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Contribution of larval growth rate variability to the recruitment of the Bay of Málaga anchovy (SW Mediterranean) during the 2000-2001 spawning seasons*

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SUMMARY: Daily growth rates were estimated from larval anchovy (*Engraulis encrasicolus*) sampled in their main nursery grounds off the Bay of Málaga (SW Mediterranean) during the 2000 and 2001 spawning seasons. Significantly higher growth rates were observed in the 2001 larval population, representing a 20% increase through the larval size classes analysed. The decimated SW Mediterranean anchovy population experienced a successful anchovy recruitment during this year estimated at 13,000 tons for the Bay of Málaga by the acoustic evaluation of small pelagic resources. The size distribution of the recruited anchovy juveniles during 2000 and 2001 showed an increase of approximately 2 cm. Their corresponding anchovy spawning seasonality agrees with the estimates from the growth model fits of each year. Data on the environmental background for the two years sampled are provided by a historical quarterly monitoring project. Zooplankton showed a two-fold significant increase during July 2001, coastwise as well as offshore. No significant changes in surface temperature were observed between years. Instead of the usual summer spawning peak, anchovy peak spawning shifted towards early spring during the 2001 spawning season. The study provides evidence from field data on the relationships of larval growth variability and recruitment.

Key words: anchovy, larvae, Mediterranean, growth, nursery ground, environment, recruitment.

RESUMEN: CONTRIBUCIÓN DEL CRECIMIENTO LARVARIO AL RECLUTAMIENTO DEL BOQUERÓN DE LA BAHÍA DE MÁLAGA EN LOS AÑOS 2000-2001. – Las tasas de crecimiento diario de larvas de anchoa (*Engraulis encrasicolus*) fueron estimadas de una población larvaria procedente de la principal zona de alevinaje de la Bahía de Málaga (Mediterráneo Sur-occidental) durante la época de puesta de los años 2000 y 2001. Las tasas de crecimiento diario de la población del 2001 fueron significativamente mas altas, representando un aumento del 20% en todas las clases de tallas larvarias analizadas. Durante el año 2001, se produjo un importante aumento del reclutamiento de anchoa estimado por el método acústico en 13,000 TM en la Bahía de Málaga. La distribución de tallas de los reclutas de anchoa presentó un aumento de 2 cm aproximadamente entre los años 2000 y 2001. La estacionalidad de la puesta se corresponde con las estimaciones del modelo de crecimiento para cada año. Los datos del medio-ambiente para los 2 años muestreados son aportados por un proyecto de seguimiento trimestral de las condiciones oceanográficas. La biomasa zooplanctónica aumentó de forma significativa, en costa como en mar abierto, durante Julio del 2001. Sin embargo, no se observaron cambios significativos en la temperatura superficial entre años. En el 2001, se observa un adelanto a primavera de la puesta de la anchoa. Este estudio evidencia a partir de datos de campo la relación entre variabilidad del crecimiento larvario y reclutamiento.

Palabras clave: anchoa, larvas, Mediterráneo, crecimiento, zonas de alevinaje, medio-ambiente, reclutamiento.

INTRODUCTION

The Alborán Sea anchovy (*Engraulis encrasicolus*) is the most economically valued of the small pelagic species. Unfortunately, its resources suffered a drastic decline during the mid-eighties (Giráldez and Abad, 2000). At its peak, landings amounted to 28,000 tons during 1982, among which 87% corresponded to catches from the Southern Alborán and 13% to catches from the Northern Alborán (Giráldez and Abad, 1991). The lowest landings occurred during 1993, coinciding with a poor recruitment that may have been caused by the bloom of a species of mesopelagic nature, *Capros aper,* in the Alborán Sea (Abad and Giráldez, 1990). Though fishing effort applied by the purse-seine fishery has decreased during the last two decades from 203 vessels in 1980 to 120 in 2001 (Giráldez and Alemany, 2002a), the anchovy resources have not recovered to the biomass levels prior to their decline. Since then, the main bulk of the anchovy resource from the northern coasts of the Alborán Sea has been concentrated in the Bay of Málaga, whose port lands on average as much as 85% of the total catch from the southern Mediterranean region. Therefore, the landings from this port represent a proxy of the stock's abundance, and since the fishery principally captures –0 age classes, it also represents the recruitment trend (Giráldez and Alemany, 2002a).

The nursery grounds of the species are concentrated near the coasts facing the city of Málaga, where in the past inshore artisanal fisheries based on beach seine fishing gear exploited its larval stages intensively as described by García *et al.*, 1981 and Reina-Hervás and Serrano, 1987.

Based on the observation of their reproductive parameters, Giráldez and Abad (1995) set their spawning season from early spring to early autumn, with a peak in June-July. With regard to ichthyoplanktonic abundance, Rodriguez (1990) and Rodriguez and Rubín (1986) find anchovy eggs from May to November, while maximums were observed in August when surface temperatures ranged from 19-23 ºC.

Within the framework of a national funded project on the "Effect of abiotic and biotic factors on the distribution, abundance, viability of eggs and larvae of exploited fish populations" (CICYT MAR1999-0328-CO·-03), larval anchovies were sampled in the nursery grounds off the Bay of Malaga during the 2000 and 2001 anchovy spawning seasons to assess the influence of environmental conditions on their daily growth.

The ECOMALAGA quarterly monitoring programme of the Instituto Español de Oceanografía provided the data on the environmental and oceanographic variables of the Bay of Málaga and its surrounding waters. To assess the impact of differential growth rates observed between the two years on the recruited population, data from the ECOMED project on the acoustic evaluation of small pelagic resources during the anchovy recruitment season were also provided.

It is generally recognised that recruitment success in most pelagic fish is determined by the degree of survival in their early life stages. Mortality in these stages can be caused by numerous reasons, such as predation, starvation and hydrological transport to unfavourable feeding grounds, yet the way that these factors interact is still a matter of debate among researchers (Bailey and Houde, 1989; Legget and DeBlois, 1994). A poor growth rate may lead to an increase in mortality due to the prolongation of time spans within vulnerable larval sizes (Folkvord and Hunter, 1986). Predation was shown to have a much higher impact on mortality than starvation in the Bay anchovy (*Anchoa mitchilli*) (Leak and Houde, 1987). Houde (1987) from literature derived data indicated that small variations in the growth rates could lead to major recruitment variations.

The analysis of otolith microstructure offers great potential for analysing the daily growth of the larval stages, which in small pelagic species are most susceptible to mortality (Houde, 1987). The daily deposition of increments on otoliths allows age determination and growth analysis (Geffen, 1982, Campana and Nielson, 1985) in a number of species. From the environmental viewpoint, otolith microstructure also provides a tool , for assessing the seasonal, environmental or geographic differences observed through the analysis of increment widths and growth rate differences (Campana and Neilson 1982; Moksness and Fossum 1991; García *et al.*, 1998).

