Larval development and growth of the European hake *Merluccius merluccius* in the northwestern Mediterranean*

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SUMMARY: The larval growth and development of the European hake, *Merluccius merluccius,* was studied from field larvae. Larvae were collected in the northwestern Mediterranean on three cruises carried out during the peak spawning months (November 1998, September 1999 and November 1999). Like other species of the genus, these larvae are characterised by a well-developed anterior part of the body, head and trunk region. Nevertheless, yolk sac larvae are much more slender than larvae at notochordal flexion stages. In the present study we analysed the allometric relationships between several body measurements and body length. This is the first attempt to infer larval growth of *Merluccius merluccius* by means of sagittal otolith analysis. Our results show the change in the otolith shape from a lenticular otolith in early larvae to an almond-shaped otolith in larger larvae. Otolith diameter showed a power relation with larval size, with no significant differences between seasons. In spite of the sea surface temperature differences between the three periods of larval collection, the early growth estimates showed no significant differences. This was explained by the similarity in the temperature at the depths at which the larvae are located. Absolute growth rates in length were estimated by relating daily growth increments in otoliths and larval size (standard length). When using the whole larval size range the values obtained were similar to those found for other *Merluccius* species. Nevertheless, the present data evidenced that growth for larvae younger than 12 days is very low, showing a significant increase thereafter. This indicates that length is probably not the best parameter for describing the growth of hake larvae in the first days of life, as allometric analysis suggested.

Keywords: hake, *Merluccius merluccius*, morphometric, larval growth, larval development, otoliths, age.

RESUMEN: DESARROLLO Y CRECIMIENTO LARVARIO DE LA MERLUZA EUROPEA *MERLUCCIUS MERLUCCIUS*, EN EL MEDITERRÁNEO NOROCCIDENTAL. – Se estudió el crecimiento y desarrollo larvario de la merluza europea, *Merluccius merluccius,* a partir de larvas capturadas en el mar. Las larvas se pescaron en el Mediterráneo noroccidental en tres campañas que se realizaron durante los meses de máxima puesta (Noviembre 1998, Septiembre 1999 y Noviembre 1999). Como otras especies del mismo género, estas larvas se caracterizan por tener la parte anterior del cuerpo, la cabeza y el tronco, bien desarrollada. Sin embargo, las larvas lecitotróficas son mucho más alargadas que las larvas en estado de flexión del notocordio. En este estudio, analizamos las relaciones alométricas entre algunas medidas del cuerpo y la longitud del mismo. Es la primera vez que se realiza un estudio del crecimiento larvario de *Merluccius merluccius* por medio del análisis de los otolitos sagitta. Nuestros resultados muestran que hay un cambio en la forma del otolito, pasando de forma lenticular en larvas pequeñas a forma almendrada en larvas de mayor tamaño. El diámetro del otolito se relaciona con la talla de la larva mediante un ajuste potencial, sin encontrarse diferencias significativas en las distintas épocas analizadas. A pesar de las diferencias en la temperatura superficial encontrada en los distintos periodos muestreados, no hubo diferencias significativas en las estimas de crecimiento larvario de las tres campañas. Esto se explicaba por la similitud de las temperaturas en las profundidades en que las larvas de merluza se distribuyen. Se estimaron tasas absolutas de crecimiento en talla relacionando el número de incrementos de crecimiento diario de los otolitos y la longitud estándar. Cuando se usó todo el rango de talla de las larvas se obtuvieron valores muy similares a los de otras especies de *Merluccius*. Sin embargo, nuestros datos evidenciaron que el crecimiento de las larvas de menos de 12 días de edad es muy bajo y aumenta significativamente en los días posteriores. Esto

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indica que probablemente la longitud no es el mejor parámetro para describir el crecimiento de la merluza en los primeros días de vida, tal como se sugería con el estudio de alometrías.

Palabras clave: merluza, *Merluccius merluccius*, morfometría, desarrollo larvario, crecimiento larvario, otolitos, edad.

INTRODUCTION

The European hake, *Merluccius merluccius* (L.) is a moderately large fish that is widely distributed in the northeast Atlantic and the Mediterranean (Alheit and Pitcher, 1995). It is one of the most important fishery species in the northwestern Mediterranean, being collected by a variety of fishing gears, particularly trawlers but also longliners and gillnetters. Bottom trawl fishery is mainly composed of juveniles living on the continental shelf. According to FAO statistics, annual catches in the Mediterranean reached a plateau of *ca*. 50,000 mt between 1993 and 1995 (representing half of the total European hake production) and had steadily diminished to 22,000 by 2002 (representing one third of total European hake production).

