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A DRIFT STUDY OF VERTICAL DISTRIBUTION AND MORTALITY  
OF *Engraulis anchoita* EGGS AND LARVAE \* ‡

by

RAMIRO P. SANCHEZ <sup>1</sup>, JANINA D. DE CIECHOMSKI <sup>1,2</sup>  
CARLOS A. LASTA <sup>1</sup> AND RAUL A. GUERRERO <sup>1</sup>

<sup>1</sup> Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP),  
Paseo Victoria Ocampo N° 1, 7600 - Mar del Plata, Argentina.

<sup>2</sup> Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET).

RESUMEN

**Estudio de distribución vertical y mortalidad embrionaria y larval de *Engraulis anchoita* mediante una boya de deriva libre.** Las variaciones lagrangianas en la distribución y sobrevivencia de embriones y larvas de anchoíta dentro de una mancha de plancton fueron estudiadas mediante un recolector de apertura y cierre múltiple, siguiendo una boya de deriva libre. La boya fue equipada con un emisor de señales, reflector de radar y luz intermitente y fue conectada con un deflector suspendido en la profundidad de 15 metros, que correspondía a la mayor concentración de huevos y larvas dentro de la mancha. El rastreador fue utilizado en aguas de la plataforma continental frente a Necochea (Prov. de Bs. Aires), durante el desove primaveral más intensivo en el año 1983.

Se muestrearon tres estratos de profundidad: sobre la termoclina, en la termoclina y por debajo de la misma, mediante el muestreador de Motoda, en la vecindad de la boya. La abundancia de huevos y larvas fue monitoreada en las muestras tomadas a intervalos de tres-cuatro horas durante tres días. Simultáneamente en cada estación se tomó una serie de datos hidrográficos y climatológicos.

La eficiencia del sistema al utilizar la boya como marcador lagrangiano fue examinada mediante la aplicación del ANOVA multifactorial con el fin de analizar la variabilidad entre los días, régimen de iluminación, estratos de profundidad muestreados, estructura poblacional y sus interacciones. Se comprobó que los vientos de superficie no afectaron en forma significativa la trayectoria de la boya.

Las características de la distribución vertical de los huevos y larvas, en diferentes horas del día fueron analizadas mediante el cálculo de las profundidades de los centros de masa, los índices de dispersión e índices de agregación para cada estadio de desarrollo. Hubo evidencia de migración vertical nocturna en larvas mayores de ocho mm de longitud estándar. Aunque la incidencia en la alimentación basada sobre la presencia de contenidos visibles en los tractos digestivos de larvas fue baja, se evidenció un período de alimentación de 14 horas, entre las 7.00 y las 21.00. La migración vertical hacia la noche de larvas mayores no pareció relacionada con la actividad trófica.

Para el cálculo de la mortalidad durante el período embrionario y larval se ha desarrollado un modelo que representa a esos estadios, mediante una única ecuación que asume que la mortalidad no es constante sino dependiente de la edad. Se comparan los resultados obtenidos con aquellos que provienen de los métodos clásicos basados en el concepto de decrecimiento exponencial constante en la numerosidad de la cohorte.

SUMMARY

Lagrangian changes in distribution and survival within an anchovy egg and larvae patch were studied by means of mul-

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multiple opening/closing sampling following a free drifting buoy. The buoy was equipped with a radar reflector and flashing light, and it was connected to a current cross drogue floating at 15 m depth, which corresponded to the main egg and larvae concentration within the patch. The drifter was launched on the Buenos Aires continental shelf, off Necochea during the spring spawning peak of 1983.

Three discrete depths (within, below and above the thermocline) were repeatedly sampled close to the drogue with a Motoda sampler. Egg and larval abundances in the vicinity of the drogue were monitored at 3/4 hour intervals for a period of three days. Each plankton station included a set of hydrographic and climatological data registered simultaneously.

The efficiency of the drogue as a Lagrangian marker was examined by means of the application of multifactorial ANOVA to test the significance of variability between days, light regime, sampling depths, population structure and their interactions. Wind drag on the surface unit did not significantly affect the trajectory of the drogue.

Patterns of embryonic and larval vertical distribution are discussed by means of the variations in the centre of mass, in the vertical dispersion and patchiness indexes for each developmental stage analyzed. There is evidence of diel vertical migration in larvae larger than 8 mm SL. Although the incidence of feeding based on observations of the presence of undigested food in the gut content of larvae was low, a daily feeding pattern over a 14-hour period starting after sunrise, was evident. Evening ascent of larger larvae was not related to feeding activity.

A single equation two-stage model, assuming age dependent mortality in the embryonic and post-larval period is derived and compared to standard models based on constant exponential decay during each developmental phase.

**Palabras clave:** Atlántico Sudoccidental, distribución vertical, mortalidad, embriones, larvas, anchoíta, seguimiento boya.

**Key words:** Southwest Atlantic, vertical distribution, mortality, embryos, larvae anchovy, drogue study.

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## INTRODUCTION

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*Engraulis anchoita*, is by biomass, the largest fish resource of the Southwest Atlantic (Ciechomski and Sánchez, 1989). The species plays a key role in the fisheries as trophic support of several commercially exploited stocks of pelagic and demersal fish (Angelescu and Fuster de Plaza, 1962; Angelescu, 1982).

The reproductive activity of the species in the sea off Argentina and adjacent waters has been extensively studied over the last 30 years. Current knowledge on the reproduction and early life history of the species in Argentine waters has been summarized by Sánchez (1990). Available information comes mostly of large-scale ichthyoplankton surveys, that served to delimit the spawning habitat (Ciechomski, 1968, 1969, 1970, 1971), describe reproduction seasonality (Ciechomski and Sánchez, 1986), assess the spawning stocks (Ciechomski and Capezzani, 1973, Ciechomski *et al.*, 1983, 1986, Sánchez and Ciechomski, 1984), and estimate embryonic mortality (Ciechomski and Sánchez, 1984). Little is known about the vertical or horizontal distribution of the species at finer scales, and this comes from investigations carried out using a Eulerian approach (Ciechomski *et al.*, 1986; Sánchez, 1986).

Large scale surveys, as those cited, often fail to improve our understanding of relevant recruitment processes, as events that affect the survival of larvae and may lead to year-class variability often take place in the micro and fine-scale. Vast spatial coverages are not easily reconciled with such concepts as synoptic representation and stationary state of the populations, which are necessary conditions for the appli-

cation of mortality models. Crucial events in the life history of a cohort, or relevant local gradients affecting the distribution of a patch may be masked by the typical arrangement of equally spaced plankton stations along transects, and cruises throughout the season (Fortier and Leggett, 1985; Heath and MacLachlan, 1987).

A much recommended alternative (Lasker, 1975; Hunter 1976; Saville and Schnack, 1981) is the study of changes occurring within a plankton patch as it is advected. During the last years, many field experiments have been reported in which free drifting drogues have been used as Lagrangian markers, in order to track distinct egg and larval cohorts (Bjorke, 1971, 1978; Dragesund and Nakken, 1971; Hempel and Schnack, 1971; Fahay, 1974; Smith *et al.*, 1978; Conte *et al.*, 1979; Shelton and Hutchings, 1982; Fortier and Leggett, 1985; Henri *et al.*, 1985; Heath and MacLachlan, 1987; Heath *et al.*, 1987, 1988, 1989; Christensen *et al.*, 1988; Owen *et al.*, 1989; Roepke, 1989; Wieland, 1989). Larval ecology studies from the Lagrangian perspective, have rendered valuable information, particularly in relation to larval transport, growth and mortality and feeding habits.

Water circulation during spring and summer in the shelf off Buenos Aires, is still a subject of controversy. Objectives of this study are to gain information on the transport routes of anchovy eggs and larvae in the area, on their vertical distribution and diel patterns of migration. We intend to compare intrapatch estimates of aggregation and mortality with those derived by multicohort data integration from mesoscale studies, and consider the validity of assumptions inherent in these methods.

## MATERIAL AND METHODS

Plankton samples, were collected on board RV Dr. E. L. Holmberg, during cruise No. 8, hereafter called EH-08/83, from November 7 to November 10 1983. The study area is located about 20 miles to the south of Necochea, in the continental shelf, off Buenos Aires province, Argentina.

As shown by several reports, the study area is included within the vast spawning grounds of the species during the spring peak in Argentine waters (Ciechowski, 1967, 1968, 1969, 1970, Ciechowski *et al.*, 1986). A more precise location was suggested by a previous cruise carried out in the same area and time (EH-07/81) which showed the presence of large amounts of eggs and larvae of the species (Sánchez, 1986).

The exact location of the beginning of the experiment was determined as the results of two preliminary oblique hauls with a Nackthai sampler. After the second tow a large patch of anchovy eggs and larvae was detected at 38°44'S and 58° 45'W. A temperature profile from a bathythermograph cast indicated the formation of a thermocline at 15-m depth.

A free drifting current cross drogue was launched on November 8 (0100 h) in order to stay with the same water mass and observe changes in the abundance and distribution of the patch as it was advected. The current cross consisted of two perpendicularly set metal panels, suspended from a surface buoy, equipped with a signal source, light, and a pole and flag to facilitate tracking. The cross was located at 15 m depth, as previous reports showed that anchovy eggs and larvae in the stratified waters off Buenos Aires, tend to accumulate over the thermocline (Ciechowski *et al.*, 1986). The drogue was tracked during 70 hours and recovered at 38° 44'S 58° 31'W, on November 10 at 2300 h.

Ichthyoplankton samples were collected in the vicinity of the drogue, with a multiple opening/closing Motoda sampler (Motoda, 1967). Three depths layers were sampled, within, above and below the thermocline. Depth of each net was determined from average readings of a clinometer. Warp length was regulated in order to keep the nets at 0-10m, 11-25m and 26-35m depth. The sampler was fitted with 200µ mesh nets. In order to calculate the volume of water filtered in each horizontal tow, digital flowmeters were mounted on the mouth of each net. The device was operated from the side of the ship at a towing speed of 3.2 kn. In average sampling took 25 minutes per station, covering a horizontal distance of 2.3 km.

The sampler operated satisfactorily in all but two stations (Nos. 336, 337) where part of the samples were lost. The efficiency of the device to catch all larval sizes was con-

trolled by means of 6 horizontal tows carried out with a Nackthai sampler (400 µ mesh net) at different levels in day and night stations. Due to the smaller mesh used, the Motoda sampler caught significantly more larvae smaller than 5.5 mm SL (preserved size) (Kolmogorov-Smirnov,  $\alpha=0.05$ ). The upper limit of the range of sampled sizes however, were coincident between the two devices.

Hydrographic and climatological measurements were taken during each plankton station. Wind speed and direction were measured on board. Water samples for temperature and salinity determination were obtained in each station by standard Nansen bottle casts. Four depths 0, 10, 20 and 40 m were repeatedly sampled.