With increasing larval age, certain advantages are observed in the analysis of otolith microstructure. Daily increments are sharper and more distinct with age, thus facilitating a greater precision of age estimates. An otolith intercalibration exercise among experienced readers showed a coefficient of variation in the readings of less than 10 day old larvae of 30%, decreasing to 10% over this age (Moksness *et al.*, 2000). Another advantage lies in the longer historical record of an individual larva registered in the otolith. The transition from the early
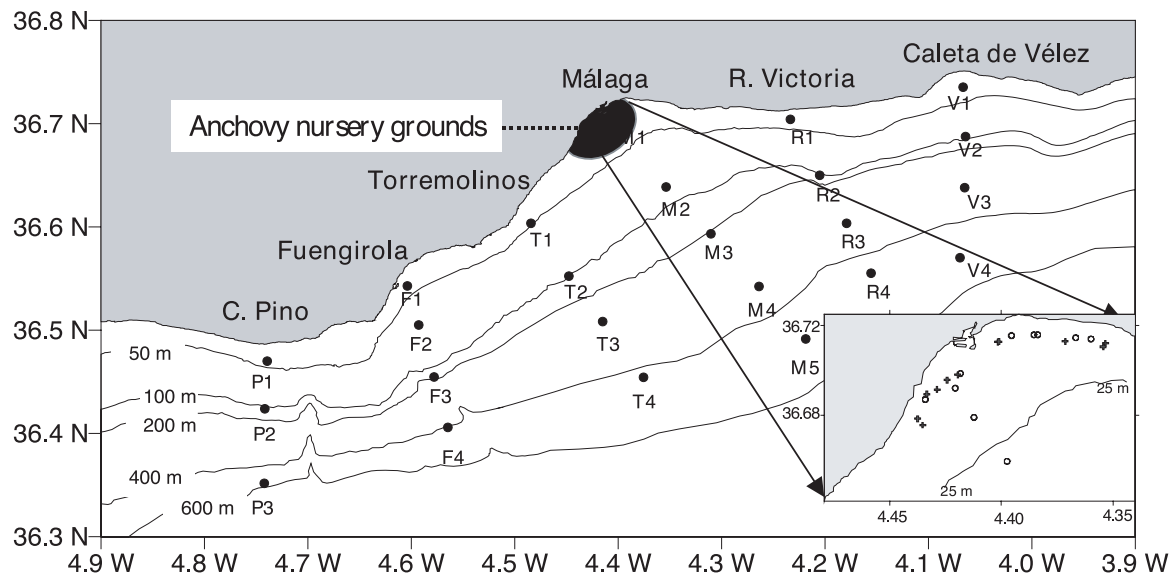
FIG. 1. – Study area of the ECOMALAGA monitoring program. Points denote CTD and Bongo 40 cm stations. The lower amplified map indicates the site of 1 m Bongo hauls (indicated as + for July 2000 and O for July 2001) carried out specifically for the anchovy daily growth study.

ontogenic stages to later developmental stages (e.g. endogenous to exogenous feeding, the initial growth bursts) and environmental changes leave check marks in the otoliths of larvae. Mortality in anchovy larvae declines with age during the developmental stages and their survival is growth-rate dependent (Rilling and Houde, 1999). Therefore, it is believed that an approximation to the pre-recruitment stage can yield a better growth to recruitment relationship (Peterman *et al*., 1988). The nursery grounds off the coasts of Malaga, once renowned for their intensive fishing capacity for anchovy/sardine fry, provide an excellent site for verifying growth characteristics and survivorship to recruitment.

MATERIALS AND METHODS

The environmental characteristics of this study on daily larval growth of anchovy is provided by the ECOMALAGA monitoring programme (Camiñas *et al.,* 1996), based on the information acquired from 24 oceanographic stations distributed in 6 transects perpendicular to the coastline (Fig. 1) with a quarterly sampling frequency.

Sampling at sea

The seawater properties of the water column were monitored by means of a Seabird 25 CTD profiler to 300 m depth where possible at each of the 24 stations. Niskin water bottle samples were taken at different depth strata (surface, 10, 20, 50 and 100 m) to estimate chlorophyll *a* content by filtering 2 litres through a Whatman GF/F filter (0.7 µm). Filters were conserved at –20ºC in plastic tubes with silicagel.

The abundance of anchovy eggs and larvae was delimitated in the area by means of Bongo (40 cm ∅) oblique tows to 100 m depth where possible, using nets of 200 µm mesh size geared with General Oceanics 2030 flowmeters. The plankton hauls were carried out at a ship speed of 2 knots, while the largest size classes of anchovy larvae used for the daily growth study were exclusively sampled in their nursery grounds off the coasts of Málaga city during July 2000 and 2001. They were sampled by a Bongo gear of cuadrangular aperture measuring 1 m diagonally equipped with a black tinted net of 1 mm mesh size to reduce avoidance of late larval stages. Moreover, all tows were carried out at night when anchovy larvae school at surface layers, inflating their gas bladders. The tows were superficial and over average depths of 10-15 m. Tow duration was fixed to 10 minutes to prevent damage to larva at a speed of 2 knots. Upon retrieval of the net, the cod-ends were washed gently in buckets filled with water so as to facilitate the sorting of larvae on board by placing the washed samples on glass trays. The sorted larvae were placed in cryogenic vials and conserved immediately in liquid nitrogen. The situation of the tows was random in the nursery area in search

of larval schools. Whenever a significant number of individuals had been fished, a tow was repeated in the same area to increase sample size.

Laboratory analysis

One of the samples of the Bongo 40 tow was used to estimate mesozooplankton biomass, while the other was used to sort the fish eggs and larvae in order to map their distribution. The sample for mesozooplankton biomass estimation was frozen on board, defrosted and weighed in the laboratory, and later dried for 24 hours at 60ºC for weighing with a precision balance.

The major and minor axis and perimeter of the sorted anchovy eggs were measured by means of an image analysis system.

Chlorophyll *a* was extracted with acetone 90% for 24 h at 4ºC in the dark, and subsequently analysed by spectrophotometry (SCOR-UNESCO 1966).

Anchovy larvae sampled in the nursery grounds with the 1 m Bongo gear were transferred from the liquid nitrogen containers to a –80ºC freezer until the moment of otolith extraction. Before extracting otoliths, larvae that were randomly selected from the vials were thawed at ambient temperature. The defrosted larvae were standard length measured by projecting them on a computer monitor using the image analysis program Image of NIH (National Health Institute of USA). After measuring, the larvae were dehydrated in the dry freezer CHRIST Alpha 2-4 for 24 hours. Larvae were then dry weighed on the precision balance Sartorius M2P 1 µg. After dry weighing, larvae were re-hydrated with distilled water to facilitate otolith extraction. The otoliths were extracted by fine needles and dropped onto the slide. They were then cleansed with a drop of distilled water. Once dried, the sagittae were fixed to the slide with nail lacquer.