European hake shows a strong variability in yearly recruitment indices, both in the Mediterranean (Oliver and Massutí, 1995) and in the Atlantic (Sánchez and Gil, 2000). In the Mediterranean, female hake spawn continuously throughout the year, although spawning activity peaks in autumn in the Catalan sea (Recasens *et al.,* 1998), leading to seasonal variability in recruitment (Maynou *et al.,* 2003; Morales-Nin and Moranta, 2004). Spawners are concentrated in the highest densities between the shelf break and the upper slope (150 to 350 m, Recasens *et al.,* 1998).

Studies on European hake eggs and larvae are scarce and mainly analyse distribution in relation to environmental features, both in the northeast Atlantic (Coombs and Mitchell, 1982; Valdés *et al.,* 1996; Motos *et al.,* 2000; Alvarez *et al.,* 2001) and in the northwestern Mediterranean (Olivar *et al.,* 2003).

The main area of hake egg distribution in the Catalan sea (western Mediterranean) is the shelf edge (Olivar *et al.,* 2003) coincident with the main fishing grounds for spawning adults (Recasens *et al.,* 1998). Additionally, the main larval distributions were located oceanwards of the main reported distributions of juveniles (Maynou *et al.,* 2003), which implies the shoreward movement of postlarvae.

The development rates of hake eggs and yolk sac larvae have been studied by Coombs and Mitchell (1982), Marrale *et al*. (1996), Bjelland (2001) and Morales-Nin *et al*. (in press) in laboratory experiments. In the Mediterranean sea, Morales-Nin and Aldebert (1997) analysed growth rates by means of the analysis of daily growth increments in otoliths of juvenile hake in the Gulf of Lions, and Arneri and Morales-Nin (2000) made a study of hake juveniles that had settled to the bottom, from a size of 16 mm. This study also provides validation of the daily increment deposition rate in juvenile hake otoliths.

The present study is the first attempt to analyse larval growth and development of *Merluccius merluccius* in field larvae based on otolith readings and morphological measurements. The results are also discussed in the context of the oceanographic situation during the sampling period.

MATERIAL AND METHODS

The larvae analysed in this study come from samples taken during three cruises made on the Catalan coast (NW Mediterranean) in November 1998 (Llucet I), September 1999 (Llucet II) and November 1999 (Llucet III) (see Olivar *et al.,* 2003 for details).

Plankton hauls were carried out following standard procedures by means of a Bongo gear of 60 cm mouth diameter and 500 and 300 μm mesh nets (Smith and Richardson, 1977). Oblique plankton hauls covering the water column from the surface to 200 m (depth permitting) were carried out. On board, the plankton samples were concentrated and fixed in 5% formalin buffered with borax. It took 5 to 10 minutes from the hauling of the net on board to the fixation of the samples.

The larvae were measured to the nearest 0.1 mm at least six months after fixation. Shrinkage was not corrected, though it may have occurred at death and preservation. According to the estimations of Bailey (1982) for small *M. productus* larvae, 9-20% of shrinkage in length might have occurred during collection. Additionally, some shrinkage might have occurred during the storage period.

The following measurements were recorded: body length, the distance along the midline of the body from the tip of the snout to the tip of the notochord (standard length, SL) or to the end of the caudal fin (total length, TL); preanal length (PA), the distance along the midline of the body from the tip of the snout to the vent; head length (HL), the distance from the tip of the snout to the posterior margin of the cleithrum; head depth (HD), the maximum depth of the head; body depth at anus level (BDA), body depth at pectoral (BDP) and body depth at the base of the pectoral fin; eye diameter (ED); caudal length, the distance from the posterior margin of the hypural elements to the end of the caudal fin in larger larvae or the distance from the last portion of the tail from the end of the caudal pigmentation to the end of the primordial finfold; and caudal peduncle depth, the maximum depth of the caudal peduncle. The allometric relationships between the various body measurements and TL were calculated by use of a power equation $y=ax^b$, where x is TL, y the other measurement being related, b the allometric factor, and a the expected value of y at x=1 (Gould, 1966). Confidence intervals were calculated at the 95% level of significance.