Ichthyoplankton material was preserved in a 5% solution of buffered formalin. In the laboratory all the ichthyoplankton material was sorted, and counted. Anchovy eggs were staged and aged according to the scale and model described by Ciechowski and Sánchez (1984). Anchovy larvae were measured to the tip of the notochord with a graduated eye-piece and grouped in size categories of 0.5 mm SL preserved size. To convert this data to real size the equation of Theilacker (1980) was used. Larval production at age was estimated by dividing the abundance of each size group by the time spent in the size category. Duration of each size category was the inverse of the instantaneous growth rate (IGR) for the category, which in turn was obtained from the derivative of the growth curves. The Laird Gompertz growth model as described by Zweifel and Lasker (1976) was adopted to describe yolk-sac and post-larval growth. The model may be formulated as:

$$LS_{(t)} = L_0 \exp\{G[1-\exp(-\alpha t)]\}$$

$t = \text{age in days}$

Data on yolk-sac and post-larval growth, were obtained from experimental data (Sánchez, 1986) and from countings of daily rings in the post-larvae otolith (Sánchez, unpublished data).

Fitted expressions are:

$LS_{(t)} = 2.75 \exp\{0.5755[1-\exp(-0.3033t)]\}$ , for yolk sac larvae (2.75mm < LS < 4.2mm) and  $LS_{(t)} = 4.20 \exp\{2.7670[1-\exp(-0.0223t)]\}$  for feeding-larvae (> 4.2 mm LS).

Instant growth rate was calculated as:  $IGR = dLS/dt$   
 $IGR_{LS_i} = a LS (\ln LS_i / L_0 - G)$

Duration of size class  $LS_i = 1/IGR_{LS_i}$

In order to interpret the behaviour and trajectory of the drogue, calculations were made of surface wind generated drift by means Ekman's transport equation. The efficiency of the drogue to track the same plankton patch, was tested by

means of multifactorial ANOVA, on log-transformed data, following the procedure described by Smith *et al.* (1978). The variables considered were: days of the cruise (3), light regimes (2), sampled levels (3), and ichthyoplankton categories (4 = anchovy eggs, yolk sac larvae, post-larvae, and other fish larvae). Samples collected during the same day at the same light regime (3) were considered replicates. In order to meet the requirements of the ANOVA in terms of balance of the information, 18 out of the 19 complete stations were considered.

Aspects of variation of the vertical distribution of anchovy eggs, larvae and post-larvae, at different times of the day, were evaluated by calculation of the depth of the centre of mass (Heath *et al.*, 1988; Wieland, 1989), and the dispersion index (Frank *et al.*, 1989). Trends in the aggregation of the early developmental stages of the anchovy was studied by the application of Lloyd's patchiness index (Lloyd, 1967) to day and night samples. Numbers of organisms/100 m<sup>3</sup>, replaced the quadrat data usually used to calculate the index. The method of calculation included the estimation by maximum likelihood of the parameter *k* of the negative binomial distribution (Hewitt, 1981).

Feeding activity was estimated from the direct microscopic observation of undigested contents in the guts of anchovy larvae. Only when necessary specimens were immersed in glycerin to facilitate inspection (Arthur, 1976).

The decline of anchovy eggs and larvae during the study was described by the standard equations for constant exponential decay, applied to data grouped by day. Parameters of the model were obtained from log-linear and non linear procedures. Log-linear analysis was used for comparisons between days. The constancy of instantaneous mortality rates (IMR) between adjacent age groups was evaluated through the calculation of rates according to the cohort method (Wieland, 1988) and the equations presented by Lo (1985, 1986) for the estimation of IMR. As ANOVA results had shown homogeneity of slopes in all the eggs and larvae mortality estimates by the exponential model, for the derivation of the IMR the total production curve obtained during the cruise was used. The application of Lo's equations showed that IMR were not constant in any of the stages analyzed, and that *t<sub>c</sub>*, the critical age defined by Lo (1985, 1986) as marking a change in the trend of IMR values, should be set at the end of the yolk sac stage. We then proceeded to estimate a single mortality model, that could describe age dependent mortality both in the embryonic (eggs+yolk sac larvae) and post-larval stage. This type of decay can be described by equations basically similar to the Pareto family of survival models (Lo, 1985; Loos and Perry, 1991). The model presented here consists in a combination of age dependent power-exponential curves for the embryonic and larval phases. Complete details on the derivation of the model to this set of data is given by Sánchez and Hernández (MS).

## RESULTS

The analysis on board of material collected during the tows previous to the launching of the drogue revealed the presence of a dense patch of anchovy eggs and larvae. Three cohort of eggs could be identified, including a very high proportion of eggs in initial cleavage stages, yolk sac larvae, and small sized post-larvae of up to 10 mm SL. The presence of other ichthyoplankton components was also observed, particularly larvae of the family Sciaenidae. Surface temperature of water at the beginning of the experiment was 14.5 °C, depth of the mixed layer was 13 m, wind blew from NNW with a speed of 0.51 m/s, and bottom depth was 47m.

Fig. 1-A describes the trajectory of the drogue during the 3 day cruise. The area covered from the beginning of the experiment was approximately 58.37 km<sup>2</sup>. Total distance travelled by the drogue was 42.1 km, with a net direction towards the E, almost parallel to the coast line, and the 50m isobath. During its course the drogue crossed its previous path only once. Drift was intense during the first and third day (16.1 km and 18.1 km, respectively) and markedly lower during the second day (7.8 km). Mean drifting speed was 0.17 m/s, with two clear maxima between stations 331-332 (0.41 m/s) and stations 347-348 (0.45 m/s) and five instances were speed was lower than (0.1 m/s) (table 1).

The stick vector diagram (fig. 1-B) shows wind speeds and direction recorded on board during the 3-day study. As customary vectors are drawn in the direction from which the wind was blowing. During first half of the cruise winds blew mainly from the North with average speed of 13 kn. During the second half winds veered to the South and later to the East slightly decreasing in speed, averaging 11 kn.

Temperature and salinity data point out the integrity of the hydrological structure investigated. T-S pairs corresponding to surface and 10 m depth conform a defined water type throughout the study (fig. 3-A). The time series analysis shows the expected variations in temperature induced by noon surface heating (fig. 4-A) whereas surface and subsurface salinity values ranged between 33.60 and 33.65 in all but one station. The thermocline throughout the whole study remained centered at 15m depth (fig. 4 - A). The layer of more intense temperature stratification is encompassed by the 33.63 - 33.66 isohalines (fig. 4-B). Bottom layers show uniformity in the sequence of temperature data, and a slight rise in salinity (>33.75) during the last day of the cruise. Interpretation of these results lead us to consider that the drogue successfully remained within the characteristic seasonally stratified intermediate shelf water mass as defined by Martos and Piccolo (1988).

The N-S, E-W displacements of the drogue (fig. 3-B), the residual displacement after subtraction of the effect of

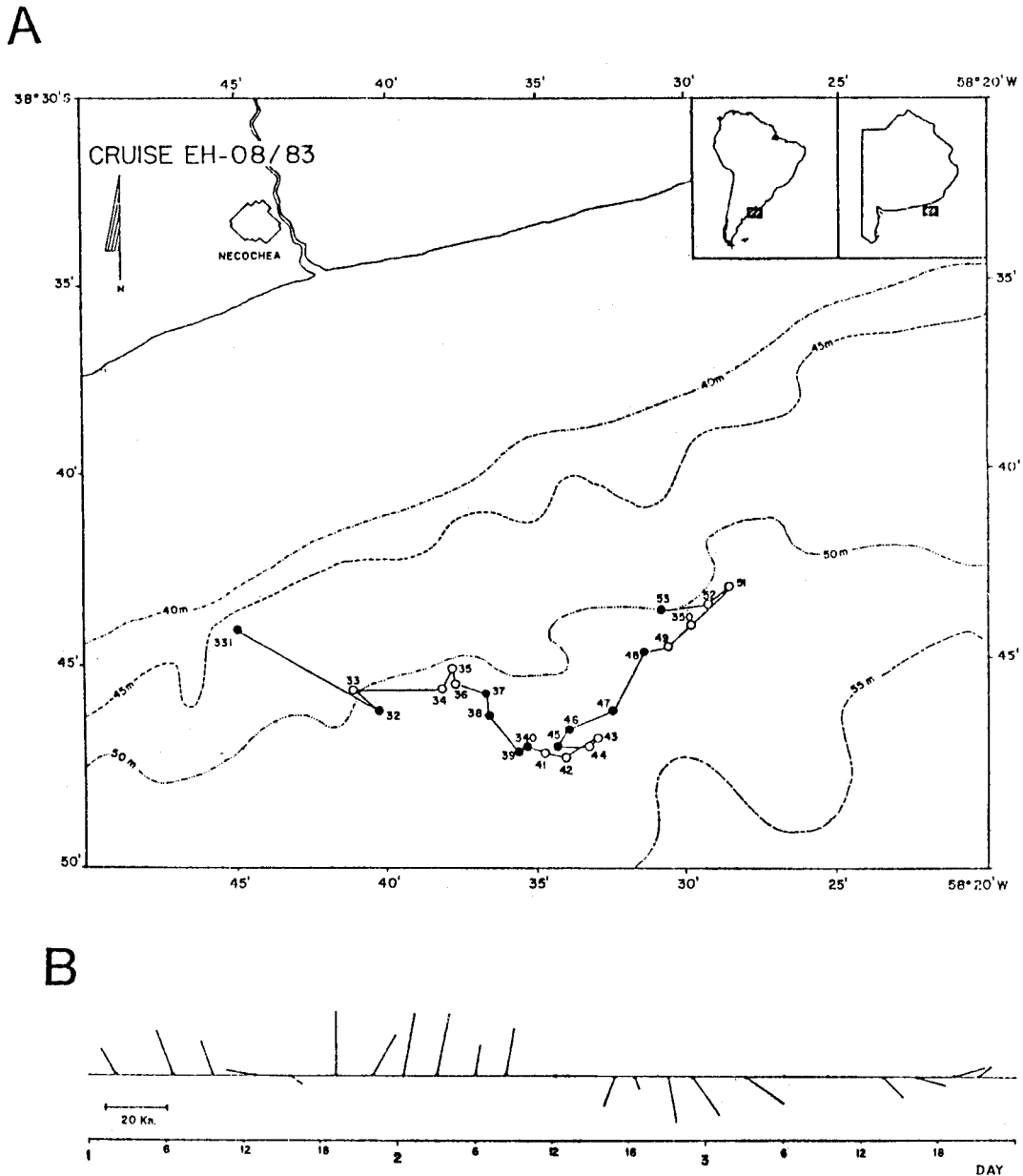


Figure 1. A) Trajectory of the free drifting drogue during cruise EH-08/83 from 0200 h (local time) on 8 November to 2100 h on 10 November 1983. Full circles indicate nights stations, open circles day stations. The insets show the location of the study area in the sea-shelf off Argentina. B) Stick vector diagram of wind speed and directions recorded at the ship during the drogue study.