The age interpretation was done with the sagittae using the OTO program designed by Andersen and Moksness (1988). To run this program, the following equipment is needed: a video monitor, a high resolution camera inserted in the microscope and a HEI digitiser connected to a Macintosh computer system. The count of increments and the measurement of widths of increments and nucleus are all done under 1000X magnitude. The criteria for interpreting the increments were established by means of an otolith intercalibration workshop held among experienced age readers (Anonymous, 1993).

Standard length-at-age data were fitted using a power model ($SL = SL_0 + \alpha \cdot Age^{\beta}$). In this model the intercept was fixed at 2.7 mm in order to minimise any possible bias due to growth rate effects (Campana and Jones, 1992). This value corresponds to the standard length at hatching for the Adriatic anchovy Dulčic (1997). Likewise, otolith radius vs age was fitted using a power model ($R = R_0 + \delta \cdot Age^{\phi}$) in which the radius at hatching date R_0 was fixed at 4.3 and 4.7 µm, the average values at hatch observed for the sampled larval anchovy populations. For the estimation of individual somatic growth rates (mm/day) we used the following equation:

$$(L_2 - L_0)/t,$$

where L_0 represents the mean size at hatch of the population (2.7 mm). In a similar manner, the individual growth rate of otoliths were estimated.

The expected growth rate at a given age was calculated through the derivative of size (SL, otolith radius) at age functions. The daily growth rate in length (mm_d^{-1}) at age=t was estimated according to the formula:

$$dSL/dt = \alpha \cdot \beta \cdot t^{(\beta-1)}$$

One factor ANOVA were applied to test differences between years (e.g. zooplankton biomass, anchovy egg sizes). ANCOVA on log transformed data was used to test differences in the somatic and otolith growth models using age as covariate, and differences in the allometric growth of SL and dry weight using otolith radius as covariate. Likewise, an ANCOVA was applied to test the differences in the individual growth rates using SL and age as covariates.

Recruitment estimation

Small pelagic fish resources are estimated from the yearly acoustic ECOMED survey carried out along the Spanish Mediterranean coasts in November-December on board the *R/V Cornide de Saavedra*. The period in which the survey is carried out is coincident with the anchovy recruitment season in the Mediterranean. The area covered in the acoustic tracking is subdivided into two strata: one extending from 30 to 100 m and the other from 100 to 200 m. The acoustic survey encompasses four zones, among which Alborán Sea constitutes an independent one that extends from the Bay of

Almería to the Strait of Gibraltar. This zone, which has a narrow shelf, has a grid of 39 transects, each one separated by 4 nautical miles. The acoustic tracking is done during daylight hours while fishing stations at night.

The estimations of abundance were obtained using an acoustic SIMRAD EK-500 unit at a frequency of 38 KHz with a split-beam transducer. The elementary sampling distance unit was 1 nautical mile (Abad *et al.,* 1998). For the identification of target species, pelagic trawls (9 and 10 trawls during ECOMED 2000 and 2001 respectively) were carried out with a net that had 20 m of vertical aperture equipped with a SIMRAD FR-500 net-sonder. The integration values of the target species related to each stratum were calculated according to the method proposed by MacLennan and Simmonds (1992). Only the catches from night trawls were used when the schools were dispersed. The target strength (TS) was: (20 log (L)-72.6) dB (Anonymous, 1986), where L is fish size.

The data provided in this study from the acoustic assessment originate from the ECOMED survey reports of an institutional nature, presented for fisheries management purposes. Data on the Bay of Málaga landings are from the IEO data base from the fisheries information network.

RESULTS

Since larval growth is mainly influenced by temperature and feeding (Buckley, 1984), it is deemed adequate to begin describing briefly the main differences observed between years with regard to the environmental characteristics that could have implications on growth at the early life stages. The anchovy larval cohorts sampled for daily growth in this study were sampled in July 2000 and July 2001, so only the environmental characteristics that conditioned their growth in this period are highlighted. However, due to the implications of spawning seasonality on recruitment, the anchovy egg and larval abundances over time are shown.

Environmental features

Hydrographic conditions

The hydrographic setting during the anchovy larval sampling for the daily growth study is shown in Figure 2, describing the respective surface (10 m) temperature and salinity distributions over the ECOMALAGA survey area in July 2000 and July 2001. The temperature regime of the water column at the 10 m and 20 m depth levels can be considered rep-
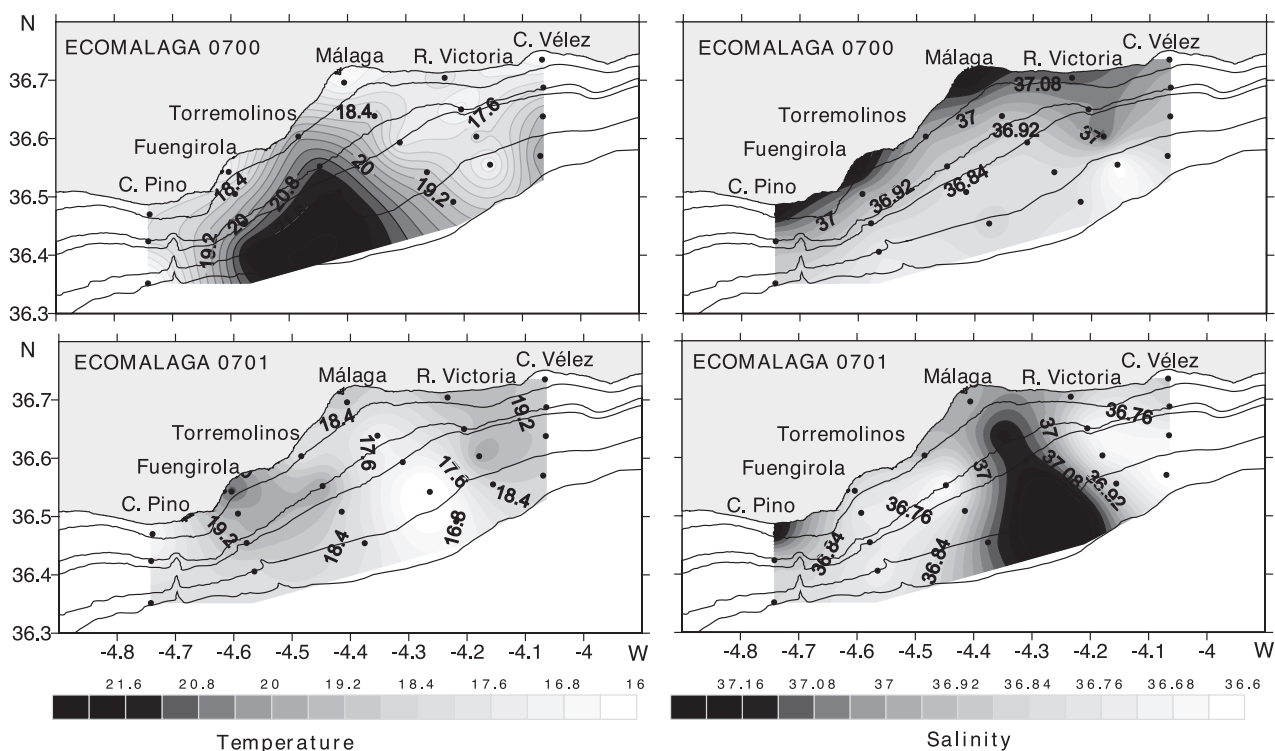

FIG. 2. – Surface temperature (ºC) and salinity distribution (PSU) of the ECOMALAGA survey in July 2000 and July 2001.

resentative of the water column occupied by the anchovy larval stages (Palomera, 1991; Coombs *et al.*, 1997).

