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Recruitment and post-settlement growth of juvenile *Merluccius merluccius* on the western Mediterranean shelf*

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SUMMARY: Young-of-the-year European hake (*Merluccius merluccius*) were sampled during four seasonal cruises between November 1998 and September 1999. The greatest numbers and biomass were found in spring 1999. Some 73% of juvenile fish in terms of number, and 81% in terms of biomass, were caught at depths between 60 and 160 m on the outer western Mediterranean shelf, where the water temperature ranged between 13.5 and 14°C. The length composition of samples showed there to be small hake all year around, with modes between 7 and 11 cm total length depending on the season. Otolith analysis was used to establish age at settlement (62.7 days) and to determine seasonal growth. The monthly growth rates ranged from 1.2 cm month^{-1} for juvenile hake captured on February 1999 to 2.5 cm month^{-1} for ones captured in June. The growth rates are related to survival, as was shown by the calculated hatch dates and relative abundances of recruits. This work provides information on the first year of life, recruitment and growth processes in an important species of the Mediterranean demersal ecosystem which is heavily exploited by a recruitment fishery.

Key words: habitat, recruitment, juvenile fish, growth, otoliths, daily growth increments, *Merluccius merluccius*.

RESUMEN: RECLUTAMIENTO Y CRECIMIENTO POST ASENTAMIENTO DE LOS JUVENILES DE *MERLUCCIUS MERLUCCIUS* EN LA PLATAFORMA DEL MEDITERRÁNEO OCCIDENTAL. – Juveniles de la merluza europea (*Merluccius merluccius*) fueron muestreados durante cuatro cruceros estacionales realizados entre noviembre de 1998 y septiembre de 1999. La mayor abundancia y biomasa se encontró en primavera de 1999. Cerca del 73% de juveniles en abundancia y 81% en biomasa, se capturaron entre 60 y 160 m de profundidad en la parte externa de la plataforma del Mediterráneo occidental, correspondiendo a un rango de temperatura del agua entre 13,5 y 14°C. La composición en talla de las muestras mostró que hay ejemplares de talla pequeña todo el año con modas a los 7 y 11 cm de talla total dependiendo de la época. El análisis de los otolitos se utilizó para determinar la edad a la que se produce el asentamiento en el fondo (62,7 días) y el crecimiento estacional. La tasa de crecimiento mensual osciló entre 1,2 cm mes^{-1} para los juveniles capturados en febrero 1999 a 2,5 cm mes^{-1} para los capturados en junio. Las tasas de crecimiento están relacionadas con la supervivencia como demuestran los resultados del retrocalculo de nacimientos y la abundancia relativa de los reclutas. Este trabajo provee por primera vez información sobre el primer año de vida, los procesos de reclutamiento y crecimiento en una importante especie del ecosistema demersal Mediterráneo que es intensamente explotada por una pesquería de reclutamiento.

Palabras clave: habitat, recclutamiento, juveniles, crecimiento, otolitos, incrementos de crecimiento diario, *Merluccius merluccius*.

INTRODUCTION

Hake *Merluccius merluccius* L. is a major demersal finfish in the marine ecosystem of the Atlantic and Mediterranean. Its economic value in Europe is relatively high, especially in northern Mediterranean mixed fisheries (Pitcher and Alheit, 1995). This species was the most frequent component of trawl surveys performed in the Gulf of Lions over a period of 14 years and was dominant in terms of bio-

mass and abundance indices, the main component being juvenile fish (Bertrand *et al.,* 1998).

Despite the hake's ecological and economic importance, data on its life history in the western Mediterranean are scarce. In the Gulf of Lions and the Catalan Sea, the spawning season runs throughout the year, peaking in autumn-early winter (Recasens *et al.,* 1998). Information from egg and larval stages is also scarce. Hake eggs and larvae appear mainly in late spring, summer and autumn, with a peak abundance in late November over the continental shelf, with peak abundances between the 100 m isobath and the edge of the shelf (Olivar *et al.,* 2003).

Hake recruitment determined from the northwestern Mediterranean has shown variability in both time and space at the short scales (Maynou *et al.,* 2003). Maynou *et at.* (2003) find some constancy in the location of nurseries but other occasional nursery areas are also significant contributors to total recruitment. According to these authors, the reduced state of surface sediments and the percentage of organic matter were higher in hake nursery areas than in occasional nursery areas.

Growth of juvenile hake has been determined using otolith growth increments and length frequency analysis (Morales-Nin and Aldebert, 1997). The daily nature of the increments has been validated for juvenile hake in the Adriatic (Arneri and Morales-Nin, 2000) and increments have been used to determine growth rates and hatch date distribution.

The purpose of this study was to examine the seasonal hatching time and growth rate of *M. merluccius.* Age and growth based on otolith microstructures were examined, under the assumption that increments are formed daily, and that increment widths reflect somatic growth. From these data, larval hatching distributions were reconstructed to reveal spawning times and growth rates. These population measurements were compared with environmental data in an attempt to explain survival processes during the first year of life. This information will contribute to the identification of essential data for understanding factors determining the recruitment of juveniles of this important species.

MATERIAL AND METHODS

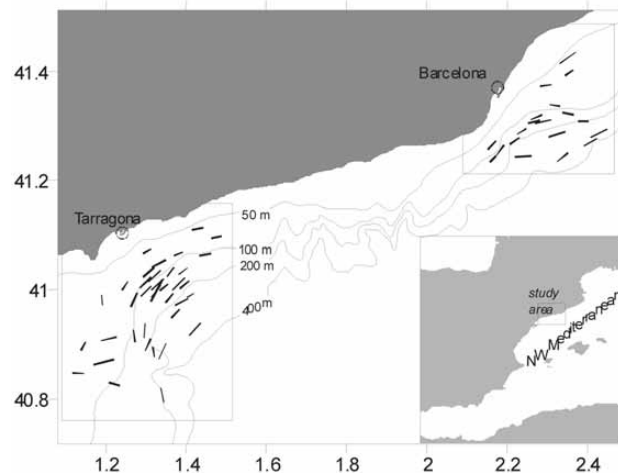Specimens of juvenile *M. merluccius* L. were sampled by trawling at depths between 50 m and

Fɪɢ. 1. – Locations of the sampling hauls on Lluç cruises.