The growth profiles of *M. merluccius* larvae were drawn according to the method proposed by Fuiman (1983). Body segment lengths were generated by sequentially subtracting a measurement from the next larger one. These data were related to the allometric growth coefficients calculated by fitting the power function between each of these segment lengths and TL.

Otolith preparation and examination

A total of 16, 35 and 38 hake larvae obtained from the three cruises Llucet 1, Llucet 2 and Llucet 3 respectively were used to analyse growth. The two sagittal otoliths were removed under a dissecting microscope and mounted onto glass slides with a clear medium (Depex). Otolith measurements and increment counts were made for both otoliths using a light microscope coupled with an image analysis system using OPTIMAS software. The otoliths were observed with immersion oil as a clarifying medium, and green light and polarising filters were used to improve the clarity of the daily growth increments (DGI).

When possible, increments were counted in both sagitta (84% of the individuals). If the two readings differed more than 2 increments, these otoliths were rejected (10% of readings). When counts differed between the right and left otolith, we used average values. We assumed daily formation of increments taking into account the findings of Arneri and Morales-Nin (2000) in juveniles of the same species in the Adriatic Sea. In larvae of other hake species, daily deposition has also been assumed for *Merluccius bilinearis* (Pannella, 1971) and validated for *M. productus* (Bailey, 1982). Increments were counted from the clear check mark that encircled the primordium (the hatch mark). The ages were estimated as the number of increments.

The diameter of this check (CD) and the maximum otolith diameter (OD) were measured. Size of larvae (SL), not corrected for shrinkage, was plotted against the otolith diameter and a power curve was fitted in order to determine the allometric relationship between otolith growth and somatic growth. The slopes of the curves were fitted for larvae from the three surveys and compared using a t-test.

The relationship between larval length (SL) and age (increment number) was analysed by fitting linear, exponential and Gompertz equations. As a first step, larvae collected on each cruise were analysed separately, and the slopes of the linear functions of the three cruises were compared using a t-test. Canonical Discriminant Analysis (Huberty, 1994) was performed on the data set defined by pairs of age and size data using the SPSS statistics package to check for differences in growth patterns through age.

RESULTS

Morphometric study of larval growth

The collected larvae ranged from the slender yolk sac specimens of 2.5 mm to a larger larva of 9.1 mm SL, although more than 70% of the larvae were smaller than 4 mm. The general morphology of these larvae agrees with the descriptions given in the literature (D'Ancona, 1931; Russell, 1976). Newly-hatched larvae do not show a well-formed and functional mouth, or completely black eyes. In the anterior digestive region remnants of the oil globule are present (Fig. 1). The only fin present in larvae smaller than 4 mm is the membranous pectoral fin. The caudal fin develops in the next stages, although it is not prominent until the 9.1 mm SL larva (11 mm TL), in which the urostyle is already flexed. The caudal fin rays are not fully formed (only 27 rays) in this larva. Pelvic fin buds and anal and dorsal fin bases appear between 5 and 6 mm, and six rays are already developed in the pelvic fin of the largest larva (Fig. 1).