During the July 2000 survey, the western sector of the sampled area showed higher temperatures in offshore waters. At the 10 m depth, the temperatures ranged from a minimum of 15.5°C to a maximum of 22.0°C, while the temperature at 20 m varied from 14.3°C to 20.8°C. During the July 2001 survey, the temperature at 10 m ranged from 15.0°C to 21.0°C, while for the 20 m level these values ranged from 14.8°C to 19.9°C. In the central part of the survey area, an intrusion of colder water masses was observed. The mean temperature at the 10 m level for 2000-2001 over the survey area was 18.7 and 18.4°C respectively, while for the 20 m level both years registered the same mean temperature of 16°C. The same result was observed when only the stations surrounding the anchovy nursery grounds were considered, that is the two most coastal stations from transects T, M and R. No significant differences (p>0.05) were observed between years (18.5 and 18.7°C for 2000 and 2001 respectively).

With respect to the salinity distribution (Fig. 2), the presence of Atlantic water masses, which is a normal characteristic of the Bay of Málaga coastal region, is evidenced. No values above the interface between Mediterranean and Atlantic water masses (37.5 PSU) were observed. The higher salinities and lower temperatures observed during July 2001 in the central part of the survey area indicate subsurface upwelling.

Chlorophyll a

The distribution of chlorophyll *a* values over the survey area at 10 and 20 m in July 2000 and July 2001 is shown in Figure 3. Coincident with the subsurface upwelling located along the Malaga transect (M), a phytoplankton bloom was observed. However, no statistical differences (p>0.05) were observed in the individual or averaged values of chlorophyll *a* over the depths 10 and 20 m between years. This bloom was particularly high at station M2, showing averaged values over the water column of 8 mg/m³.

Mesozooplankton biomass

Mesozooplankton biomass showed contrasting differences between the July 2000 and 2001 ECO-MALAGA surveys (Fig. 4). These differences were statistically significant (ANOVA p<0.01). The averaged values of zooplankton biomass during 2001 represent on the whole more than a two-fold
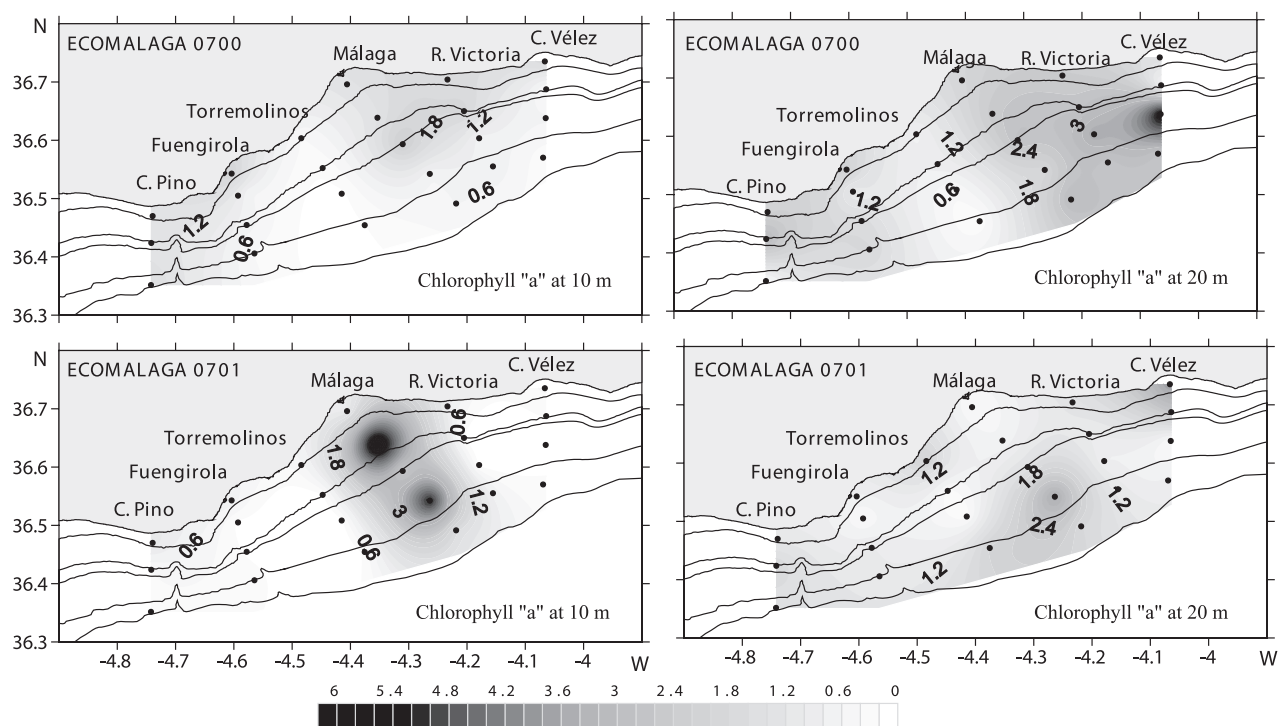