350 m during four Lluç research cruises off the Catalan coast (Fig. 1). The start positions of the trawls were allocated proportionally with respect to sea bed surface area corresponding to each depth stratum, following a random stratified design. The depth strata used were: 50-100, 100-150, 150-250 and 250-350 m. At sea, trawl positions were measured by GPS. The standard effective trawling duration was 30 minutes. The mean towing speed was around 2.5 knots. The trawling net used was a Maireta system (Sardà *et al.,* 1998) with a cod-end mesh-size of 40 mm and a cod-end liner mesh-size of 6 mm. The trawl depth and net configuration (net opening) were monitored using acoustic net sensors (Scanmar). Table 1 shows details of sampling periodicity, location and number of hauls. At each sampling depth a conductivity, temperature and depth instrument (CTD) was lowered to obtain water column characteristics. All the fish were individually identified, counted, measured and weighed. The abundance and biomass of juvenile hake in each haul was estimated in relation to the swept area.

Total fish length to the nearest mm was recorded. Sagittal otoliths were sampled in a length-stratified way. A total of 1158 otoliths were obtained corresponding to fish length (FL) of 2.5 to 25 cm. The otoliths were stored dry in paper or plastic bags. Once in the laboratory, they were weighed (OW, otolith weight) with a precision of 0.001 g, measured (OL, otolith length) to the nearest 0.01 mm, and morphometric relationships (OL-FL, OW-OL) were determined.

Growth increments in the otoliths of juvenile hake from the Adriatic have been shown to be laid down daily (Arneri and Morales-Nin, 2000). Thus,

TABLE 1. – Cruise characteristics and *Merluccius merluccius* abundance in number and biomass. D: Depth range, T: Trawled time (min), SA: Swept area, A= Total number of individuals, B= Total biomass. (m=meters, min=minutes, ha=hectares, g=grams).

Cruise	Date	Hauls	D (m)	T (min)	SA (ha)	A	B (g)
Lluç-I	12-20/11/98	56	60-349	2032	197.52	581	20751
Lluç-II	04-10/02/99	43	60-346	1388	138.34	393	13248
Lluç-III	01-05/06/99	40	46-350	955	100.08	2899	43831
Lluç-IV	17-22/09/99	43	61-352	1039	132.00	1074	33799
Total		182	46-352	5414	567.94	4947	111629

age was determined from daily growth increments (DGI). For their observation, thin sections along the frontal plane were obtained. The hake otolith is optically dense due to its high protein content (Morales-Nin, 1986), requiring different preparation depending on fish size. Otoliths from fish in the 2.5-8 cm length range were mounted on glass slides with the inner side downward using Eukitt as the mounting medium. Otoliths from fish in the 8.5-12 cm length range were polished on their inner side until the core was reached, and then mounted as above. The otoliths from fish larger than 12 cm were polished on the external side until the core was reached, and then mounted with the external side downward. The internal side was then ground. All mounts were ground and polished with frequent microscopic control until the core plane was reached.

The otoliths were viewed using a microscope equipped with green light and a polarising filter, employing immersion oil as a clarifying medium. The microscope was connected to a high resolution video camera and a PC with an image analysis system. The otoliths were viewed on the screen at magnifications of 650 to 2000. In some otolith areas, sub-increments were very abundant and were differentiated by fine focussing. DGI were enumerated from the otolith core to the edge following the dorsal prism, which provides the most complete increment sequence (Morales-Nin and Aldebert, 1997). DGI were counted twice from the nucleus to the dorsal margin and *vice-versa*. The mean of the two readings was considered the specimen's age in days. A third reading was taken if the first two differed by more than 10%. If the discrepancy persisted, the otolith was discarded. A linear relationship was fitted to length-at-age data for each cruise to describe the growth of juvenile hake in the first year of life.

The hatch date distribution of each specimen was computed by subtracting fish age from each sampling date. This was weighed by the length frequency distribution of each cruise and plotted at monthly intervals. No correction for mortality was made.

The width of the outer otolith increments, or the recent otolith growth (ROG), can be used as an indicator of the previous somatic growth, although due to the conservative nature of otolith growth, differences in ROG must be caused by even larger differences in somatic growth (Hovenkamp, 1990). The otolith radius (OR) at each DGI and the width of the outer DGI corresponding to the last days of life were measured in the dorsal otolith prism using Optimas software. OR was closely related to FL (OR = $0.0067*FL^{1.0626}$ $F_{1,151} = 898$, $R^2 = 0.8552$, p<0.0001, n = 153). Moreover, age (number of increments) and OR were correlated (DGI= $-0.0952 + 0.0054$OR, $F_{1,151} = 264$, $R^2 = 0.6973$, p<0.0001, n = 153), therefore allowing OR to be used as a proxy for both variables. The data were standardised by OR intervals of 0.2 mm and the mean and s.d. were calculated. ROG was analysed for the four cruises (N = 47 for Lluç-I, N = 44 for Lluç-II, N = 36 for Lluç-III and N = 26 for Lluç-IV).

Statistical analysis

One-way analysis of variances was used to compare the number of daily growth increments (DGI) in primordia by cruise. Tukey's HSD test for unequal number of samples was used to test post-hoc comparisons of means. The relationship of age, estimated by DGI, to fish length (FL) was examined by using regression analysis, and analysis of covariance (ANCOVA) was used to test the null hypothesis that there were no differences in growth with respect to season. The assumptions involved in regression analysis were checked in terms of residuals (Christensen, 1996). Thus, to fit with the assumption of normality of the residuals and homoscedasticity of its variance, the continuous variable (DGI) was transformed to ln(*x*). In the two analyses the parametric assumptions of normality and homoscedasticity were evaluated using the Kolmogorof-Smirnov and Lev-
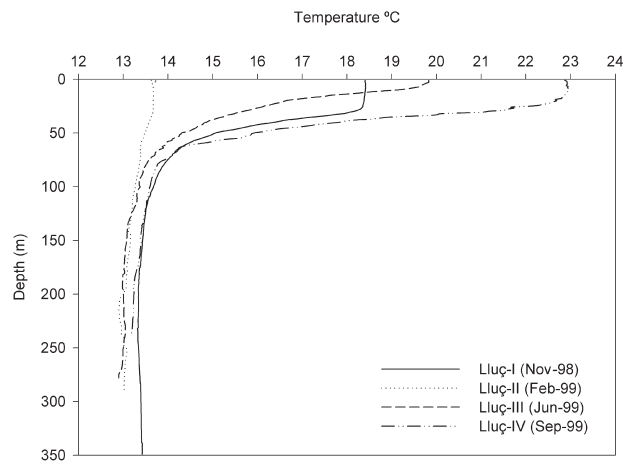
Temperature ºC

FIG. 2. – Vertical temperature profiles at the studied depths by cruise.

