supports both the “the bigger is the better” and “the faster is the better” hypothesis (Miller *et al.*, 1988; Folkvord and Hunter, 1986).

The general pattern of daily microincrement width development in juveniles involved an increasing trend until maximum values over 5 μ m were reached in late spring, followed by a later decreasing phase in which values fluctuated. This is the same pattern found previously in other daily growth studies on sardine juveniles (Álvarez and Butler, 1992; Álvarez and Morales-Nin, 1992; Alemany, 1993; Álvarez and Alemany, 1997; Álvarez, 2002), and even in other winter spawned pelagics off the Iberian peninsula, as *Scomber scombrus* (Cotano and Álvarez, 2003; Villamor *et al.*, 2004). These patterns are probably influenced by endogenous factors, such as the decrease in potential growth with age; but they are also modulated by environmental factors, such as temperature and food abundance (Catalán *et al.*, 2006; Ramírez *et al.*, 2004). Since in all the aforementioned cases the start of the fluctuating and

decreasing second growth phase was synchronic among autumn, winter and early spring spawned juveniles, and coincided with the beginning of stratification processes which produce a decrease of production in surface waters, we hypothesise that it is triggered by the end of the planktonic bloom. From satellite-derived phytoplankton pigments in the Alborán Sea, García-Gorriz and Carr (1999) stated that the algal bloom period lasts from November to March and the non-bloom period from May to September. Transitional periods occur in April-May, when thermal stratification starts, and in October-November, coinciding with maximum wind variability and loss of stratification within the basin. These figures are coherent with our findings, since the phase of increasing daily growth rates would coincide with the high production period and the decreasing trend would match with the non-bloom period. Mid- and late winter spawned specimens would grow relatively faster than those born earlier because their larval and early juvenile phase, when their growth potential is highest, match the maximum planktonic production. This cycle of annual production could also influence the survival of larval sardines. According to our results, survivors' birthdates match the algal bloom period, in agreement with Cushing's (1975, 1990) "match-mismatch" theory. However, shorter temporal scale phenomena would modulate these global figures, both in juvenile growth rates and in larval survival. Some of the inflexions observed in daily microincrement width evolution during the first growth phase would be attributable to endogenous factors, as would be expected for the metamorphosis process and their inherent behavioural changes, which would lead to a temporal stabilisation in the increasing trend of microincrement widths. Other changes in otolith microincrement width must be driven by environmental factors. The results of this study suggest that wind stress plays a crucial role in the recruitment process of the Alborán Sea sardine, by both determining larval survival and modulating juvenile growth. The three first periods of northern and western wind predominance coincided exactly with the estimated birthdates of the three detected recruit sub-cohorts. It could be hypothesised that both the increased food abundance, resulting from coastal upwelling events, and calm sea weather conditions in the inshore bays (nursery areas) induced by northern and western winds enhance larval survival. Thus,

these periods of northern and western winds would be those in which "Lasker events" (Lasker, 1978; Peterman and Bradford, 1987; Mendelssohn and Mendo, 1987; Cury and Roy, 1989) occur, favouring larval survival. On the other hand, stormy conditions in coastal areas induced by Levantine winds modify spatial and temporal availability of food to fish larvae and thus negatively influence their feeding and growth (Maillet and Checkley, 1991), and hence their survival. A parallel study on larval condition based on the same postflexion larvae analysed in this study (García *et al.*, 2006) suggests that the growth strategy of sardine larvae in the Alborán Sea is adapted to pulses of low food availability, which would agree with the fluctuating daily growth rates observed.

According to our results, wind stress and direction also directly influence daily growth rates during the juvenile period, mainly during late autumn-early spring, when water masses are not stratified. Taking into account the immediacy of the biological response (variation in growth rates) to the considered wind index—both increasing growth rates during NW winds and decreasing growth rates during SE episodes—the effect of wind must not only be related to enhancement of production through upwelling processes, but also to a more direct impact on juvenile feeding rates or metabolism, as occurs in larval stages. Of course, as the low correlation values between the two indices considered suggest, environmental factors other than wind determine larval and juvenile growth. With regard to larval growth, temperature and food availability have been defined as the main factors affecting larval growth and condition (Buckley, 1984; Heath, 1992). Their importance for sardine larvae development has been demonstrated in other Mediterranean populations (Ramírez *et al.*, 2004; Catalán *et al.*, 2006). Several studies have shown the direct impact of temperature on the otolith accretion rate (Mosegaard *et al.*, 1987; Fitzhugh and Nixon, 1997). However, during periods in which these factors remain more stable, as is the case for temperature during winter, when the water column is mixed, the wind must become a more important factor modulating larval and juvenile sardine growth in the Alborán Sea. This study has therefore detected a relationship between wind stress and sardine juvenile growth and sardine larval growth and survival, but further studies will be required to understand the mechanisms driving this relationship.

ACKNOWLEDGEMENTS

This work has been supported by the project “Definición de ventanas óptimas que condicionan la supervivencia de huevos y larvas de peces pelágicos en zonas de alto contraste ambiental” (REN2002-04205-C04-03), funded by the Spanish Ministry of Science and Technology. We want to thank Drs. Cástor Guisande, Jesús García Lafuente and Sebastià Monserrat for their useful comments on the manuscript, as well as the editor of *Scientia Marina* Dr. M. Pilar Olivar for her help in the revision process of the original manuscript.

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Received November 14, 2005. Accepted May 11, 2006.
Published online September 26, 2006.