FIG. 3. – Chlorophyll *a* (mg/m³) distribution of the ECOMALAGA survey in July 2000 and July 2001 at the 10 and 20 m depths.
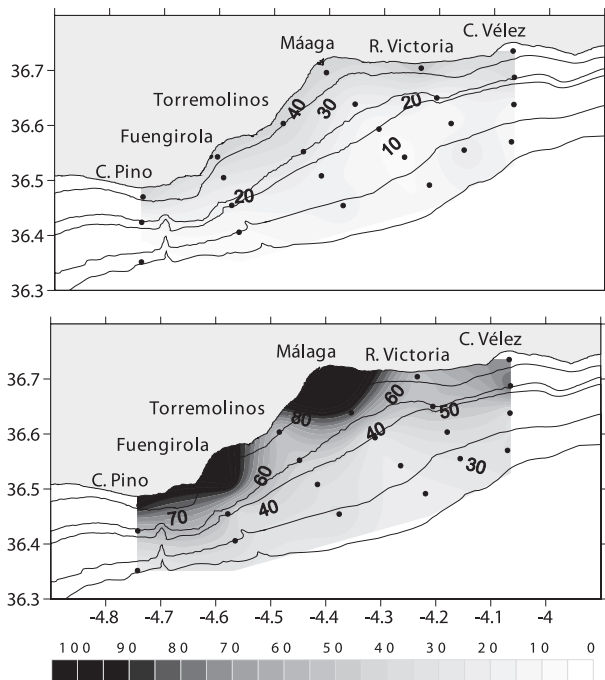
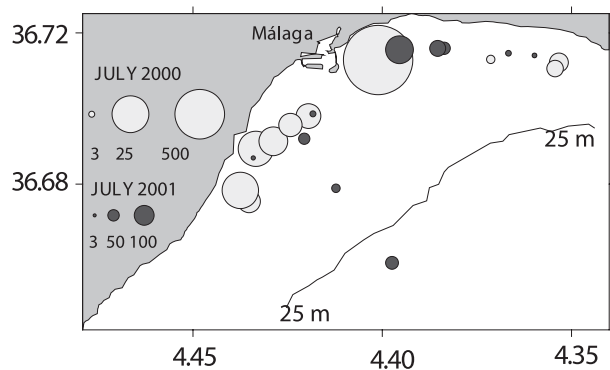Fig. 4. – Mesozooplankton biomass (mg/m³) distribution of the ECOMALAGA survey in July 2000 and July 2001.

Fig. 5. – Larval catch and positions of the 10 minute surface hauls off the nursery grounds facing the city of Málaga carried out with the Bongo 1 m quadrangular opening are represented by proportional light-shaded (July 2000) and dark-shaded circles (July 2001).

increase in comparison to the previous year (average values of 22.7 and 58.3 mg/m³ respectively).

The mesozooplankton distribution pattern shows a strong coastal gradient. As expected, coastal stations show higher values than the offshore stations, generally doubling the offshore values during both years.

Anchovy larval growth

A total of 1215 and 294 anchovy larvae were captured from 11 and 10 tows by the 1 m Bongo gear during the 2000 and 2001 anchovy spawning season (July) respectively. All the tows were carried out in the nursery grounds facing the eastern and western beaches of the city of Málaga (Fig. 5). Nevertheless, during both years, the highest catch rates occurred in the neighbouring waters off the port of Málaga.

A total of 193 and 188 anchovy larvae were randomly selected from each of the series of tows carried out during the 2000 and 2001 spawning season. Both larval populations were normally distributed over a mean size of 13.6 and 13.7 mm respectively (Table 1).

The somatic growth pattern for each anchovy larval population, expressed as somatic gain in body size (SL) or body mass (dry weight) with age follow power fits (Fig. 6). The results show that the larval population from the 2001 spawning season grows faster in length and in body mass than in the previous year. The ANCOVA test on the linear relationship of Ln SL and Ln Dry Weight versus Ln Age showed significant differences between years (p<0.01). However, this difference did not stand for otolith growth (Fig. 7).

TABLE 1. – Basic statistics of the principal parameters used in the daily growth analysis of the post-larval anchovy populations from July 2000 and 2001 (numbers in brackets correspond to standard deviation values).

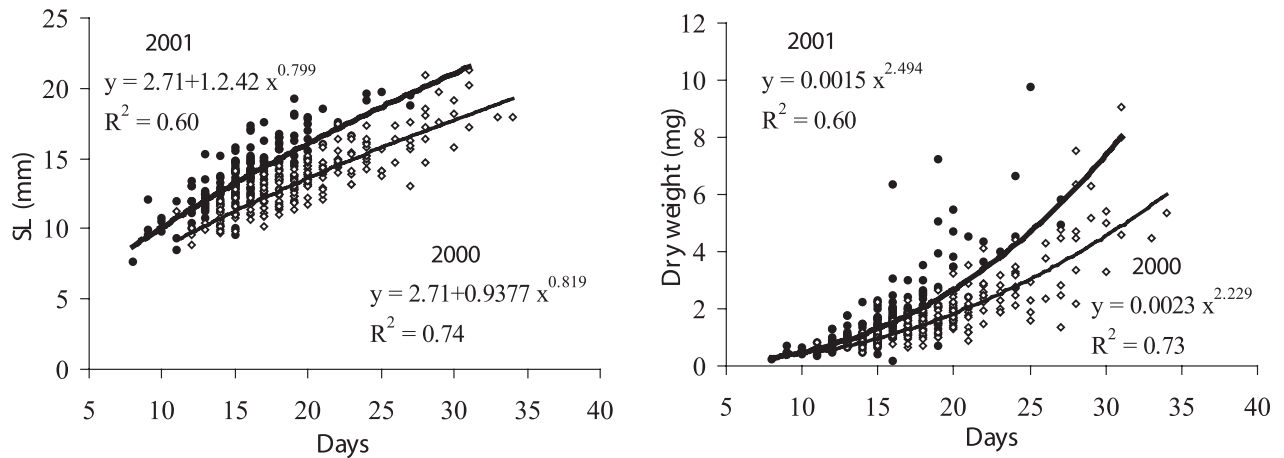| Survey	Variable	Mean (Std. Dev.)	Min (Max)	N
July/00	Standard length (mm)	13.62 (2.28)	8.86(21.33)	193
	Dry weight (mg)	2.08 (1.379)	0.485 (9.053)	
	Nucleus	4.7 (0.38)	4 (6.4)	
	Otolith radius (μm)	55.59 (14.61)	39.8 (110.8)	
	Days	20 (4.42)	11 (34)	
July/01	Standard length (mm)	13.79 (2.24)	7.62 (19.69)	188
	Dry weight (mg)	1.77 (1.33)	0.182 (9.75)	
	Nucleus	4.3 (0.45)	3.4 (5.9)	
	Otolith radius (μm)	42.61 (11.64)	15.2 (86.8)	
	Days	16 (3.13)	8 (27)	

FIG. 6. – Somatic growth models of larval size (SL) and dry weight from the anchovy larval populations spawned during July 2000 and 2001.

The estimated growth rates for the larvae sampled during 2001 were 20% higher than those of larvae sampled in 2000. The estimated growth rate for a 10 mm larva during the 2000 spawning season was 0.49 mm/day, while this value increased to 0.62 mm/day for the 2001 population. At the 15 mm size class, the estimated daily growth rates of the 2000 and 2001 populations were 0.43 and 0.54 mm/day respectively. At the 20 mm size class, these values were 0.40 and 0.50 mm/day respectively. Throughout the size classes, there was an average difference of 0.1 mm/day in favour of the 2001 population. This means a temporal difference of a week to reach a 20 mm size.

The differences observed in the daily growth rates are clearly shown in Figure 8, which represents the individual estimates of growth rates of the respective populations. An ANCOVA test was applied to test whether these differences were significant, using age as covariate and likewise with size. Both tests showed significant differences (p<0.01). However, the estimates of otolith growth

rates do not show these differences which is caused by the relationship of otolith radius and increments (Fig. 7), meaning that for a similar otolith radius size, similar ages are attributed. In general, slower-growing larvae have larger otoliths than fast-growing larvae in the same size class.