ene test respectively. When significant differences on the slopes of the regressions were obtained between seasons, univariate test of significance for planned comparisons between pairs of seasons were applied for least squares means, computed for covariates at their means.
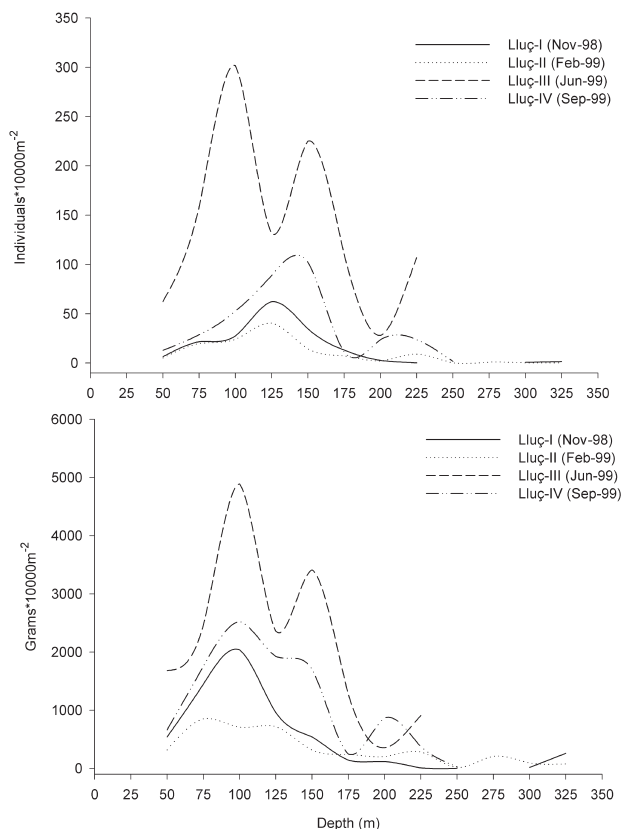

FIG. 3. – *Merluccius merluccius* bathymetric distribution of abundance (number of individuals) and weight (grams) per 10,000 m^{-2} by cruise.

RESULTS

Seasonal abundance and length composition

The water temperature was considered the best indicator of seasonal oceanographic conditions and was plotted against depth for the four cruises. The vertical profiles (Fig. 2) show water at <14°C below 75 m depth. The water column was stratified in all cruises except in Lluç-II (February 1999), in which the water was mixed with a temperature of 13.5°C. At the surface, water can reach 18.4°C in November, 19.8°C in June and 22.9°C in September.

The abundance (number of individuals and biomass) showed great recruitment in June that decreased progressively, reaching a minimum in February (Fig. 3). 73% of all hake in terms of numbers and 81% in terms of biomass were caught between 60 and 160 m depth. In general, the number of individuals in the four cruises presented the same
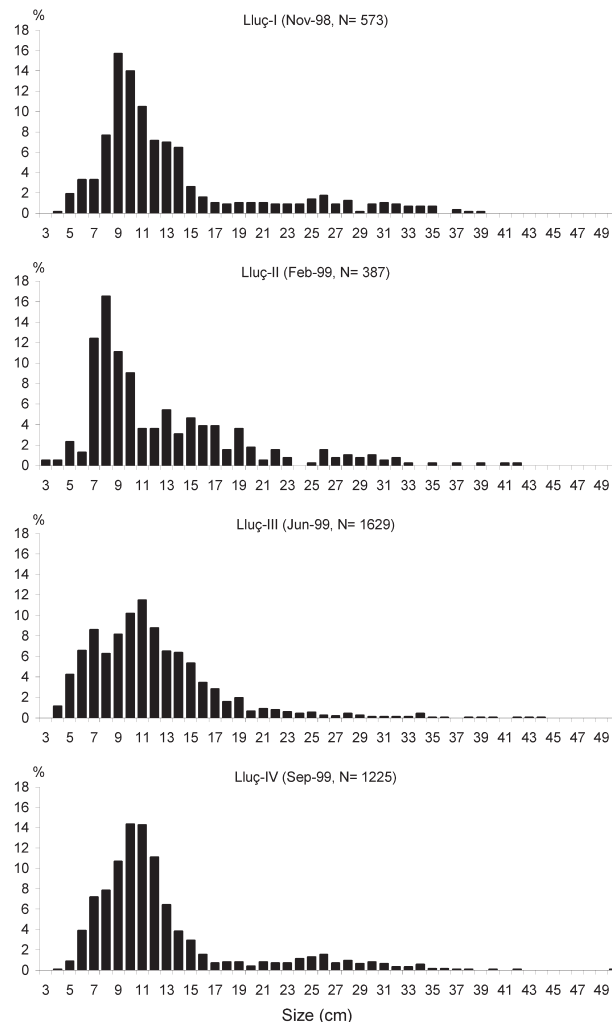

FIG. 4. – *Merluccius merluccius* length catch composition by cruise.

depth distribution, with a peak at 125-150 m, while the biomass presented a bimodal distribution with a marked peak at 75-100 m depth, and a second less well-defined peak at 125-150 m. A clear second peak in both variables was observed in the Lluç-III cruise both at 90 and 160 m depth, where the greatest number of hake juveniles was captured.

The captured hake ranged from 2.5 cm FL to 50 cm FL, although in this study the length range was limited to 25 cm for otolith morphometry and to 18 cm for age determination, corresponding to fish slightly older than 1 year (Morales-Nin and Aldebert, 1997; Arneri and Morales-Nin, 2000). Length differences in catch composition were seen between cruises (Fig. 4). Continuous recruitment is shown by the presence of small lengths on all four cruises. The length composition was bimodal in Lluç-III, when hake abundance was highest.

Otolith characteristics

Hake otoliths have a central core of around 8 mm surrounded by narrow DGI (1.4 mm ±0.2 μm) (Fig. 5a), followed by DGI increasing in width from 2.6 to 7.1 μm. This central area of the otolith, called the primordium, is irregular in shape (Fig. 5b) and composed of around 63 DGI. The last increments of the primordium are thick and dense, with a clear discontinuity around which accessory centres are seen
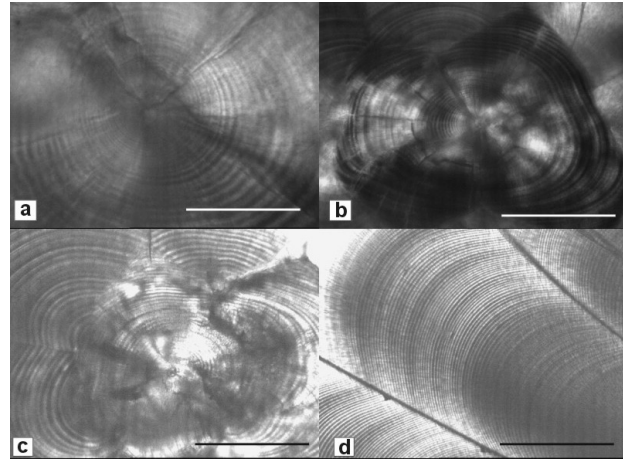

FIG. 5. – *Merluccius merluccius* otolith microstructure; a) otolith core and first increments; b and c) primordium with the discontinuity and accessory centres; d) regular growth on a prism. Scale bar: a) 50 μm, b,c,d) 100 μm.