Figura 1. A) Trayectoria del muestreador de deriva durante la campaña EH-08/83 desde las 0200 hs. (hora local) del 8 de Noviembre hasta las 2100 hs del 10 de Noviembre de 1983. Los círculos rellenos indican las estaciones nocturnas y los círculos vacíos las estaciones diurnas. B) Dirección y velocidad del viento registradas a bordo durante el estudio de deriva.

Table 1. Distance travelled by the drogue and average speed between stations.

*Tabla 1. Distancia recorrida por el rastreador de deriva y velocidad promedio entre estaciones.*

Station No.	Distance travelled (km)	Time (h)	Average speed (m/s)
331-332	6.622	4.5	0.409
332-333	1.325	3.0	0.123
333-334	2.018	3.5	0.160
334-335	0.705	2.5	0.078
335-336	0.755	3.6	0.059
336-337	2.968	2.9	0.283
337-338	1.794	2.5	0.199
338-339	1.152	2.5	0.128
339-340	0.746	3.0	0.069
340-341	0.754	2.5	0.084
341-342	1.631	5.0	0.091
342-343	0.469	3.5	0.037
343-344	0.937	1.5	0.174
344-345	1.140	2.5	0.127
345-346	0.939	2.2	0.120
346-347	1.682	3.8	0.122
347-348	4.851	3.0	0.449
348-349	2.483	3.3	0.212
349-350	2.651	4.5	0.164
350-351	1.296	2.6	0.139
351-352	2.417	2.7	0.252
352-353	2.746	3.0	0.254
Total	42.119	mean	0.170
		s. dv.	0.104

wind induced Ekman surface drift (fig. 3-C) and of the wind generated displacement at 15 m depth (fig. 3-D) are analyzed by means progressive vectors diagrams. Comparison of figs. 3-B and 3-C indicate that the effect of wind on the surface unit of the drogue system may be considered negligible, as the correction does not introduce any evident change in the observed track. Progressive vectors (fig. 3-D) show that during the first two days of the study much of observed displacement (24 km) could be accounted for by the effect of wind induced Ekman drift at the depth of the drogue. Discrepancy during the last day may be related to the reversion of winds, which seem to be counteracting a more intense displacement to the NE, probably accounted for mean water circulation in the Argentine shelf, with the constraints imposed by topography. Although no clear periodic signal was observed, the fact that displacement of the drifter is nearly parallel to the coast may be indicative of tidal currents

influencing the trajectory.

Results of the analysis of variance do not permit to reject the null hypothesis that we stay within the same ichthyoplankton patch during the study as no significant differences in the mean abundance of organisms during each day were observed (table 2). Significant differences were obtained when comparing the mean values of night and day catches, catches at the different levels, and mean abundance of the ichthyoplankton categories. There was no significant differences between catches of the different days within the same light regime and within ichthyoplankton stages.

Density variation by depth stratum in the collections of anchovy eggs and larvae in cruise EH-08/83 is presented in fig. 2. The vertical distribution of anchovy eggs and larvae is mostly within and above the thermocline, with total eggs more abundant and more homogeneously dispersed in the three layers. Night peaks in total anchovy egg catches are

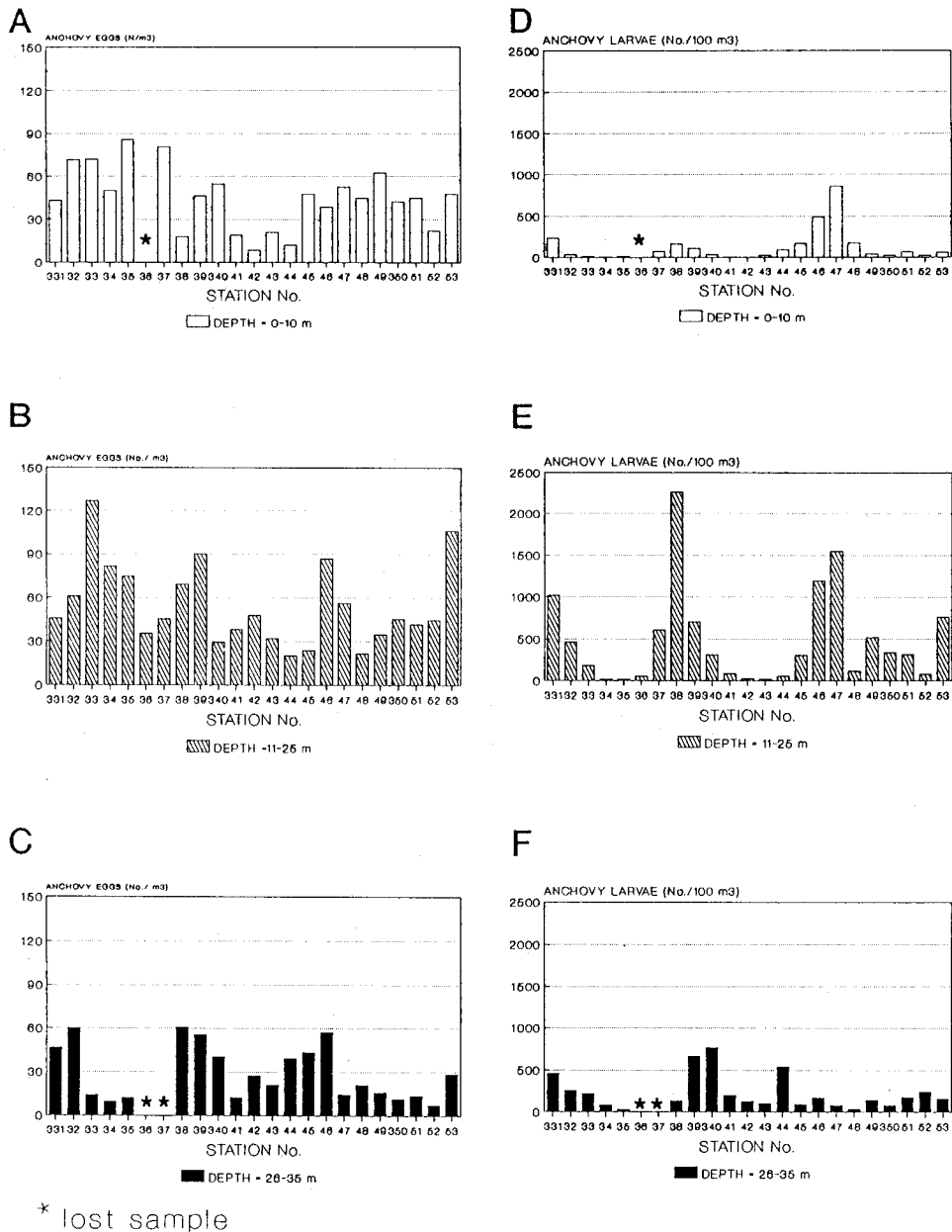


Figure 2. A-B-C) Variation in anchovy egg catches (N / m<sup>3</sup>) by depth level during cruise EH-08/83.

D-E-F) Variation in anchovy larvae catches ( N / 1000 m<sup>3</sup>) by depth level during cruise EH-08/83.

Figura 2. A-B-C) Variación en las capturas de huevos de anchoíta (N / m<sup>3</sup>) por nivel de profundidad durante la campaña EH-08/83. D-E-F) Variación en la captura de larvas de anchoíta (N / 1000 m<sup>3</sup>) por nivel de profundidad durante la campaña EH-08/83.



evident in the thermocline and bottom depth (B and C) while no clear pattern is observed in the upper layer (A). During the first day of cruise the peak over the thermocline corresponds not to a night collection but to a station just before sunrise. The analysis of percent variation in the abundance of anchovy eggs collected in each depth layer at different times of the day (fig. 5) emphasizes the marked increase observed during the night in the bottom layer and a more uniform pattern in the other two levels. The time series representation of fig. 4 (C and D) shows similar patterns for age-0 and other anchovy eggs in the samples. Peak densities in the time series of age-0 eggs (fig. 4-D) which at the observed water temperature comprise stages I, II and III in the scale of Ciechowski and Sánchez (1984), points out the nightly

spawning rhythm, reported for the species. Stage I eggs were collected from 1900h to 0200h, with peaks at 2400h, 2200h and 2100h, in the successive nights.

The observed densities of all anchovy larvae in each station and stratum (fig. 2 D-E-F) and the percent distribution in each depth at different hours (fig. 5) indicate clear peaks during the night stations of the two upper layers, and a less evident pattern in the bottom layer. The time series analysis shows the predominance of the thermocline level for yolk sac (fig. 4-E) and post-larvae (fig. 4-F). Post-larvae in densities over 20/100 m<sup>3</sup> were only collected during night stations, mostly in stations on and above the thermocline. The time series of fig. 4-E reveals that the peak densities exceeding 500/100 m<sup>3</sup> correspond to a large extent to yolk sac larvae.

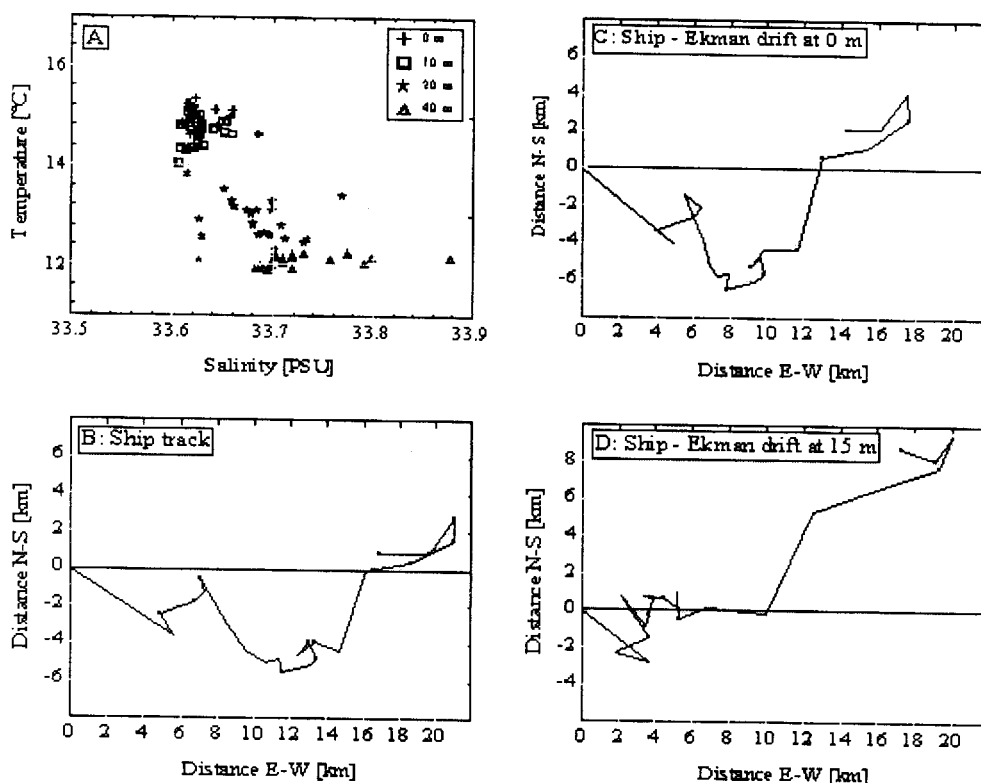


Figure 3. Hydrographic and meteorological data during the drogue study. A) Composite Temperature-Salinity diagram from T-S pairs measured at four depth levels. B) N-S and E-W displacement of the drogue. C) Correction of the buoy track for wind drag on the surface unit. D) Difference between buoy track and wind generated displacement at 15 m depth.