The relative growth of a body constituent such as SL or dry weight to another body element such as the otolith radius also provides an insight into the differences observed. The allometric relationship between SL and dry weight with otolith radius show higher larval sizes and weights per otolith radius

TABLE 2. – Allometric growth models of SL and dry weight relationship on otolith radius of the anchovy populations from the 2000 and 2001 spawning seasons.

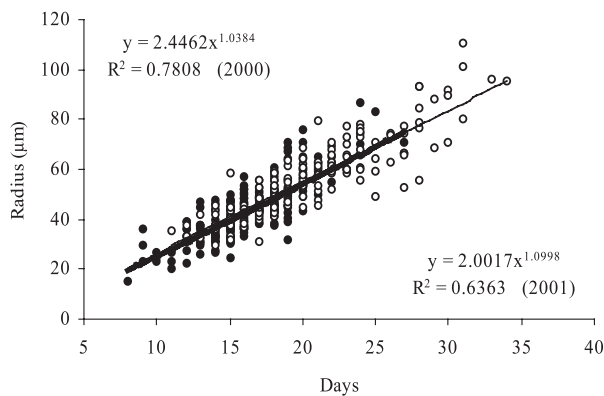| Independent variable: Otolith radius				
Survey	Dependent variable	Relative growth equation	R^2	N
07/00	SL (mm)	$y = 1.2314 * x^{0.5996}$	0.86	193
	Dry weight (mg)	$y = 0.0005 x^{2.0486}$	0.85	
07/01	SL (mm)	$y = 1.6829 * x^{0.5625}$	0.85	188
	Dry weight (mg)	$y = 0.0005 * x^{2.1501}$	0.85	

FIG. 7. – Otolith growth model for larval *E. encrasicolus* population spawned during July 2000 and July 2001.
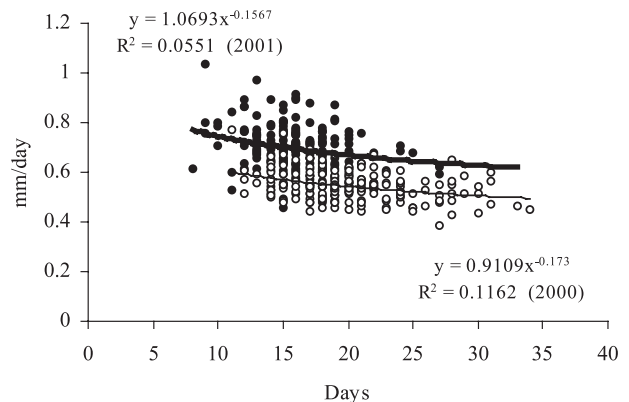

FIG. 8. – Individual growth rates of the *E. encrasicolus* larval populations spawned during July 2000 and 2001.
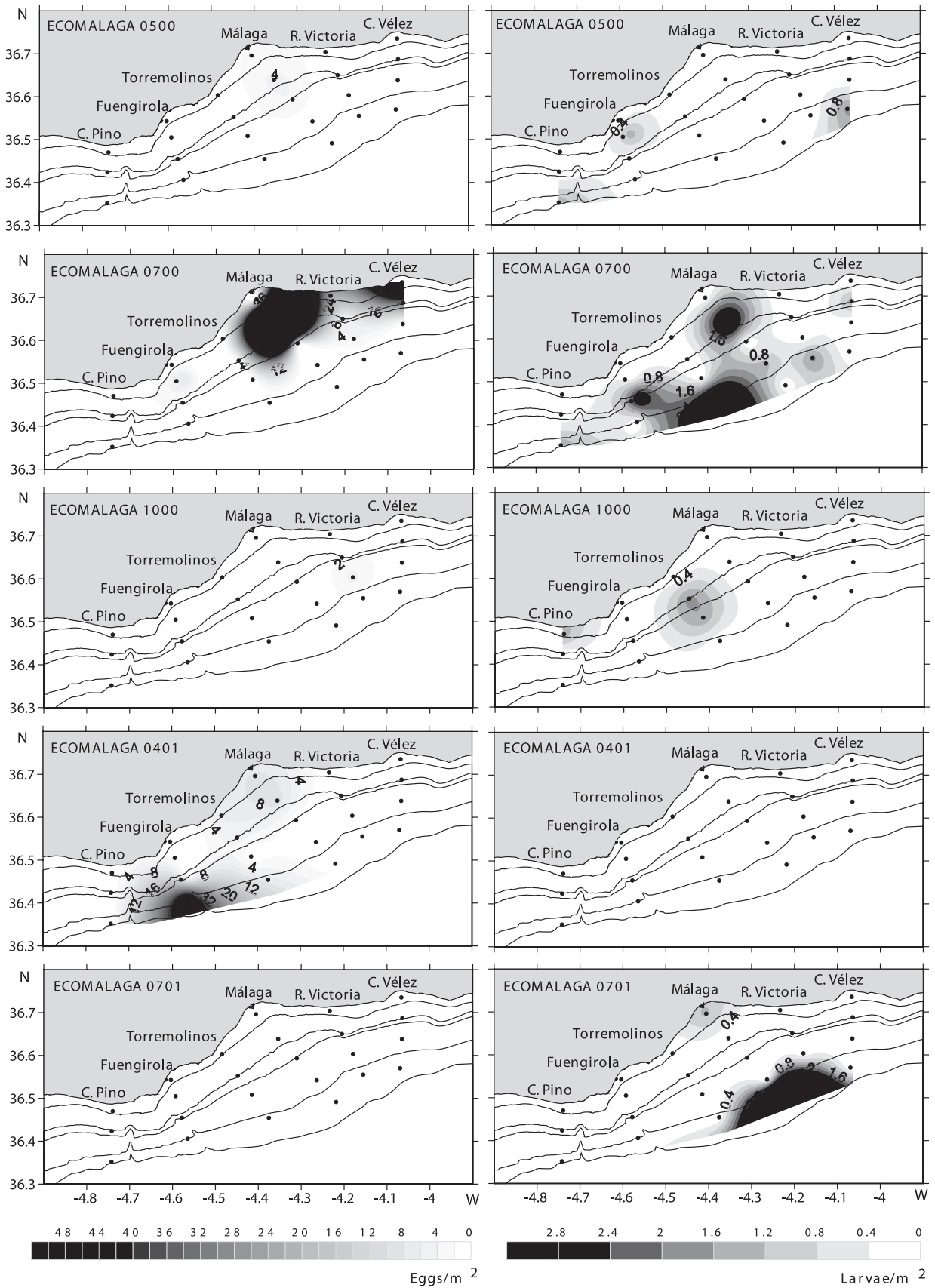
FIG. 9. Anchovy (*E. encrasicolus*) egg and larval distributions off the Bay of Málaga from the ECOMALAGA surveys series during years 2000 and 2001.
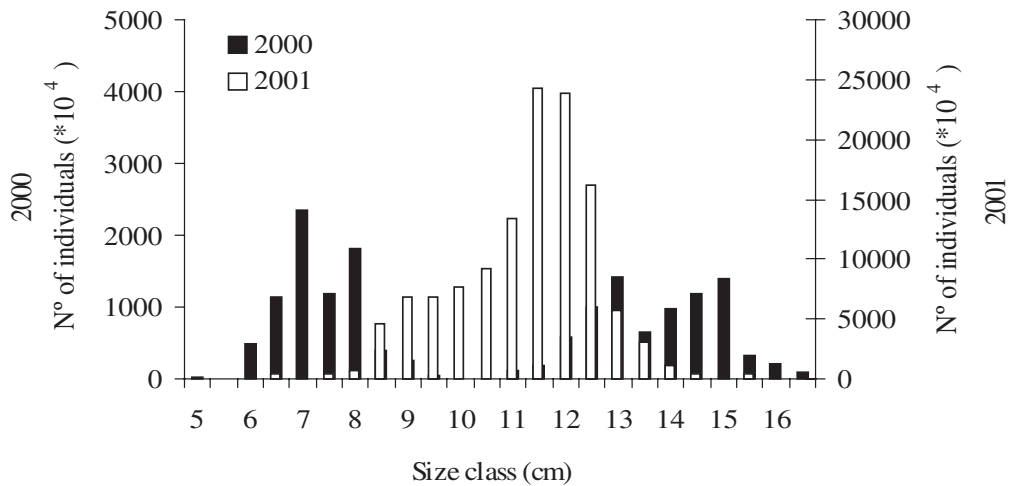
Fig. 10. – Acoustic estimates of *E. encrasicolus* individuals by size classes from the 2000 and 2001 ECOMED surveys.