(Fig. 5c). These accessory centres gave rise to the prisms that are characteristic of hake otoliths (Morales-Nin and Aldebert, 1997), in which the increments are laid down in regular patterns (Fig. 5d). The number of accessory centres or primordia is variable between fish and between left and right otoliths (Arneri and Morales-Nin, 2000). In the smallest specimens from the Catalan Sea (2.5 cm FL), one accessory centre was laid down in the rostral area and another in the postrostral area, indicating a recent transition to demersal life. The number

TABLE 2. – Summary results of the statistical differences in the number of daily growth increments (DGI) in the primordium calculated for each cruise (SE=standard error, K-S= Kolmogrof-Smirnov test, N= number of otoliths, df=degrees of freedom, SS= sum of squares, MS= mean squares, F= statistic)

a) Descriptive statistics

Cruise	N	DGI±SE	Minimum	Maximum	Normality
LL-I (Nov-98)	58	59.54±1.09	47.54	87.11	K-S[1]
LL-II (Feb-99)	91	63.18±0.96	40.00	93.00	K-S[1]
LL-III (Jun-99)	46	67.10±1.32	50.19	87.35	K-S[1]
LL-IV (Sep-99)	89	62.50±1.02	40.35	94.83	K-S[1]

b) Levene test of homogeneity of variances

Main effects	df	SS	MS	SS Error	df Error	MS Error	F	P
Increments	3	88.18	29.39	9021.42	280	32.22	0.92	0.43

c) Analysis of variances

Main effects	df	SS	MS	SS Error	df Error	MS Error	F	P
Increments	3	1414.67	471.56	23220.24	280	8293	5.69	0.00*

d) Post-host comparisons of means (Tukey's HSD test for unequal N)

	LL-I	LL-II	LL-III	LL-IV
LL-II	0.14			
LL-III	0.00*	0.20		
LL-IV	0.30	0.96	0.09	

1 Denote normal distributions
* Mark significant differences

$O_L = 0.0366 \cdot F_L^{1.0525}$ ($R^2 = 0.9786$, $F_{1,1156} = 52832$, $p < 0.0001$)

$O_W = 0.0366 \cdot O_L^{2.6356}$ ($R^2 = 0.9833$, $F_{1,1156} = 52832$, $p < 0.0001$)
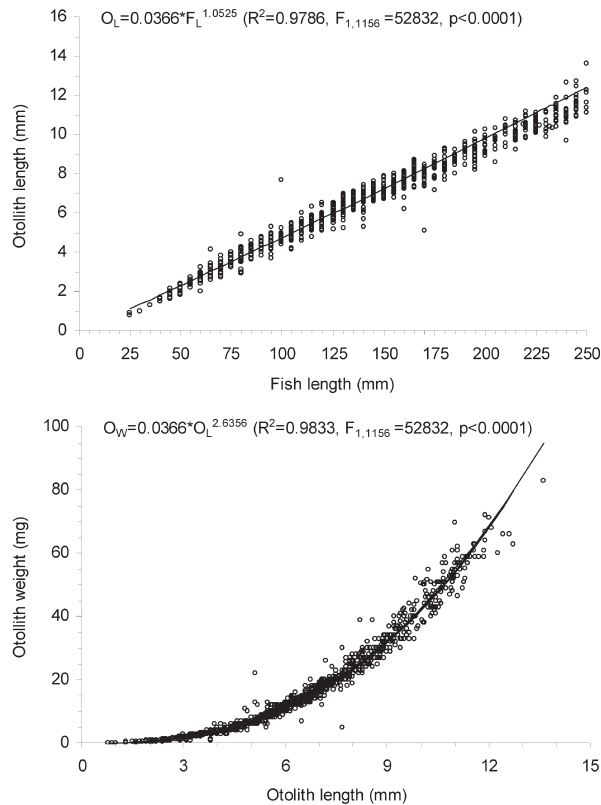
FIG. 6. – Juvenile *Merluccius merluccius* otolith morphometric relationships.

of DGI in primordia, which corresponded to around two months of life, was compared showing signifi-

cant differences between the Lluç-I and Lluç-III cruises (Table 2).

Age composition of juvenile hake and hatch date distribution

The OL/FL and OW/OL relationships showed a goodness of fit with R^2 equal to 0.9786 and 0.9833 respectively (Fig. 6), thus allowing fish growth patterns to be inferred from otolith dimensions.

The opacity of the otoliths and the presence of translucent bands corresponding to the multiple false rings on hake otoliths (Morales-Nin *et al.*, 1998) caused many otoliths to be over-polished. Only 527 otoliths showed a complete increment sequence and were accepted as adequate (less than 10% difference in the two readings). The age-length relationships (Fig. 7) in the four cruises were significant, and the ANCOVA results also showed significant differences between the slopes (Table 3). The age-length keys were calculated for monthly intervals and the juvenile hake growth rates determined were 1.21 for Lluç-I, 1.18 cm month[-1] for Lluç-II, 2.53 cm month[-1] for Lluç-III, and 1.78 cm month[-1] for Lluç-IV (Fig. 8).