Figura 3. Análisis hidrográfico y climatológico durante la campaña. A) Diagrama T-S compuesto, a partir de valores registrados a cuatro profundidades estándar. B) Derrota del rastreador en las direcciones N-S y E-O. C) Derrota del rastreador corregida por efecto del viento sobre la unidad de superficie. D) Derrota del rastreador corregida por efecto del viento a la profundidad de 15 m.

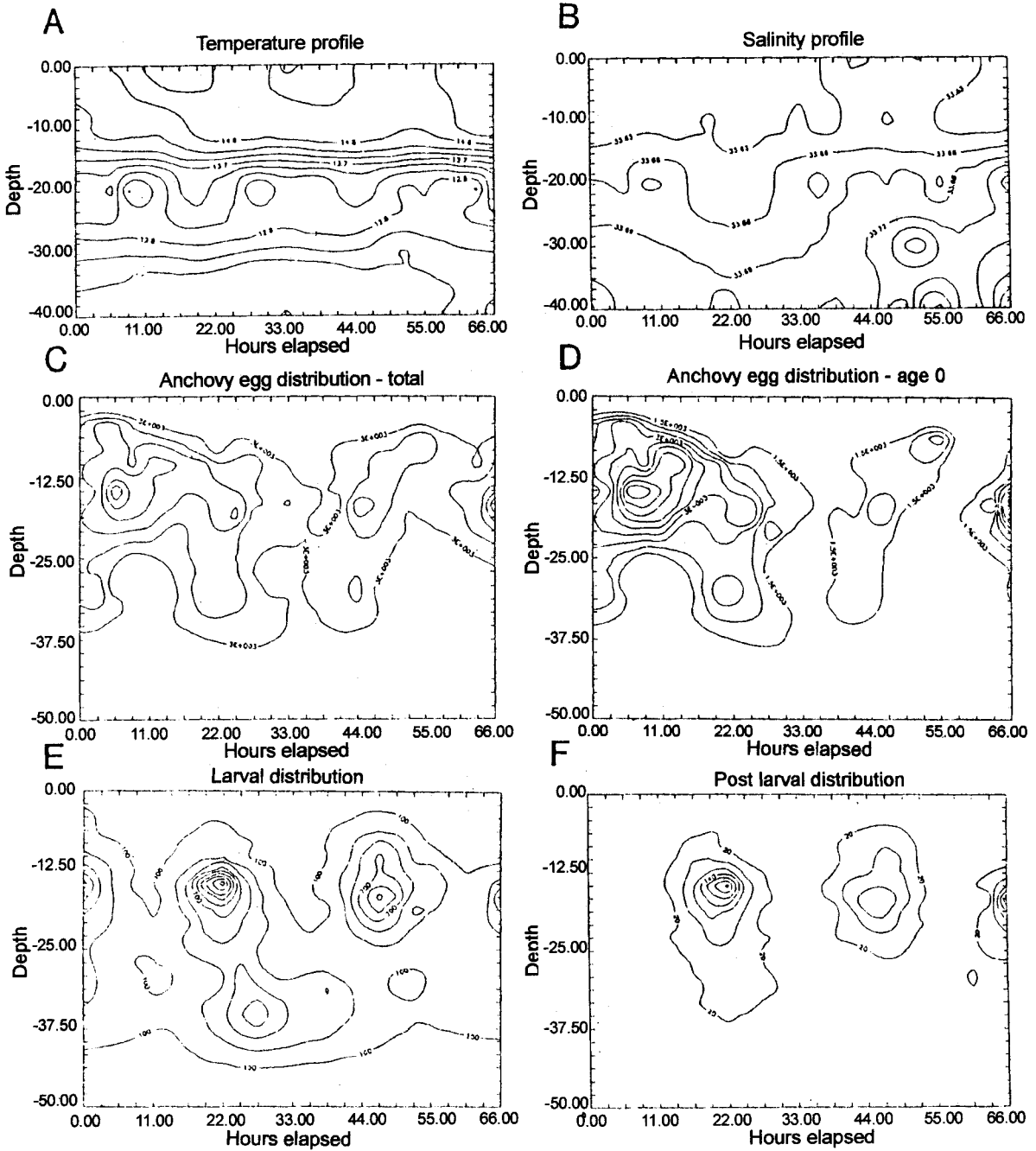


Figure 4. Vertical profiles of temperature (A), salinity (B), total anchovy eggs (C), anchovy -0 eggs- less than 1 day old- (D), total anchovy larvae (E) and postlarvae (F).

Figura 4. Perfiles verticales de temperatura (A), salinidad (B), huevos de anchoíta totales (C), huevos de anchoíta de edad 0 - menores de un día- (D), larvas de anchoíta totales (E), y postlarvas (F).

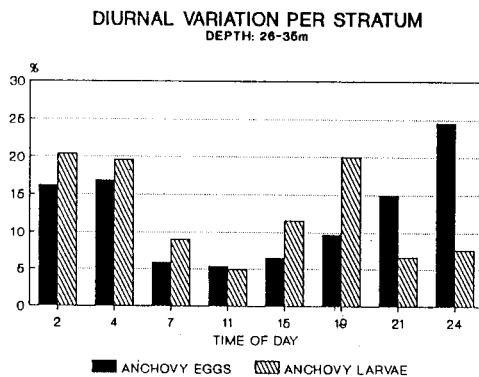
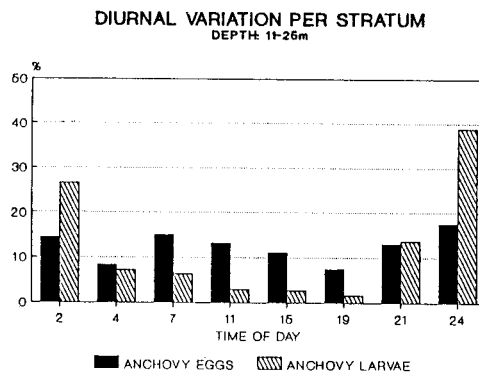
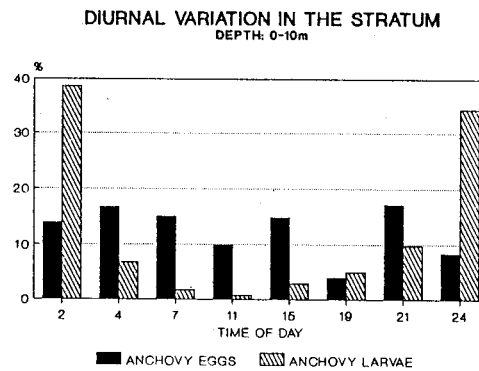


Figure 5. Diurnal variation in the distribution of anchovy eggs and larvae in different depth strata, from catch percentages at 3- 4 hour intervals.

Figura 5. Variación horaria en la distribución de huevos y larvas de anchoíta en diferentes estratos de profundidad, porcentajes de captura a intervalos de 3- 4 horas.

Table 2. Multifactorial ANOVA on log-transformed data, from cruise EH-08/83. Included variables are: days, light regime, sample depth, and ichthyoplankton stage categories (anchovy eggs, larvae and post-larvae, and other fish larvae).

Tabla 2. ANOVA multifactorial de los datos transformados logarítmicamente, correspondientes a la campaña EH-08/83. Las variables incluyen: días, régimen de iluminación, profundidad de muestreo, estadios de desarrollo del ictioplancton (huevos de anchoíta, larvas y postlarvas, y otras larvas de peces).

Source	D.F.	S.S.	M.S.	F.S.	Level of Significance
Days (A)	2	1.4993	0.7496	0.9077	n.s.(a=0,25)
Light (B)	1	89.9263	89.9263	108.8855	**
Depth(C)	2	28.6546	14.3273	17.3479	**
Stages(D)	3	1077.7490	359.2497	434.9907	**
A x B	2	1.2753	0.6376	0.7721	n.s.(a=0,25)
A x C	4	15.0174	3.7543	4.5459	**
A x D	6	7.5345	1.2558	1.5205	n.s.(a=0,10)
B x C	2	8.8388	4.4194	5.3512	**
B x D	3	18.2913	6.0971	7.3826	**
C x D	6	26.5315	4.4219	5.3542	**
AxBxC	4	0.6470	0.1618	0.1959	n.s.(a=0,75)
AxBxD	6	5.7572	0.9595	1.1618	n.s.(a=0,25)
AxCxD	12	6.4838	0.5403	0.6542	n.s.(a=0,75)
BxCxD	6	20.1244	3.3541	4.0612	**
AxBxCxD	12	9.8063	0.8172	0.9895	n.s.(a=0,25)
Replicates	144	118.9266	0.8259		
Total	215	1437.0633			

Fig. 6 shows results on the vertical distribution of larvae grouped in 1 mm SL size categories. Larvae of the two smaller length groups are predominant in the three levels both in night and day stations. During day time the full range of larvae was only caught in the bottom layer (C). Day stations on and above the thermocline contained only larvae up to 7.5 mm SL. The full range of larval sizes during night stations was observed on and above the thermocline (A-B), though at this level mean larval densities of the two larger sizes are lower than  $1/100 \text{ m}^3$ . Catch ratios for each size and level, are presented in fig. 6 (D-E-F). The two upper levels show an evident incidence of the night catches in all length groups. The bottom stratum, indicates more uniformity in ratio of catches during night and day stations for larvae up to 8.5 mm SL. The fact that no larger larvae were caught during the night stations at this level may be indicative of diel migration pattern towards surface waters for these size categories.

The centre of mass of the vertical distribution of anchovy eggs remained nearly constant (range 13-20) at the depth of the thermocline (fig. 7-A). The descent in the centre of mass takes place at the hour of first appearance of ferti-

lized eggs in the samples. The centre of mass of yolk sac larvae follows an almost similar trend, but located a few meters below, although always remaining within the middle stratum sampled. Anchovy post-larvae are more active, showing a more clear diel movements. The depth of the centre of mass ranged from 30 m at sunrise to 11 m at 2100 hs.

The vertical dispersion index is a measure of how homogeneously distributed the organisms are in the water column. Values tending to 0 indicate similar abundances in each level. Increasing values, reflect the tendency to aggregate in one stratum. The trend for eggs and larvae is similar, though the distribution of eggs is more homogeneous in the three levels. Anchovy post-larvae show a maximum peak in the dispersion index at sunrise and a tendency to a more homogeneous distribution at night (fig. 7-B).