unit in the 2001 population (Table 2). ANCOVA tests using Ln SL and Ln Dry weight using Ln Otolith radius showed significant differences (p<0.01).

2000-2001 anchovy spawning seasonality

From the quarterly monitoring surveys carried out during 2000 and 2001, anchovy spawning was observed from spring to autumn (Fig. 9). The highest egg and larval abundances among all the ECO-MALAGA surveys occurred in July 2000, while the lowest egg and larval abundances occurred during spring and autumn of that year. During 2001, early anchovy spawning is observed from the results of the April survey, which was not accompanied by the presence of larvae. In contrast to the preceding year, the summer survey of July 2001 showed insignificant egg abundances at two stations. Likewise, only two stations presented anchovy larvae in this survey.
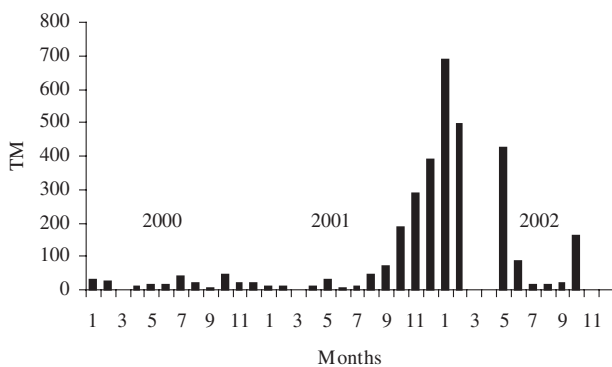

Fig. 11. – Anchovy landings by months during years 2000, 2001 and 2002 (March and April 2002 was a biological stop for the fishing fleet).

The area, perimeter, major and minor axis of 68 and 62 anchovy eggs produced during the respective peak spawnings of 2000 (summer) and 2001 (spring) were measured by an image analysis system. A one factor ANOVA presented significantly greater egg area, perimeter and major axis of the eggs spawned during 2001 (p<0.01).

Anchovy recruitment

The results of the acoustic estimates (in number of individuals by size class) for the Alborán Sea anchovy are shown in Figure 10. The anchovy stock estimates were 13,000 tons for the year 2001 (Giráldez, 2002). For the year 2000, a lack of ship time hampered the coverage of the westernmost sector of the Alborán Sea. Nevertheless, 1716 tons were estimated by Giráldez and Alemany, (2002b) for the NE Alborán zone (from Cape Gata to Fuengirola). The size frequency distributions of the acoustic estimates differ greatly. Whereas during 2000 a bi-modal distribution of sizes was observed, in which the juveniles (sizes from 6 to 9 cm) are completely segregated from the adult stock, in 2001 the distribution is unimodal, with a slight negative skew in which the recruit size classes showed a significant increase. Whereas during the 2000 recruitment season the anchovy recruits were distributed over the 7 cm size class, in the 2001 recruitment season the recruitment size increased towards the 9 cm size class (Fig. 10).

This increase in the anchovy stock during the 2001 recruitment was substantiated in the landings of anchovy recorded in the port of Málaga (Fig. 11). Landings showed an increasing trend at the start of the recruitment season, from September onwards.

DISCUSSION

There is growing evidence from field-based research that enhanced growth rates in the larval stages play an important role in the survival rate of the early life stages of a wide range of species (Hovenkamp, 1992; West and Larkin, 1987; Post and Prankevicius, 1987; Wilson and Meekan, 2002; Rilling and Houde, 1999), showing their influence on recruitment success in a number of species (Campana, 1996; Bergenius *et al.*, 2002). It is reasonable to expect a relationship between larval growth and recruitment because studies on other anchovy species have shown that survival within each ontogenic larval stage is size-specific and growth-dependent (Rilling and Houde, 1999), that mortality declines with age, and that one of its main causes is predation (Leak and Houde, 1987; Folkvord and Hunter, 1986). It is believed that the results of this study will shed some new evidence on the influence of upgraded anchovy larval growth on recruitment success.

It is also significant to highlight the role of Bay of Málaga as a nursery ground that formerly commercially fished the larval shoals, similar to the actual Japanese "*shirasu*" fishery, which is currently researched for conservation and assessment of small pelagic resources (Maki and Kishida, 1997).

For Agostini and Bakun (2002), the Bay of Málaga represents an example of an eastern ocean anchovy-spawning habitat, a sheltered bight downstream from an upwelling centre located on the western Alborán coast. During July 2001, a subsurface upwelling was detected in the central part of the survey area (see Fig. 2). This hydrographic feature is produced by the effect of cyclonic gyres released from the Atlantic mainstream (Cano and Gil, 1984; Vargas *et al.,* in press). As a result, higher primary production in the surface layers is induced, as demonstrated by the extreme chlorophyll *a* values in the Malaga transect (see Fig. 3). This swell of higher primary production may have caused the two-fold increase of mesozooplankton biomass (Fig. 4). The mesozooplankton biomass increase was especially noteworthy in the coastal region, hence affecting the nursery grounds that constitute a narrow strip of shallow inshore turbid and mixed waters, where larval shoals concentrate. Their concentration mainly at night facilitates their sampling, as many as 500 larvae being obtained in a single tow (see Fig. 5).