The back-calculated hatch dates showed continuous hatching over the year (Fig. 9). The main peaks in relative abundance were in October-February, with secondary peaks in April and September. The hatch-

TABLE 3. – Summary results of the ANCOVA analysis comparing the age-length relationship (daily growth increments vs fish length) between cruises (D: statistic, K-S= Kolmogorof-Smirnov test, SR=standard residuals, df=degrees of freedom, SS= sum of squares, MS= mean squares, F= statistic, E= error).

a) Residual analysis

| Cruise/season | K-S test for normality | | Effects | Levene test of homogeneity of variances | | | | |
	D	P		df	SS	MS	F	P
LL-I (Nov-98)	0.56	>0.05	SR	3	0.21	0.08	0.23	0.88
LL-II (Feb-99)	0.78	>0.05	Error	521	178.46	0.34		
LL-III (Jun-99)	0.28	>0.05						
LL-IV (Sep-99)	0.07	>0.05						

b) Analysis of covariance

Main effects	df	SS	MS	F	P
Ln(DGI)	1	5331.5	5331.5	1685.8	0.00**
Season (S)	3	92.78	30.93	9.78	0.00**
Ln(DGI)*S	3	350.2	116.73	46.63	0.00**
Error	517	1294.4	2.50		

c) Univariate test for planned comparisons (least squares means)

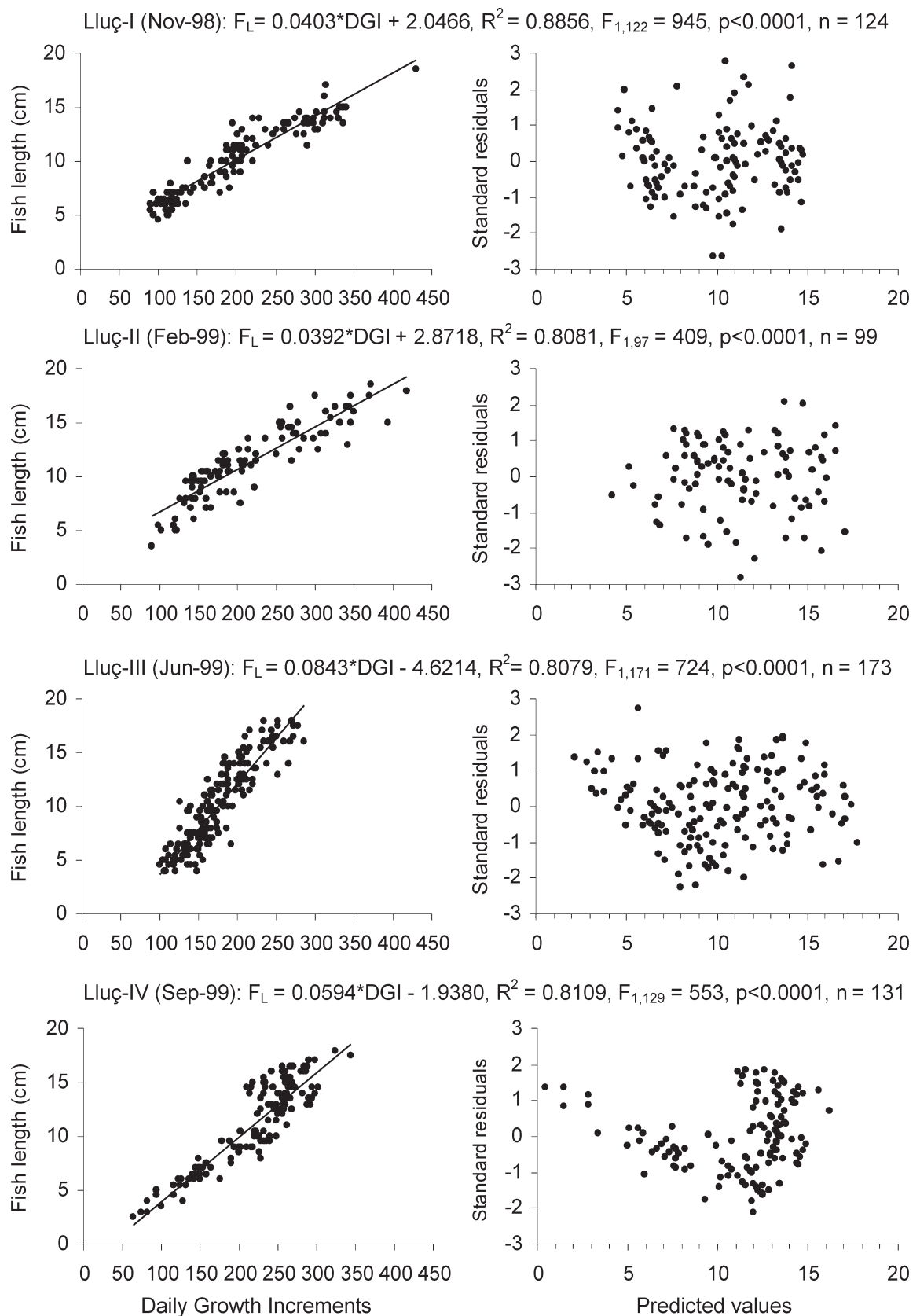| Comparison	df	SS	MS	df E	SS E	MS E	F	P
Lluç-I vs Lluç-II	1	12.20	12.20	517	1294.4	2.50	4.87	0.03*
Lluç-I vs Lluç-III	1	131.84	131.84	517	1294.4	2.50	52.66	0.0**
Lluç-I vs Lluç-IV	1	2.67	2.67	517	1294.4	2.50	1.07	0.30
Lluç-II vs Lluç-III	1	49.72	49.72	517	1294.4	2.50	19.86	0.00*
Lluç-II vs Lluç-IV	1	24.86	24.86	517	1294.4	2.50	9.93	0.00*
Lluç-III vs Lluç-IV	1	169.99	169.99	517	1294.4	2.50	67.90	0.00*

*Mark significant differences

FIG. 7. – Regression of fish total length versus daily growth increments and plots of residuals versus predicted values from juvenile *Merluccius merluccius* captured on each cruise.
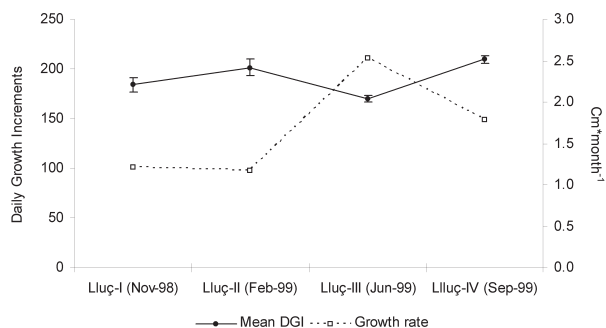
FIG. 8. – Evolution of the mean age in daily growth increments (±standard error) and the calculated fish length growth rate by cruise.

dates corresponded to an interval 2-14 months before capture on each cruise. The back-calculated peak in abundance was found about 6 months before the capture. This might be due in part to the fish size-range, which always had a mode at 8-11 cm. The hatch-dates are bimodal, except in the Lluç-III cruise, which corresponded to the period of maximum growth.

Analysis of recent otolith growth

The number of outer increments measured varied between 12 and 163, depending on the relative otolith size and the clarity of the increments on the slide. For the analysis of ROG we considered the last two months of life (i.e. outer 60 DGI), which were measured in 30.72% (47 observations) of otoliths. The plot of ROG against otolith radius (or age or fish length, due to their correlations) showed

different trends depending on the season (Fig. 10). The rhythmical pattern of thin and wider increments observed microscopically (Fig. 5) is also reflected in IW (Fig. 10).