Lloyd's patchiness index is a measure of the actual crowding of an individual, relative to the average crowding expected in randomly dispersed population. As defined by Mc Gurk (1986) the index is equal to the numbers of "crowders" sharing the space with one individual. The index is independent of mean abundance and can therefore be used to compare aggregation for stages of different overall abundance. Five stages were considered for this analysis, age-0

eggs, age 1+2 eggs, yolk-sac larvae, first-feeding larvae, and post-larvae which in this case include size classes over 5.6 mm SL. All day and night samples, regardless of the level, were pooled to obtain the maximum likelihood estimators of the  $k$  parameter. Results show a decrease in the aggregation

from age-0 to age 1+2 (fig. 7-C). This stage is the less aggregated during night and day, thereafter patchiness gradually increases with the progress of development. Anchovy larvae and post-larvae were more aggregated during day-time, probably in relation to trophic activity. Larger values of

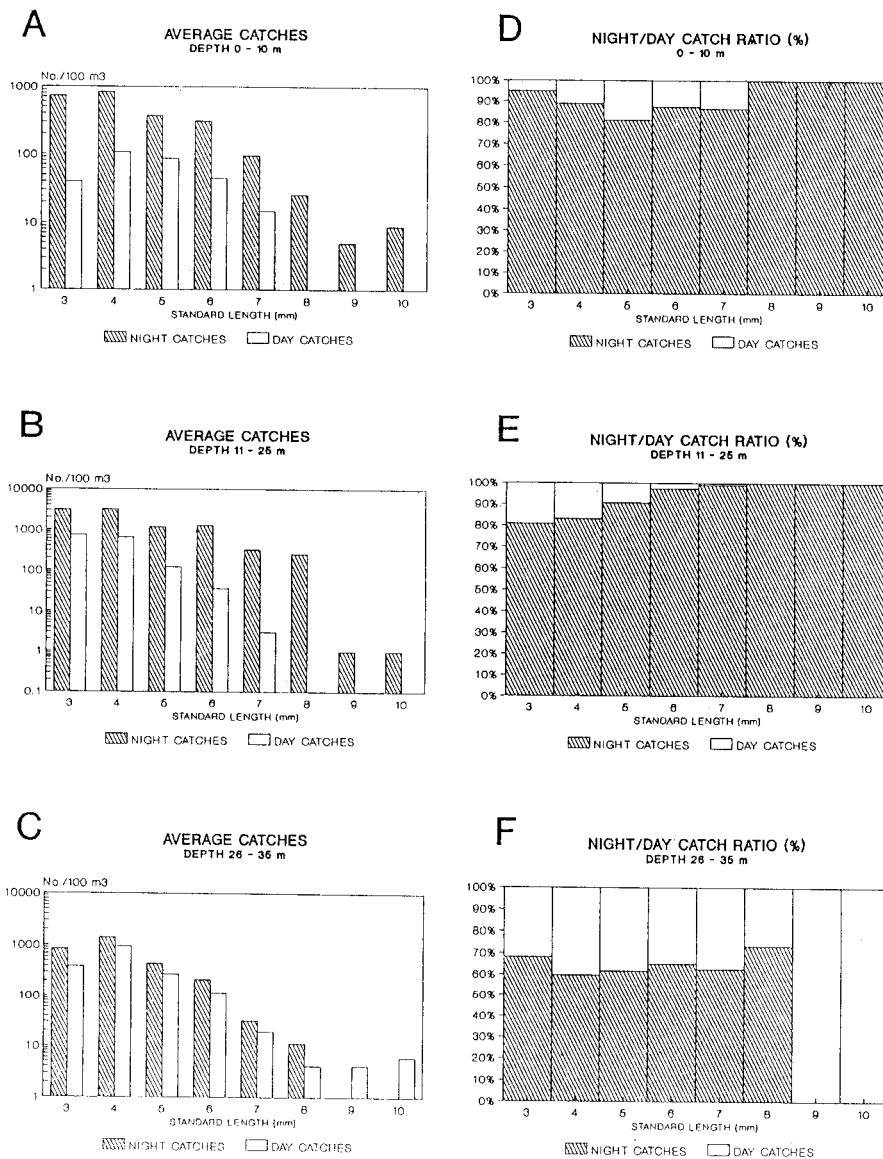


Figure 6. Night/day variation in larval catches. Data grouped by size and depth level. A-B-C: average catches; D-E-F: catch percentages.

Figura 6. Variación noche/día de las capturas larvales. Datos agrupados por tamaño y nivel de profundidad. A-B-C: capturas promedio; D-E-F: porcentajes de captura.

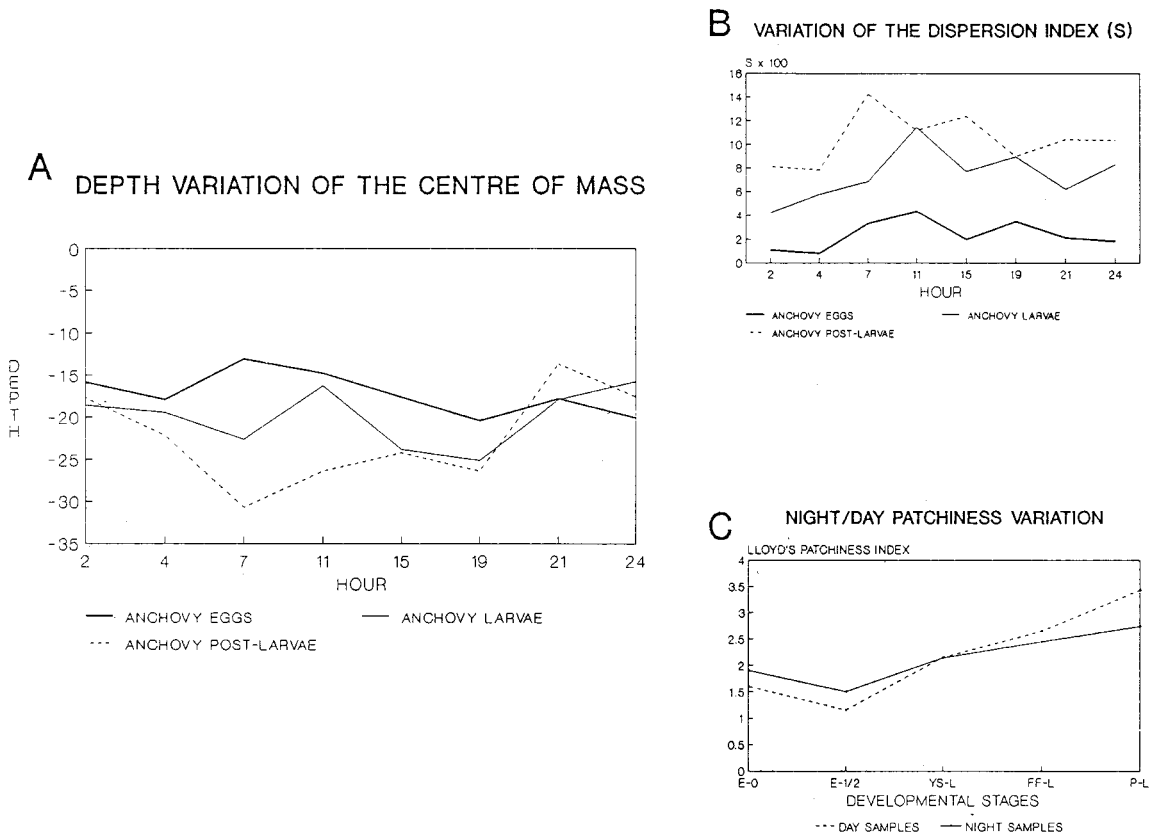


Figure 7. Characteristics of the vertical distribution within a patch of anchovy eggs and larvae. A) Depth variation of the centre of mass - mean values of the 3-day study. B) Mean values of the index of the vertical dispersion. C) Variation of the patchiness index, for different developmental stages in night and day samples.

Figura 7. Características de la distribución vertical dentro de una mancha de huevos y larvas de anchoíta. A) Variación de la profundidad del centro de masa - valores medios de 3 días de estudio- B) Valores promedio del índice de dispersión vertical. C) Variación del índice de contagio, correspondiente a diferentes estadios de desarrollo, en estaciones diurnas y nocturnas.

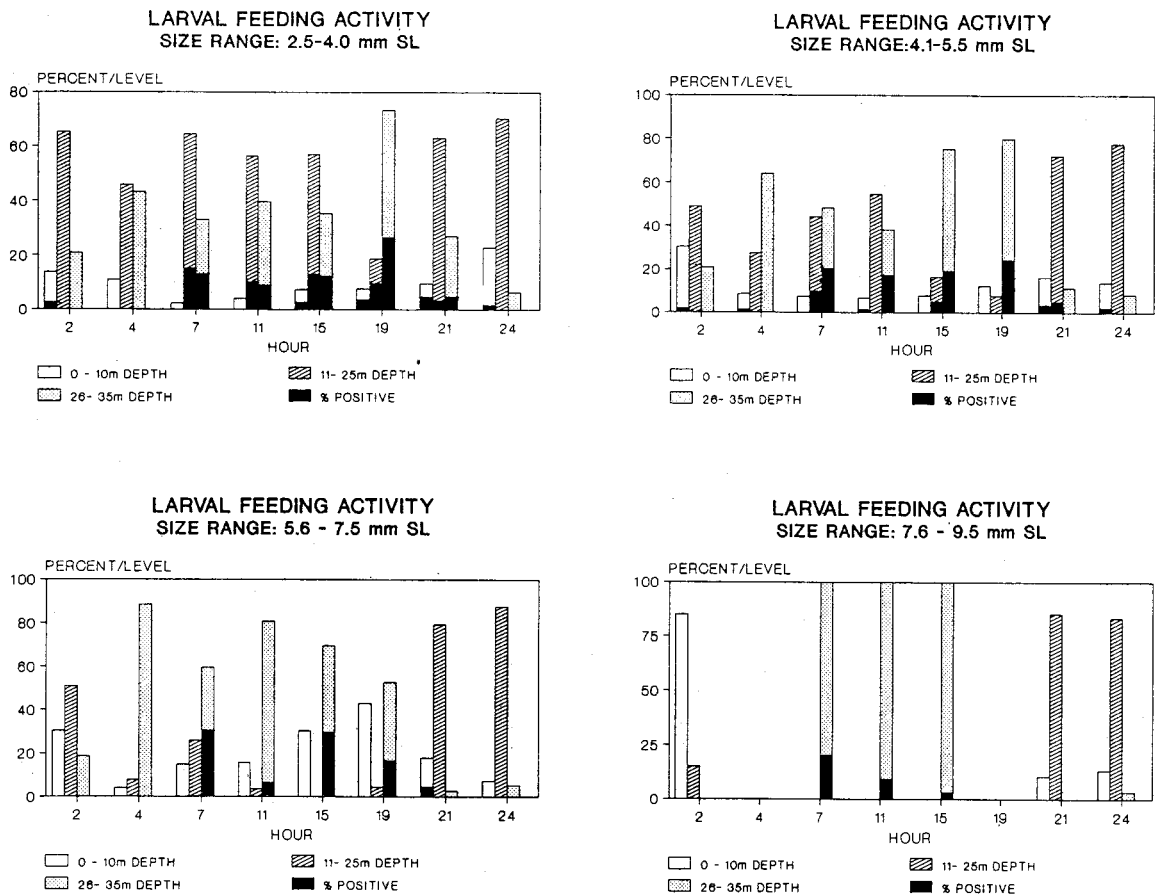


Figure 8. Percentage of different length categories (preserved size) of anchovy larvae by depth and time of the day, and estimation of feeding activity from percent of larvae with undigested gut contents.