The estimation of age by otolith microstructure requires a consistent degree of precision that in the long term benefits the reliability of growth rate estimates. Precision is gained with the age of larvae over 10 days old (Moksness *et al.,* 2000) by showing sharper and clearer edges of increments, thus also allowing more accurate increment measurements. Most of the larval stages analysed fall under this category, since the mean age for the 2000 population was 20 days, and that of the 2001 population was 16 days (Table 1).

The SL and dry weight at age relationships (Fig. 6) showed a higher growth pattern of the anchovy larval cohort sampled during the 2001 spawning season. Contrarily, this was not so for the relationship of otolith radius at age, in which for an equal size of otolith radius a similar age was ascribed. The allometric relationship of somatic growth expressed in SL and dry weight in relation to otolith radius showed greater larval size in length and in weight per otolith unit measurement in the 2001 larval population. Generally, for a given larval size, a slow-growing larva has a larger otolith size than a fast-growing one. This is due to the greater time span to deposit increments in a slow-growing larva than a fast-growing one, unless great differences occur in the widths of increments. Increment width is highly influenced by temperature (Pavlov *et al.*, 2000; Karakiri *et al.*, 1989), and in our case, the temperature regime between years was similar, thereby not showing significant differences in the sampled area.

The variability of growth rates at the early stages can provide another perspective to the problem of fluctuating recruitment levels (Houde, 1987). As a result of the differential daily growth observed during the 2000 and 2001 spawning seasons, the estimated daily growth rates showed an increase of 20% in terms of SL increment during the latter spawning season. Houde (1987) indicated that small variations in the growth rates could lead to major recruitment oscillations, and in the present case the variation of the daily growth rate observed between 2000 and 2001 cannot be considered small. From the ontogenic stage duration viewpoint, there would be a time span difference of 17 days in favour of the 2001 population to attain a size of 40 mm, which corresponds to the metamorphic stage of squamation (D'Ancona, 1931) from the larval to the juvenile stage, assuming that each of the anchovy larval populations had followed their respective daily growth model to the metamorphic size. This difference increases to 32 days to reach the size of a 7 cm juvenile anchovy. Since mortality is stage-duration and size specific (Rilling and Houde, 1999), this time-

span difference has immense consequences on survival rates.

The size frequency distributions of the recruitment acoustic surveys provided by the pelagic trawls (see Fig. 10) seem to respond to the different growth patterns observed during the 2000 and 2001 spawning seasons. Since the Mediterranean anchovy's size at first maturity is 10.9 cm (Giráldez and Abad, 1995), below this threshold size can be considered as –0 age class. During the 2000 spawning season, most recruits were in the modal size class of 7 cm, which would correspond to an estimated birthdate distribution of mid-June calculated from the date of capture by the pelagic trawls (mid-December), while for the 2001 population this size class would have been born by mid-July. These estimates are based on the assumption that the respective larval daily growth patterns for each year are followed throughout their developmental stages. This spawning seasonality is in agreement with the observations of Rodríguez, (1990) and Rodríguez and Rubín (1986). The fact that practically no recruits of 7 cm appeared in the size distribution of the 2001 pelagic trawls is consistent with the egg survey carried out during July 2001, which showed negligible egg catches in the samples (Fig. 9). On the other hand, the modal size class of recruits during the 2001 recruitment season was 9 cm (Fig. 10). From the estimates of the daily growth model, this size class would have been born by the beginning of May, which agrees with the early spring spawning observed during that year and the much lower larval catch rates observed in July in the nursery grounds (Fig. 5). However, such differences in the recruit size classes could also be attributed to daily growth differences, as observed by Waldron (1995) in the South African anchovy (*Engraulis capensis*). A difference of 0.1 mm/day between years of high and low daily juvenile growth rates, similar to our estimates, could cause interannual variations of 2 cm in the recruit size classes.

Bearing in mind that the sampled anchovy larvae belonged to by far the most important nursery grounds of this species in the region (García *et al.*, 1981), and that the anchovy landings in the port of Málaga represent on average 85% of the total amount landed in the SW Mediterranean region, i.e. the Alborán Sea (Giráldez and Alemany, 2002a) (see Fig. 11), it is reasonable to draw a direct relationship from the higher growth rates observed in late larval stages and the successful recruitment for the 2001 year class.

The causes of the substantial increase in daily growth rates in the late larval stages of anchovy during the 2001 spawning season seem to be related to an enhanced production in the Bay of Málaga, possibly induced by the subsurface upwelling detected in the central part of the ECOMALAGA survey area, evidenced by the high values of chlorophyll *a* in this area. This may have caused the higher production at the higher trophic level as observed by the two-fold increase in the mesozooplankton biomass values during July 2001. Higher productivity induced by hydrographic phenomena, such as upwelling or river outflows, has been related to anchovy recruitment success in other regions (Borja *et al.*, 1998; Cury *et al.*, 1996).

Considering that the Mediterranean anchovy larvae feed mainly on the developmental stages of copepods, mainly nauplii (Tudela and Palomera, 1995; Conway *et al.*, 1998), and that the predominant groups of zooplankton in the Bay of Málaga are composed of copepods and cladocers (Pérez-Martin and Camiñas, 1995), whose relative proportion is 60/20 in favour of the former (Rodríguez, 1983), a great increase in zooplankton production could have led to a greater availability of feeding resources. Rilling and Houde (1999) observed in the Bay anchovy (*Anchoa mitchilli*) a positive relationship of larval growth rate with temperature and zooplankton abundance as a proxy for prey abundance.

Nonetheless, the maternal effects on growth cannot be overlooked. Monteleone and Houde (1990) studied the influence of maternal size of striped bass (*Morone saxatilis*) on the growth of larvae, finding that smaller maternal sizes produced smaller offspring that rendered lower growth rates. Maternal effects can also be due to parental genetic qualities, as observed in herring (Høie *et al.*, 1999). The measurement of egg dimensions was thought adequate to assess quality traits of the parental population and enhanced larval characteristics that may favour survival, as documented extensively in the literature for a number of species (Marteinsdottir and Steinarsson, 1998; Gamble *et al.*, 1985; Moodie *et al.*, 1989; Duarte and Alcaraz, 1989). The area, perimeter, major and minor axis of 68 and 62 anchovy eggs showed significantly greater egg area, perimeter and major axis of the eggs spawned during 2001 (p<0.01). Hence, the higher growth rates of the 2001 offspring could also be attributed to the parental quality of their spawners.

Regardless of which factors may have caused higher growth rates in the 2001 anchovy larvae,

either parental quality or the more than suitable production-related environmental conditions prevailing during their development, or a combination of both, this study provides evidence on the influence of growth rates estimated from field captured anchovy larvae on recruitment.

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