The growth trajectories shown in Fig. 10 correspond approximately to the time elapsed between 20 September and 20 November 1998 for fish captured in autumn (Lluç-I), 10 December 1998 and 10 February 1999 for fish captured in winter (Lluç-II), 25 April and 5 June 1999 for fish captured in summer (Lluç-III), and 21 August and 22 September 1999 for fish captured in spring (Lluç-IV). The lack of temporal overlapping precludes determining whether there is a common seasonal trend, but there seems to be a deceleration of growth in autumn, more o less stable growth rates in winter and spring, and an acceleration of growth in summer.

DISCUSSION

Our results should have a bias due to the underestimation of true age because the interval between hatching and the formation of the first increment for *Merluccius merluccius* is unknown. In rearing conditions larvae start feeding at day 6, yolk and oil globule being depleted by day 11 after hatching (R.M.Bjelland, University of Bergen, unpublished master thesis, 2001). An error of around one week is therefore assumed in the observed ages, but neither the age nor the age-size related mortality were corrected.

Lluç-I (n=124, N=573; period of capture:16-20/11/1998)
Luç-II (n=102, N=387; period of capture: 4-10/02/1999)
Lluç-III (n=177, N=1629; period of capture: 1-4/06/99)
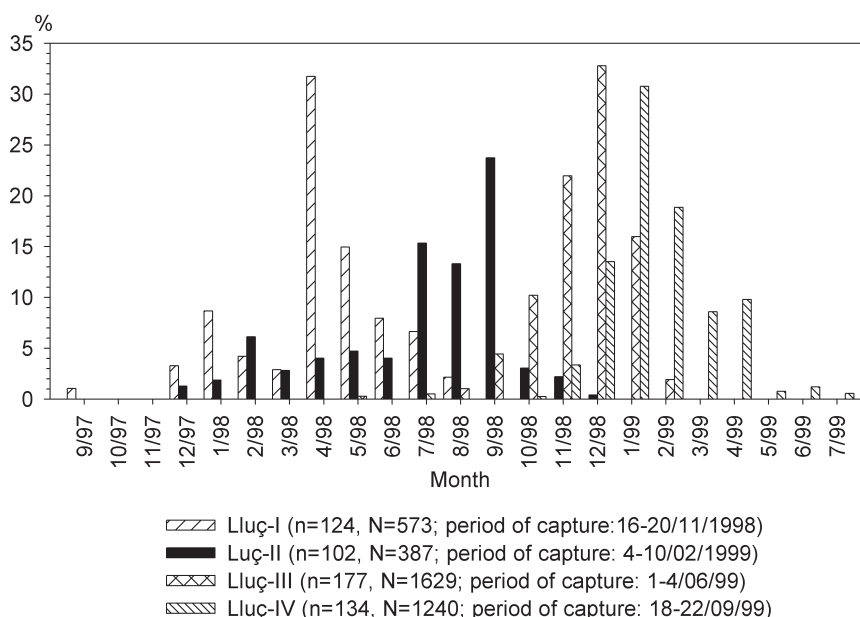Lluç-IV (n=134, N=1240; period of capture: 18-22/09/99)

FIG. 9. – Juvenile *Merluccius merluccius* relative frequency in percentage of the hatch dates estimated from daily ages and date of capture, summarised by monthly intervals (n= number of otoliths analysed, N= number of specimens captured).
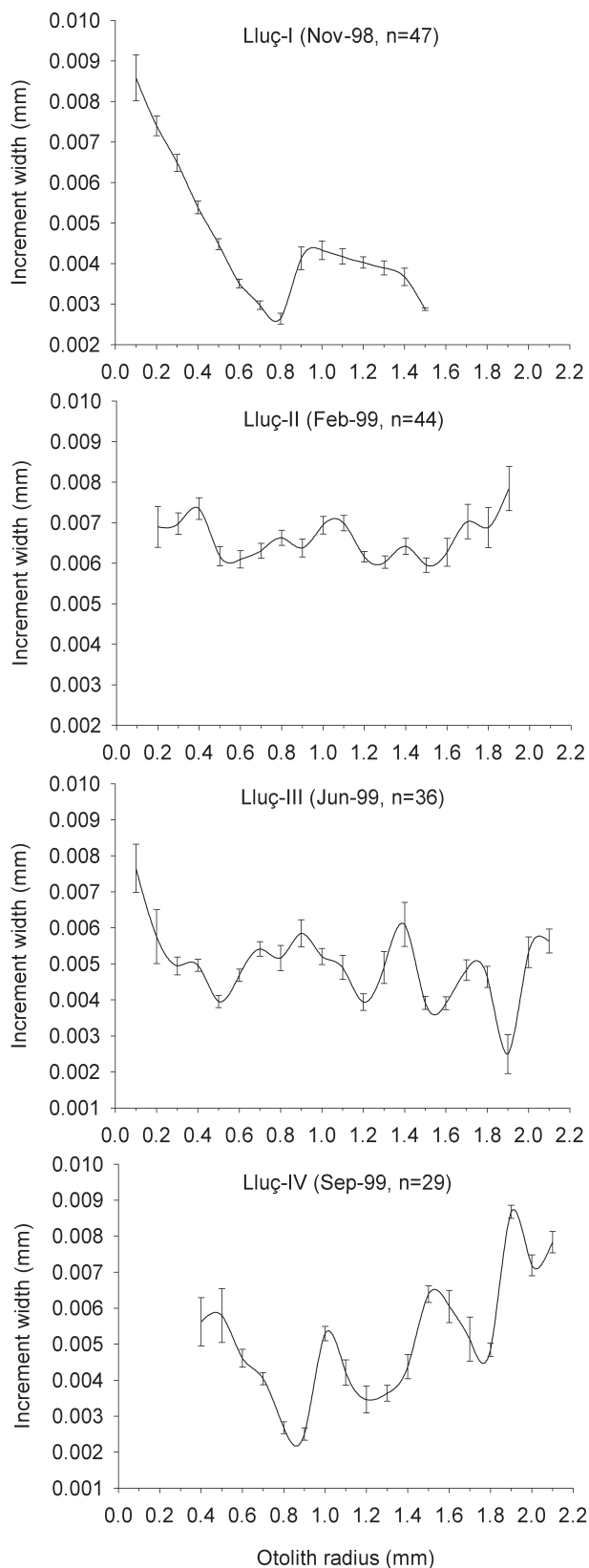
FIG. 10. – Evolution of the mean increment width (±standard error) for the 60 outer increments related to the otolith radius for each cruise. The radius 0.0 corresponds to the otolith core (n= number of otoliths analysed).