Figura 8. Porcentaje de diferentes categorías de longitud (tamaño preservado) de larvas de anchoíta por profundidad y hora del día, y estimación de la actividad alimentaria de los porcentajes de larvas con contenidos intestinales no digeridos.

patchiness index correspond to larvae over 5.6 mm collected in day stations.

Only 7.05% of all collected larvae contained visible gut contents. The larvae of the 4 size groups considered showed a similar diel trophic pattern, with most feeding activity taking between 0700h and 2100h, covering a 14-h feeding period (fig.8). Only incidental feeding was observed at night, always in the upper mixed layer, but not corresponding to the size group undergoing vertical migration. Feeding seemed to start shortly after sunset, within and below the thermocline. Larvae in the 25-36m stratum showed higher feeding percentages in all size groups. Predominance of feeding activity in the bottom layer increased with the size of larvae, nearly 100% of positive larvae larger than 5.6 mm SL were collected below the thermocline. Highest feeding incidence for the smaller larval group (27% of all larvae collected at that hour) occurred at sunset. Also larvae of sizes 4.1- 5.5 mm showed a feeding peak (22%) at 1900 hs. Larvae of the two smaller groups showed some feeding activity in all depth strata sampled. In both cases incidence of feeding in the upper mixed layer increased towards the first hours of darkness.

Several sets of data were used in order to estimate egg mortality during the cruise. Fig. 9 represents the observed abundance of eggs of different ages collected each day of cruise EH-08/83 (A-C), and totals (D), and the results of tracking of the initial cohort (E). By this we mean the group of eggs that were in stage I, II and III in the first day, in stages IV, V and VI in the second day, and in stages VII, VIII and IX during the third day. Eggs numbers were assumed to decline at a constant exponential rate according to the model,

$$N_t = N_0 * \exp(-Z_{ht})$$

where  $N_0$  is the initial number,  $N_t$  is the egg abundance at age  $t$ , and  $Z_{ht}$  is the hourly instantaneous mortality rate.

Table 3 gives details of the results of the regression analysis both by nonlinear and log-linear procedures. In all cases, the model explained over 65% of total variance of the data. The nonlinear regression gave values of  $Z_h$  ranging from 0.016 to 0.023, whereas the log-linear procedure produced higher estimates 0.021 to 0.032. These values render daily losses in numbers of about 31.8 to 54.2 %. Estimates of initial numbers ranged from 1810 to 3766 eggs/100m<sup>3</sup>. The test of homogeneity of slopes on the log-transformed values produced no significant differences ( $F=1.6761$ ,  $P=0.1720$ ) between the different data sets, and significant difference when testing the null hypothesis of 0 mortality against the common slope (0.026) ( $F=200.60$ ,  $P=0.039$ ).

Length frequencies distributions of larval anchovy collected during each day of the cruise are presented in Fig. 10

(A-C). The size range of larvae collected increased during the cruise. Larger larvae collected were 8.0 mm in SL (preserved size) in the first day, 9.0 mm in the second day, and 9.5 during the last day. Mean length per day increased slightly from 3.54 to 3.81. These averages may be considered as highly dependent on the very abundant smaller size groups and do not reflect possible differences in the length distributions due to growth of the larger but less abundant specimens. However, differences in the evolution of the size of the 90th percentile (5.28- 5.47), do not seem to vary more markedly as the cruise progressed.

The conversion to real size, and then to age, permits the calculation of mortality rates per day for each of these length frequency distribution (fig. 10-D). Nonlinear regression gave values of the daily instantaneous mortality rate  $Z_d$  ranging from 0.14 to 0.21, which imply a daily loss in numbers of 13.5 to 18.9% per day (table 4). The exponential model explained large percentages of total variance of the data (78.5-89.5%). As for the egg mortality estimates, the instantaneous mortality rates produced by the log-linear method were much higher. The test of slopes homogeneity render no significant differences between the 3 days ( $F=0.8172$ ,  $P=0.4499$ ), and a common slope (0.25) which was significantly different from 0 ( $F=255.09$ ,  $P=0.020$ ).

Although the exponential decay model fitted the data acceptably, an examination of residual plots for the different sets of egg data, indicated that in most cases, the constant rate model underestimated mortality for the younger individuals and overestimated mortality for the older ones. As regards larvae, there is no apparent decay in number for the smaller four size classes. It could be thought that length distributions are biased due to mesh selectivity. However, no significant escapement should be expected as the sampler was fitted with 200 $\mu$  mesh nets. As to the larger specimens, it has been shown in related species (Saila and Lough, 1981; Lo, 1985; Loos and Perry, 1991) that mortality rates may decrease with age and size of the larvae.

Wieland (1988, 1989) uses a different approach, the so called cohort-method to estimate the mortality of cod and sprat eggs. This method is particularly adequate to estimate mortality from repeated sampling of a single patch of eggs or larvae. Although the method was originally designed for eggs with longer incubation periods, the calculations involved may be adapted to describe the mortality of faster growing eggs. The application of the method is presented in table 5. Stages I and IX were discarded from the analysis as they may be underrepresented depending on sampling time or hatching. This method assumes constancy of mortality rates over adjacent stages. Fager (1973) provides methods to estimate ranges of values of that are consistent with the observed relative numbers of individuals. The obtained results show that mortality between successive stages is not constant indicating changes in egg mortality during develop-



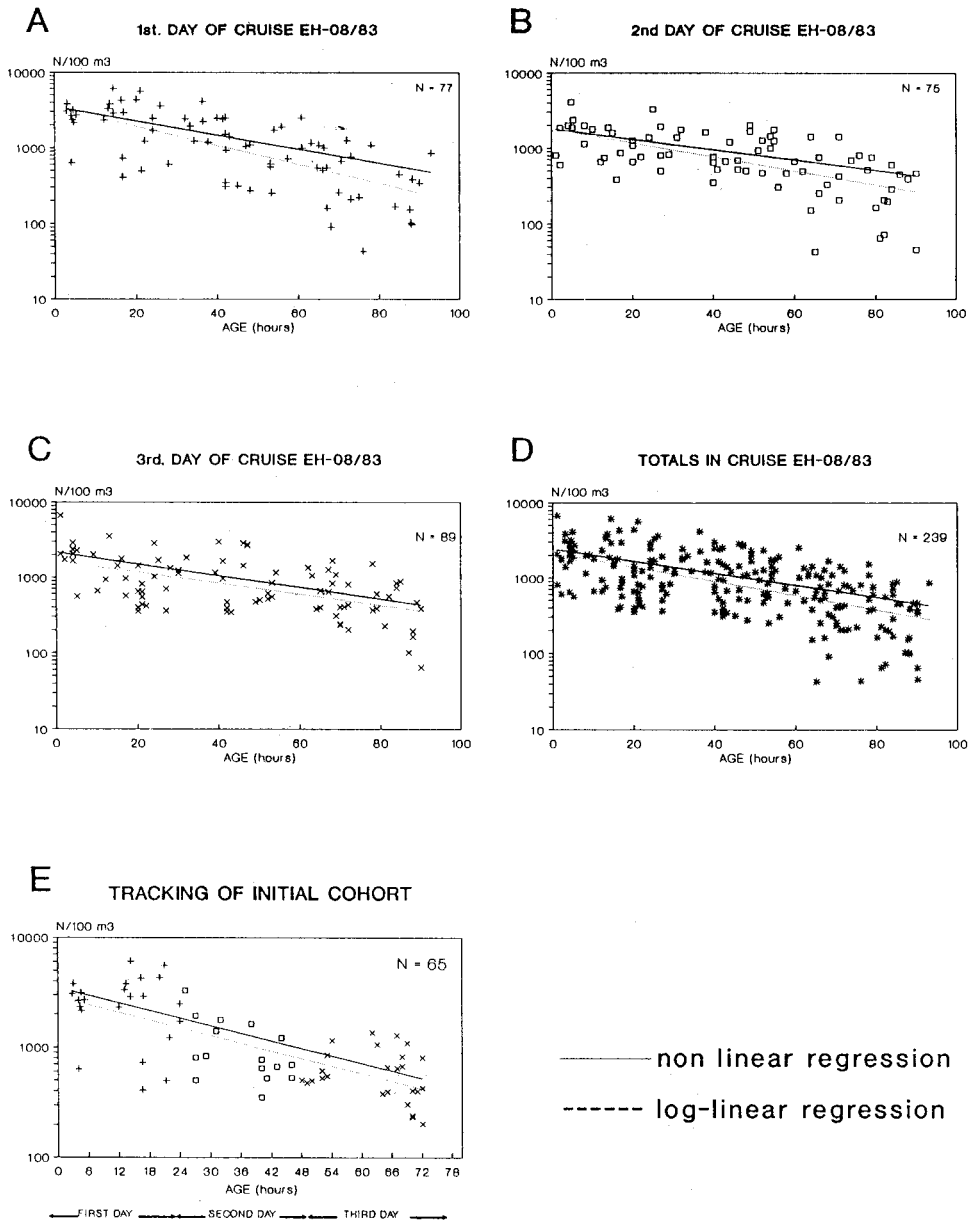


Figure 9. A - E. Egg mortality curves for the anchovy from constant exponential decay regression analysis applied to different sets of data from the drogue study.

Figura 9. A - E. Curvas de mortalidad para los huevos de anchoíta de análisis de regresión con disminución exponencial constante aplicado a diferentes conjuntos de datos del estudio de deriva.

Table 3. Summary of regression analyses for the estimation of egg mortality of the anchovy, assuming constant exponential decay [ $N_t = N_0 * \exp(-Z h t)$ ].  $Z h$  is the hourly instantaneous mortality rate,  $Md \%$  is the daily decay in numbers.

Tabla 3. Análisis de regresión para la estimación de la mortalidad en la fase huevo de anchoíta, a partir del modelo exponencial constante [ $N_t = N_0 * \exp(-Zht)$ ].  $Zh$  es el coeficiente instantáneo de mortalidad horaria.  $Md \%$  es el porcentaje diario de disminución en la abundancia.