The pre-settlement period for *M. merluccius* has a duration of around two months, with small differences (up to 10 days) perhaps corresponding to the hatch date period. The observation in the smallest specimens (2.5 cm FL) of at least two accessory growth centres at the primordium edge suggests a relationship with the transition to demersal life. The formation of accessory growth centres takes place over more than one month, probably corresponding to more than a single event in their life history, as observed in the Adriatic (Arneri and Morales-Nin, 2000). Thus, the number of DGI in the primordium acts as an indicator of the duration of the pelagic life. Juveniles with the smallest primordia (59.54 DGI) were captured on the first cruise (autumn) and were born in spring (peak hatching on April-May 1998) oceanographic conditions, while the juveniles caught on the summer cruise, with larger primordia (67.1 DGI), were born in autumn-winter conditions (peak hatching October 1998-February 1999). These results show similarities with *Merluccius productus* which recruits to the bottom at 88 days of age at a mean temperature of 13 ºC (Bailey, 1982), whereas *Merluccius bilinearis* settles to the bottom at an age of 34.5±0.52 days, corresponding to 1.5 cm FL and a mean temperature of 9 ºC (Steves and Cohen, 2000). These differences might be due to the irregular shape of primordia in all hakes with different numbers of increments depending on the otolith axis. In this study, the maximum number of increments was counted in the primordium irrespective of a reading direction, so some of the supposed differences between the species might be due to different methods used to determine their settlement ages.

The mean growth rates for the four cruises lie between 1.2 and 2.5 cm month[-1], depending on the season. A growth rate of 1.15 cm month[-1] has been reported for juvenile hake in the NW Mediterranean (Morales-Nin and Aldebert, 1997), and between 0.7 and 1.2 cm month[-1] for the Ligurian Sea (Orsi-Relini *et al.*, 1989). These estimates were obtained by modal progression analysis of length frequencies, and refer to specimens larger than 6-8 cm whose absolute ages were unknown. Our growth rates agree with results obtained from otolith readings in the Adriatic (Arneri and Morales-Nin, 2000), so over 1 cm month[-1] is a common growth rate in juvenile hake. Therefore, the present results show growth plasticity with marked inter-seasonal variation which resulted in variable fish growth rates and IW. This might be due, in part,

to the different age ranges captured on each cruise and differential length-related mortality (Butler and Nishimoto, 1997). These quite fast growth rates were directly confirmed in the Atlantic hake by a recent tagging experiment which also confirmed the great individual growth variability observed in our study (Pontual *et al*., 2003).

There is a direct relationship between growth rate and the abundance of juvenile *M. merluccius*. The maximum growth was found during the summer cruise, when a greater abundance in terms of number and biomass was obtained. Similarly, the interannual variation of *M. productus* growth is directly related to abundance (Woodbury *et al*., 1995).

The observed interseasonal variability in growth rates derived from age-FL relationships (Fig. 8) was confirmed by the analysis of recent otolith growth in fish captured during the four cruises, indicating better rates in summer-fall. The ROG is an indicator of somatic growth (Methot, 1981), as seems to be the case in *M. merluccius* where there is a direct relation between fish size and otolith radius (R^2=0.8552, p< 0.0001). Juvenile hake shows great growth plasticity with oscillations and complex tendencies (Fig. 10). Although the sample design precludes reaching more detailed conclusions, ROG seems to hold potential that should be explored further.

There are no estimates of mortality for the hake juvenile period, but in a study of juvenile *M. productus*, the mortality decreased five-fold with fish length (M=0.05 for 10-35 mm FL, M=0.02 for 35-60 mm FL, and M=0.01 for 60-110 mm FL) (Hollowed, 1992). The mortality in the larvae seemed to be inversely related to growth performance (Butler and Nishimoto, 1997). However our data do not allow correcting for these effects, so the abundance of the hake at hatching may have been much greater than that obtained in our results. Moreover, the back-calculated hatch date distribution is biased on species with a long spawning season due to the different length of time over which mortality has been acting (Campana and Jones, 1992). Given natural mortality, representatives of the larvae hatched earlier in the season will inevitably experience greater cumulative mortality than those hatched late. Accordingly, early season larvae will be underrepresented in the back-calculated hatch date distribution relative to late season larvae. Also, some bias should be expected from the unequal number of otoliths aged by length interval. However, the back-calculated hatch date distribution obtained in the present study indicates that spawning in the Mediterranean takes place through-

out the year, with a main period in autumn. Moreover, the relative abundance of back-calculated births is in agreement with the spawning data for hake in the same area (Recasens *et al*., 1998; Olivar *et al*., 2003; Recasens pers. comm.).

This protracted reproductive period might be an adaptive strategy to maximise the survival of fish which can best use the opportunities presented. This strategy of protracted spawning is contrary to that observed in other Gadiforms such as Atlantic cod, in which spawning is concentrated in two months (Anderson and Dalley, 2000), depending on water temperatures. This longer recruitment may be related to the more stable Mediterranean conditions, which have little variation with respect to water temperatures at the outer shelf and beginning of the slope where the fish dwells (Fig. 2). Our data suggest a relationship between survival and growth rate. Thus, survival during the early juvenile life is related to growth, since the periods characterised by faster growth rate produce greater abundances. The hake main abundance was found in June 1999, corresponding to fish born in autumn 1998, which had the highest growth rates (Figs. 7-8, Table 3).

It is concluded that *M. merluccius* recruits all year round on the western Mediterranean shelf. The intensity of the recruitment and the survival depends on the season and growth rate, with a maximum in summer corresponding to fish hatched the previous autumn. The main abundance of recruits occurs on the outer part of the shelf at 100-150 m depth, where the water temperature at the recruitment depth is almost constant (13.5-14ºC). Thus, the Mediterranean hake recruits at higher temperatures than those reported for other hakes, but does so at similar depths (Steves and Cowen, 2000). Mediterranean juvenile hake show great growth plasticity at individual and seasonal levels, with intense growth rates depending on the season but with a mean growth superior to 1.6 cm · month^{-1}.

REFERENCES

Anderson, J.T. and E.L. Dalley. – 2000. Interannual differences in hatching times and growth rates of pelagic juvenile cod in Newfouland waters. *Fish. Res.,* 46: 227-238.

Arneri, E. and B. Morales-Nin. – 2000. Aspects of the early life history of European hake from the central Adriatic. *J. Fish Biol.,* 56: 1368-1380.

Bailey, K.M. – 1982. The early life history of Pacific hake, *Merluccius productus. Fish. Bull. US,* 80:585-598.

Bertrand, J.A., L, Gil de Sola, C. Papaconstantinou, G. Relini and A. Souplet. – 1998. An international bottom trawls survey in the Mediterranean. The MEDITS programme. *IFREMER Actes et Colloques,* 26: 76-96.

Butler, J.L. and R.N. Nishimoto. – 1997. Growth and cohort dynamics of larval Pacific hake (*Merluccius productus*). *Cal-COFI Rep.,* 38: 63-68.

Campana, S. and C.M. Jones. – 1992. Analysis of Otolith Microstructure Data. In: D.K. Stevenson and S. E. Campana (eds.) Otolith microstructure examination and analysis. *Can. Spec. Publ. Fish. Aquat. Sci.,* 117: 73-100.

Cartes, J.E., M. Elizalde and J.C. Sorbe. – 2001. Contrasting life-histories, secondary production, and trophic structure of the bathyal suprabenthos from the Bay of Biscay (NE Atlantic) and the Catalan Sea (NW Mediterranean). *Deep-Sea Res.,* 48: 2209-2232.

Christensen, R. – 1996. Analysis of variance, design and regression. Applied statistical methods. *Chapman & Hall/CRC, London.*

Coombs, S.H. and C.E. Mitchell. – 1982. The development rate of eggs and larvae of the hake, *Merluccius merluccius* (L.), and their distribution to the west of the British Isles. *J. Cons. Int. Explor. Mer.,* 40: 119-126.

Demirov, E. and N. Pinardi. – 2002. Simulation of the Mediterranean Sea circulation from 1979 to 1993: Part I. The interannual variability. *J. Mar. Syst.,* 33-34: 23-50.

Froglia, C. – 1973. Observazioni sull'alimentazione del merluzzo (*Merluccius merluccius* L.) del medio Adriatico. *Atti. V Congr. Naz. Soc. It. Biologia Marina,* 327-341.

Hollowed, A.B. – 1992. Spatial and temporal distribution of Pacific hake, *Merluccius productus*, larvae and estimates of survival during early life stages. *California Coop. Oceanic Fisheries Investigation Report,* 33: 100-123.

Hovenkamp, F. – 1990. Growth differences in larval plaice *Pleuronectes platessa* in the Southern Bight of the North Sea as indicated by otolith increments and RNA/DNA ratios. *Mar. Ecol. Prog. Ser.,* 58: 205-215.

Maynou, F., J. Lleonart and J.E. Cartes. – 2003. Seasonal and spatial variability of hake (*Merluccius merluccius* L.) recruitment in the NW Mediterranean. *Fish. Res.,* 60(1): 65-78.

Miquel J.C., S.W. Fowler, J. La Rosa and P. Buat-Menard. – 1994. Dynamics of the downward flux of particles and carbon in the open northwestern Mediterranean Sea. *Deep-Sea Res.,* 41(2): 243-261.

Morales-Nin, B. – 1986. Structure and composition of *Merluccius capensis* otoliths. *S. Afri. J. Mar. Sci.,* 4: 3-10.

Morales-Nin, B. and Y. Aldebert. – 1997. Growth of juvenile *Merluccius merluccius* in the Gulf of Lions (NW Mediterranean) based on otolith microstructure and length-frequency analysis. *Fish. Res.,* 30: 77-85.

Morales-Nin, B., G.J. Torres, A. Lombarte and L. Recasens. – 1998. Otolith growth and age estimation in the *M.merluccius*. *J. Fish Biol.,* 53: 1155-1168.

Olivar, M.P., G. Quílez and M. Emelianov. – 2003. Spatial and temporal distribution and abundance of European hake, *Merluccius merluccius*, eggs and larvae in the Catalan coast (NW Mediterranean). *Fish. Res.,* 60: 321-331.

Orsi Relini, L., M. Cappanera and F. Fiorentino. – 1989. Spatial-temporal distribution and growth of *Merluccius merluccius* recruits in the Ligurian Sea. Observation on the O group. *Cybium,* 13**:** 263-270.

Pinot, J.-M., J.L. López-Jurado and M. Riera. – 2002. The CANALES experiment (1996-1998). Intrannual, seasonal, and mesoscale variability of thecirculation in the Balearic Channels. *Prog. Oceanogr.,* 55: 335-370.

Pontual, H. de, M. Bertignac, A. Battaglia, G. Bavouzet, P. Moguedet and A.L. Groison. – 2003. A pilot tagging experiment on European hake (*Merluccius merluccius*): methodology and preliminary results. *ICES J. Mar. Sci.,* 60: 1317-1328

Pitcher, T.J. and J. Alheit. – 1995. What makes a hake? A review of the critical biological features that sustain global hake fisheries. In: J. Alheit and T.J. Pitcher (eds.) *Hake-fisheries, ecology and markets, Fish and Fisheries Series,* 15, pp. 1-14. Chapman and Hall, London.

Recasens, L., A. Lombarte, B. Morales-Nin and G.J. Torres. – 1998. Spatio-temporal variation in the population structure of the European hake in the NW Mediterranean. *J. Fish Biol.,* 53: 387-401.

Sabatés, A. – 1990. Distribution patterns of larval fish populations in the Northwestern Mediterranean. *Mar. Ecol. Prog. Ser.,* 59: 79-82.

Sánchez, F. and J. Gil. – 2000. Hydrographic mesoscale structures and Poleward current as a determinant of hake (*Merluccius merluccius*) recruitment in southern Bay of Biscay. *ICES J. Mar. Sci.,* 57(1): 152-170.

Sardà, S., J.E. Cartes, J.B. Company and A. Albiol. – 1998. A modified commercial Trawl Used to Sample deep-sea Meagabenthos. *Fish. Sci.,* 64(3): 492-493.

Steves, B.P. and R.K. Cowen. – 2000. Settlement, growth, and movement of silver hake *Merluccius bilinearis* in nursery habitat on the New York Bight continental shelf. *Mar. Ecol. Prog. Ser.,* 196: 279-290.

Tupper, M. and R.G. Boutilier. – 1995. Size and priority at settlement determine growth and competitive success of newly settled Atlantic cod. *Mar. Ecol. Prog. Ser.,* 118: 295-300.

Woodbury, D., Hollowed, A.B. and J.A. Pearce. – 1995. Interanual variation in growth rates and back-calculated spawn dates of juvenile Pacific hake (*Merluccius productus*) In: D. Secor, J.M. Dean and S.E. Campana (eds.), *Recent developments in fish otolith research*, pp. 481-496. University Press, South Carolina.