Data set			Log-Linear Regression Analysis		Non Linear Regression Analysis		
	Zh	s.e.(Zh)	N0	%Expl.	r	N	Md%
1 st Day of cruise	0.0325	0.00402	3766		0.6819 **	77	54.2
	0.0214	0.00342	3484	74.1	0.6541 **		40.2
2 st Day of cruise	0.0215	0.00321	1810		0.6181 **	75	40.3
	0.0160	0.00295	1817	74.6	0.5658 **		31.8
3 st Day of cruise	0.0250	0.00364	1500		0.5960 **	89	45.1
	0.0186	0.00364	2225	65.5	0.5212 **		36.1
Total	0.0262	0.00235	2394		0.6243 **	239	46.7
	0.0190	0.00248	1899	67.9	0.5560 **		36.6
Tracking of Initial Cohort	0.0252	0.00347	2874		0.6720 **	65	51.8
	0.0239	0.00433	3403	74.6	0.6508 **		48.5

Table 4. Summary of regression analyses for the estimation of larval mortality of the anchovy, assuming constant exponential decay [ $N_t = N_0 * \exp(-Z d t)$ ].  $Z d$  is the daily instantaneous mortality rate,  $Md \%$  is the daily decay in numbers.

Tabla 4. Análisis de regresión para la estimación de la mortalidad en la fase larval de anchoíta, a partir del modelo de disminución exponencial constante [ $N_t = N_0 * \exp(-Zd t)$ ].  $Zd$  es el coeficiente instantáneo de mortalidad diaria.  $Md \%$  es el porcentaje diario de disminución en la abundancia.

Data set			Log-Linear Regression analysis		Non Linear Regression analysis		
	Zd	s.e.(Zd)	N0	%Expl.	r	N	Md%
1st Day of cruise	0.2193	0.04141	2215		0.8585 **	12	9.7
	0.2092	0.04608	3165	89.5	0.9096 **		18.9
2st Day of cruise	0.3071	0.05119	4432		0.8659 **	14	26.4
	0.1463	0.04802	2136	78.5	0.7965 **		13.6
3st Day of cruise	0.2817	0.04090	2525		0.8859 **	15	24.5
	0.1457	0.03925	1893	84.4	0.8463 **		13.5

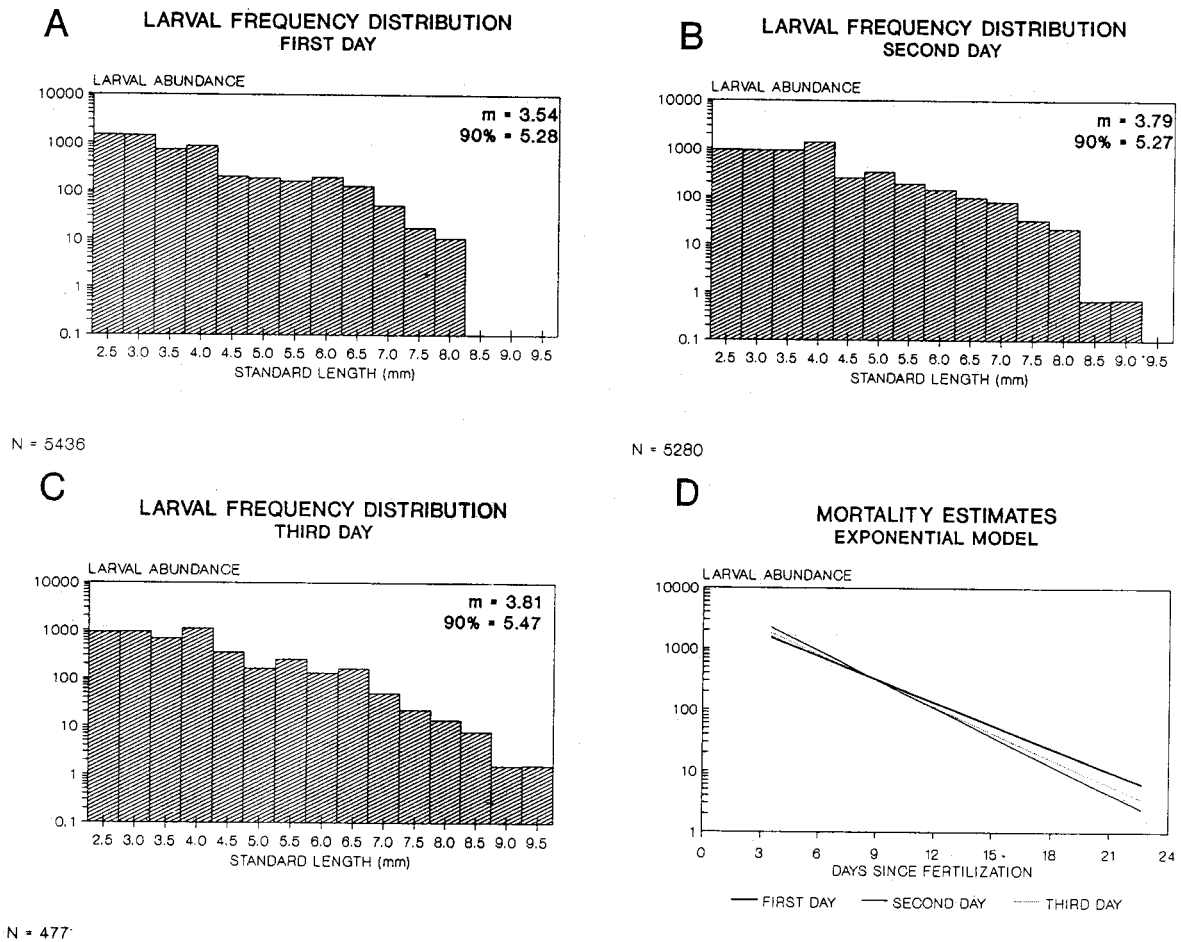


Figure 10. A-C. Length frequency distributions of anchovy larvae during each day of cruise EH-08/83. References:  $m$  = mean length (SL preserved size); 90 % = SL of the ninetieth percentile. D) Comparison of constant exponential decay regression curves.

Figura 10. A-C. Distribución de las frecuencias de tallas de larvas de anchoíta durante cada día de la campaña EH-08/83. Referencias:  $m$  = talla media (L S material fijado), 90 % = LS correspondiente al percentil 90. D) Comparación de las curvas de regresión correspondientes a una disminución exponencial constante.

Table 5. Estimates of anchovy eggs mortality from the production of successive developmental stages. An adaptation of the cohort method (Wieland, 1988). Ranges of Z h (Instantaneous mortality rate per hour) were calculated according to Fager (1973).

Tabla 5. Estimación de la mortalidad en la fase huevo de anchoíta a partir de los valores de producción correspondientes a estadios de desarrollo sucesivos. Adaptación del método de Wieland (1988). Los rangos de Zh (el coeficiente instantáneo de mortalidad horaria) han sido calculados según Fager (1973).

Stage	Midstage age (days)	Sampling day	Sampling interval (hours)	Cumulative abundance (N/1000 m3)	Stage duration (hours)	Hourly production (N/100/D m3)	Zh (IHMR) (range)	% Daily loss
II	0.393	1	9	36670.572	9.860	3719.125	0.040	62.005
III	0.685	1		10814.705	4.180	2587.250	0.026-0.052	
III	0.685	1	7	10814.705	4.180	2587.250	0.037	58.408
IV	0.877	1		10035.867	5.010	2003.167	0.028-0.056	
IV	0.877	1	11	10035.867	5.010	2003.167	0.021	39.112
V	1.249	2		20489.212	12.840	1595.733	0.013-0.025	
V	1.249	2	15	20489.212	12.840	1595.733	0.027	47.431
VI	1.721	2		10516.106	9.850	1067.625	0.018-0.035	
VI	1.721	2	18	10516.106	9.850	1067.625	0.026	46.181
VII	2.233			9868.145	14.710	670.846	0.019-0.038	
VII	2.233	3	18	9868.145	14.710	670.846	0.024	44.453

ment. Highest values were obtained between stages II and III and lowest between stage IV and V and between stages VII and VIII.

The IMR calculated according to the equations derived by Lo (1985) (open squares in fig. 11-A) show a similar tendency. The examination of the figure shows that in fact mortality during the yolk sac stage could be considered as part of the same decreasing trend observed in the egg stage. The transition to exogenous feeding is coincident with a marked increase in the IMR. As expected from previous results in the literature there follows an age dependent decay in the IMR values. The forms of the curves of the embryonic and larval phase are somewhat different, though in fact both are a combination of power and exponential equations. According to Lo (1985) the Californian anchovy shows constant mortality for ages below  $t_c$  the critical age marking a change in the evolution of the IMR. The obtained model for egg and larval anchovy from age 0 to 23 d, assuming multiplicative distribution of errors is:

$$\ln(N_t) = a - bt_1 \ln(x_1) - c \cdot x_1 - d \cdot (x_2 \cdot t - t_c \cdot h)$$

$$\text{where } a = 10.25 \quad x_1 = \begin{cases} t & t \leq t_c \\ t_c & t > t_c \end{cases}$$

$$b = 0.203 \quad t_c$$

$$c = 0.684$$

$$d = -15.26 \quad x_2 = \begin{cases} t_c & t \leq t_c \\ t & t > t_c \end{cases}$$

$$h = -0.492$$

Fig. 11-B shows the convenience of using this approach instead of the classical fitting of constant exponential decay models for separate stages of development. Values of mortality, however, do not differ much between the models. Mortality from fertilization to the end of the embryonic period is 86.3%, according to single equation model, and 85.6% according to the exponential model. The former model predicts a larval mortality of 93.7% during the period analyzed, whereas the constant exponential decay would predict a mortality of 92.6%.

## DISCUSSION

Although *E. anchoita* spawns in the continental shelf off Buenos Aires, throughout the year, major spawning to the south of Mar del Plata occurs only during spring and summer (Sánchez, 1990). Bakun and Parrish (1991) rightly observed that stability of the water column, induced by seasonal thermocline formation could condition the duration of reproductive period in the area. Temperature does not seem to be the limiting factor. During September, for instance, the spawning

grounds of the anchovy, in the sea off Argentina and Uruguay, occupy only 13% of the "potential habitat" of the species (i.e. areas comprised within the temperature-salinity tolerance ranges of the embryonic stages as defined by Ciechowski (1967) and Ciechowski and Sánchez, (1984), whereas in October, in relation with water stratification and the resulting spring phytoplankton bloom (Carreto *et al.*, 1981), the percentage reaches a maximum of 60.2%. After the decay of the spring phytoplankton bloom, the study area, remains as one of the poorest trophic ecosystems of the Argentine sea shelf (Akselman *et al.*, 1986) but spawning activity continues, covering in November an area of 260,000

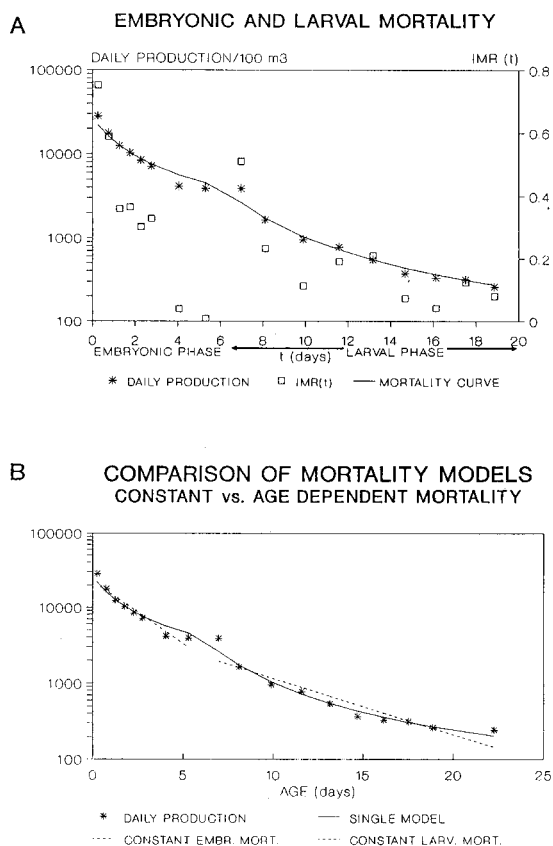


Figure 11. A) Weighted daily production, instantaneous mortality rates and mortality curve with increasing age, estimated for the embryonic (egg and yolk sac larvae) and free larval stages. B) A comparison between a single -age dependent mortality model, and constant exponential decay models for each stage.

Figura 11. A) Producción diaria ponderada, tasas de mortalidad instantánea y curva de mortalidad con el incremento de la edad, estimada para los estadios embrionarios (huevos y larvas vitelinas) y de vida libre. B) Comparación entre un modelo de ecuación única y modelos de decrecimiento exponencial constante para cada fase de desarrollo.

km<sup>2</sup>. Pycnoclines which in the study area are mainly dependent on temperature gradients become crucial mechanisms of food particle accumulation. Results presented here confirm the strong dependence of the early stages of development upon the thermocline layer.

Water circulation in the Argentine Shelf has been estimated by means of theoretical models based on surface wind stress and horizontal density gradients (Zyryanov and Severov, 1979, Lusquinos and Schrott, 1983, Forbes and Garraffo, 1988): In all cases surface velocities show a NNE orientation and magnitudes ranging between 0.10 and 0.20 m/s. Shelf waters off Buenos Aires during winter, are clearly of Subantarctic origin, and follow, both in intensity and direction, the average circulation pattern. During spring and summer, however, the situation is more confusing on account of a southward flow of warm water the origin of which is still unclear (Sánchez and Ciechomski, 1995).

The absence of larger larval sizes in our samples, reflects that offsprings from the massive October spawning are not retained in the surveyed area. Our historic data set (Sánchez, 1990) show that larger post-larvae and pre-metamorphic juveniles resulting from spring spawning are not found in the mid shelf (50-180m depth) but appeared to be concentrated along the coastal area, particularly in a shallow expansion of the sea shelf, some 60 nmi to the SW of the surveyed area. Without discarding the possibility of a southern drift, that would take the patch to that shallow area, and with the limitations imposed by the short period covered by the survey, it seems reasonable to suppose that this patch could reach the coastal region favoured by the general pattern of NNE transport characteristic of the Argentine shelf, and by the effect of average Ekman transport, which in the area is directed towards the coast (Bakun and Parrish, 1991). Average speed (0.17 m/s) of the drogoue during the cruise fall reasonably within the range predicted by the theoretical models cited.

A review of the literature suggests several ways in which the behaviour of free drifting drogues as Lagrangian markers could be assessed. Fortier and Leggett (1985), for instance, measured current speed and direction by means of instruments positioned above and below the sail of their Challenger-type drogoue in order to represent the displacement of the drifter relative to the surrounding waters. Heath and MacLachlan (1987) combined Lagrangian observations obtained with a conventional parachute drogoue with Eulerian current measurements from moorings laid before their drogoue study. Wieland (1989) evaluated the trajectory of an Argos drifter in relation to the characteristics of the dynamic topography and the induced geostrophic flow, as observed one day prior to their drift study. In other cases (Shelton and Hutchings, 1982) the lack of significant changes in physical properties and accompanying zooplankton, were taken as good evidence that the drogoue approximated closely to the

drift of the initial water mass. A common observation in these studies is that drogoue displacements are bound to be influenced by surface winds on the drifter (Dooley, 1974; Fortier and Leggett, 1985; Christensen *et al.*, 1988). On the basis of available data, we inspected the uniformity in physical properties and adopted the methodologies proposed by Heath *et al.* (1989) to estimate the effect of wind drag on the surface supporting buoy, and by Smith *et al.* (1978) to assess uniformity in patch composition throughout the study.

The ANOVA results should be considered with caution. Shelton and Hutchings (1982) discarded this procedure in their transport study of *E. capensis* eggs and larvae by a frontal jet current, on account of the narrow range of collected larvae (mostly under 5 mm SL), rapid growth rate over this length range, and an expected high mortality rate.

Taking these objections into account, we have selected stages so that the time spent in each category would exceed the duration of the cruise, and included in the analysis data on accompanying ichthyoplankton. The high mortality rates, which have been estimated during this study, seem to be compensated by the night renewal of stage I eggs, observed throughout the cruise. This may be indicative of aggregation of adult anchovies at scales larger than the surveyed area, maintaining a sustained spawning rhythm during the period considered. These results could then lend support to the assumption of constant birth rate inherent in the usual application of mortality models to data deriving from large time-space scale studies. No significant differences were obtained in the average abundance and composition of the plankton patch during the 3 day study. The differences between night and day catches may be due to nightly spawning rhythm, and to the effect of avoidance. Avoidance could also account for observed differences in the depth distribution of anchovy larvae. It should be noted however, that night catches were not larger than day catches for all levels and sizes considered. No larvae larger than 8 mm SL were caught in the bottom layer during the night.

Significant interactions between light and depth, depth and stages, and light and stages, are in agreement with the obtained results on the variation of indexes describing characteristics of the vertical distribution of the different developmental stages. There are several references in the literature about diel vertical migration of larval sizes similar to that reported here. Hunter and Sanchez (1976) reported for Californian anchovy larger than 11.75 mm a night/day catch ratio of 20,1. Less than 10% of these larvae occupy the upper 10m layer during the day, and over 50% by night. Ida (1972) described diel vertical migration of Japanese anchovy larger than 10 mm. Most of them were near the surface at night, and at 20-30m during the day. Shelton and Hutchings (1982) results on the diel pattern of migration of larvae of the South African anchovy are particularly relevant for comparison as they worked with a similar size range, and their data also

derive from a drogue study. The results show that day catches were 2.1 times higher than night catches, but the relative proportion of larger larvae increased during the night. A diel vertical migration was found, the larvae being particularly concentrated at about 25 m by day but being more generally spread between that depth and the surface by night.

Results on the variation of the depth of centre of mass of post-larvae and in their dispersion index are in agreement with these results. It should be noted however, that the ascent of larger larvae at sunset is not related to trophic activity, since no feeding could be observed in the larger group, except during day time and at the deepest stratum. Migration may be related to a diel rhythm of swimbladder inflation. Hunter and Sánchez (1976) observed that sea-caught larvae at night show expanded swimbladders, probably to facilitate passive buoyancy.

Results of variation of the patchiness index with the different stages are different in absolute values and in the relative trend from those reported in the literature, which are derived from material collected by oblique tows in meso-scale surveys (Hewitt, 1981, Sánchez and Ciechowski, 1989). These results show that smallest larvae are highly contagious, dispersing until achieving a size of about 10 mm and then reaggregating. Lloyd's index of patchiness is calculated as  $1 + \frac{1}{k}$  the inverse of the parameter  $k$  of the negative binomial distribution. As regards ichthyoplankton distributions, the negative binomial model may arise from the combination of a Poisson distribution of plankton patches in the sea, and a logarithmic distribution of the organisms within the patch. Variations in the parameter  $k$ , and consequently in the patchiness index may be driven by dispersal which tends to decrease the distance between patches while increasing the distance between individuals within the patch. Patchiness may also change on account of density dependent mortality (Hewitt, 1982). From our Lagrangian perspective, we understand that dispersal can only account for the decrease in patchiness from Age-0 to Age 1+2 eggs. The dispersion index, which in fact measures aggregation and is rightly called "aggregation index" by Heath *et al.* (1988), shows that, in general terms, within the patch yolk sac larvae are more aggregated than eggs, and post-larvae than larvae. Accordingly it should be expected that values of patchiness index for larger larvae should increase, particularly during day time when they are aggregated in the bottom layer. Hunter and Coyne (1982) report that the onset of school formation starts at 10 mm SL for the Californian anchovy. This is the length at which larvae acquire the diel rhythm of vertical migration. We can conclude then, that if no dispersal from the patch is assumed, and no density dependent mortality is operating over one particular stage, the increase in patchiness reflects the capacity of larvae to regulate their position in the water column, and their diel migratory habits.

Some aspects on the derivation of mortality estimates

deserve further comments. The examination of our data showed that mortality during the egg stage is not constant. This should not be surprising if we take into account that younger eggs are not only more vulnerable to physical damage (Ciechowski, 1967) but also to predation by cannibalism, as suggested by the studies of Valdes *et al.* (1987) who showed that within an area of intense spawning, eggs were most frequently encountered in anchovy stomachs during the evening spawning period.

We have not accounted for possible dispersion or concentration of planktonic larvae within a drifting patch. Fortier and Leggett (1985) estimated the decrease due to dilution around the drifting drogue, from variations in salinity in the St Lawrence estuary. Heath and MacLachlan (1987) modelled dispersion of larvae using simple turbulent diffusion theory. Possible bias introduced by dispersion or concentration on mortality estimates are discussed by Reed *et al.* (1989).

Values for egg mortality were consistent during the cruise, but much lower than those obtained in meso-scale studies (Ciechowski and Sánchez, 1984).

In order to fit the single model we divided the set of data in two periods, setting  $t_c$  at the transition between the embryonic and the larval period. In previous studies (Ciechowski and Sánchez, 1984, Sánchez, 1986, 1990) mortality rates were calculated as customary for eggs and larvae, (yolk sac + post-larvae). This was also the criterion for the inter-day comparison during this study. The early developmental phases of the species could be more significantly divided, from a biological standpoint, on the basis of life-history models derived from the theory of saltatory ontogeny proposed by Balon (1984). According to Balon the term yolk sac larva, should be considered a "misnomer", since as long as a fish uses endogenous yolk supply as a source of energy it is an embryo. He proposes the term free embryo, irrespective of being inside or outside the chorion. Hatching is not a developmental threshold, in contrast the transition to exogenous feeding is one of the decisive thresholds of ultimate survival value. Mortality rates during the yolk sac stage were the lowest during early development, increasing at the transition to post larval stage.

Results of Fortier and Leggett (1985) and Heath and MacLachlan (1987) also indicate a low mortality rate prior to the onset of feeding. These results are interpreted by the authors as supporting evidence of Hjort's critical period hypothesis (Hjort, 1914, 1926). The described scarcity of food in the area, the absence of enrichment mechanisms of the type found elsewhere in the Argentine sea, that could maintain high production levels after the decay of the spring bloom, the massive characteristic of the spawning, and the protracted reproductive season seem to create a favourable scenario for starvation at the transition to exogenous feeding to become a major cause of larval mortality and a powerful regulator of the population.

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