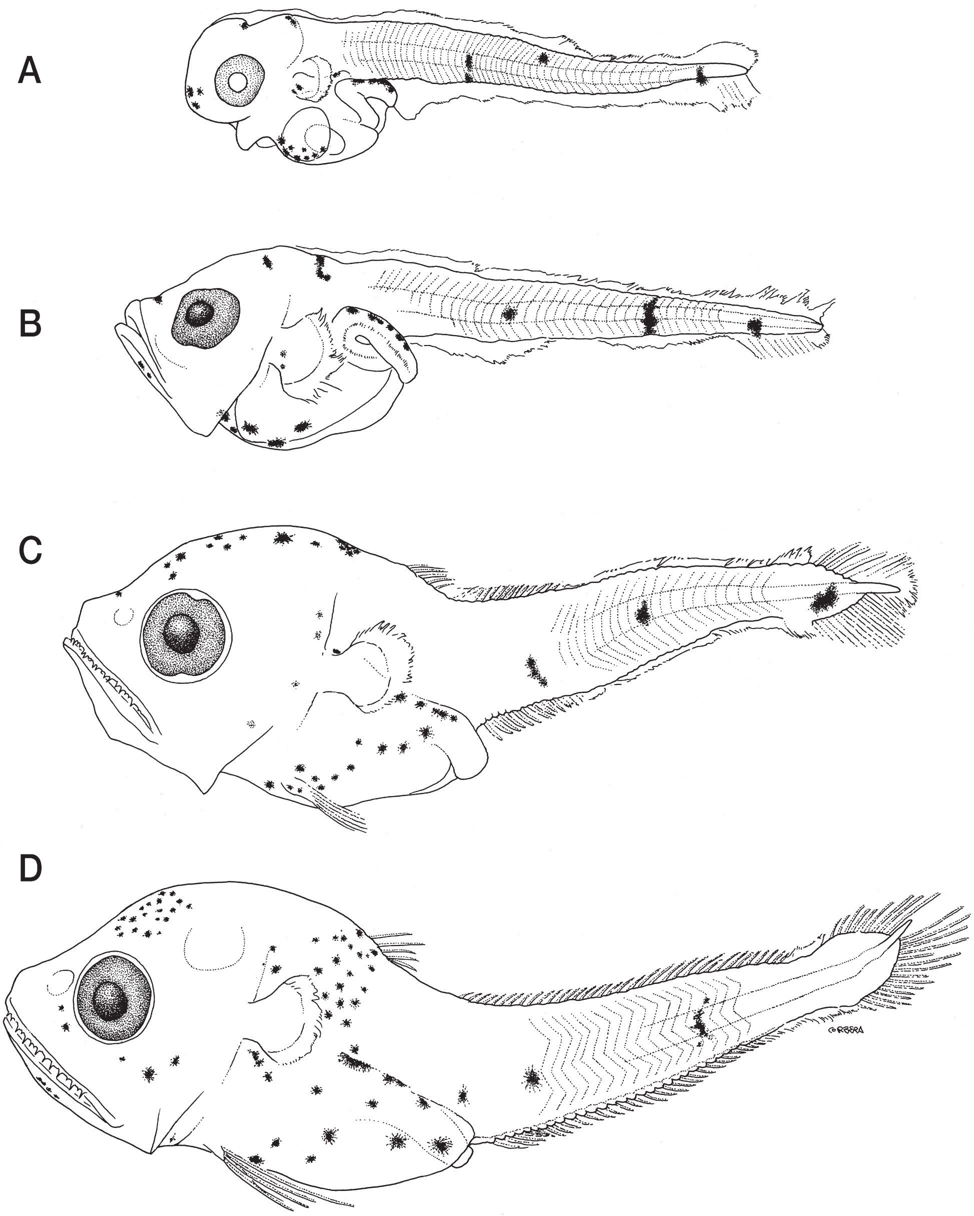

FIG. 1. – Larval development of *Merluccius merluccius*. A) newly hatched larvae 2.5 mm SL, B) larva 3.8 mm SL C) larva 6.5 mm SL, D) larva 9.1 mm SL (Drawing by J. Corbera).

Hake larvae undertake a progressive shape transformation as their body length increases (Fig. 1) (Table 1). Newly-hatched larvae are more slender than in the next developmental stages, in which the larvae are characterised by a well developed anterior part of the body. Growth in length of the head and digestive tract (head length and preanal length) has a significantly positive allometry in relation to TL. Eye diameter shows an isometric growth during development. All the measures related to the depth of the anterior part of the body (HD, BDP, BDA) progressively increase, showing a significant positive allometric relationship with body length. The caudal peduncle shows a considerable increase (both in length and depth) during development.

The growth profiles constructed for segment lengths showed a U-shaped pattern, with the lower growth coefficient for tail segment (Fig. 2a). The growth profiles for depth segments highlight the strong growth of the caudal peduncle (Fig. 2b).

Growth of larvae from otolith analysis

The larvae have relatively small otoliths with poorly contrasted increments that required strong

TABLE 1. – Values of the allometric coefficient (b), after fitting the power function between the several body measures to the body length. Confidence intervals at 95% significance (CI) and number of data points (n).

Body measures	n	b	CI
Preanal length	109	1.31	0.08
Head length	97	1.36	0.12
Eye diameter	96	1.06	0.08
Head depth	77	1.25	0.17
Body depth at pectoral	87	1.39	0.20
Body depth at anus	121	1.45	0.11
Tail length	109	0.76	0.06
Caudal length	85	1.38	0.15
Caudal depth	47	2.43	0.27

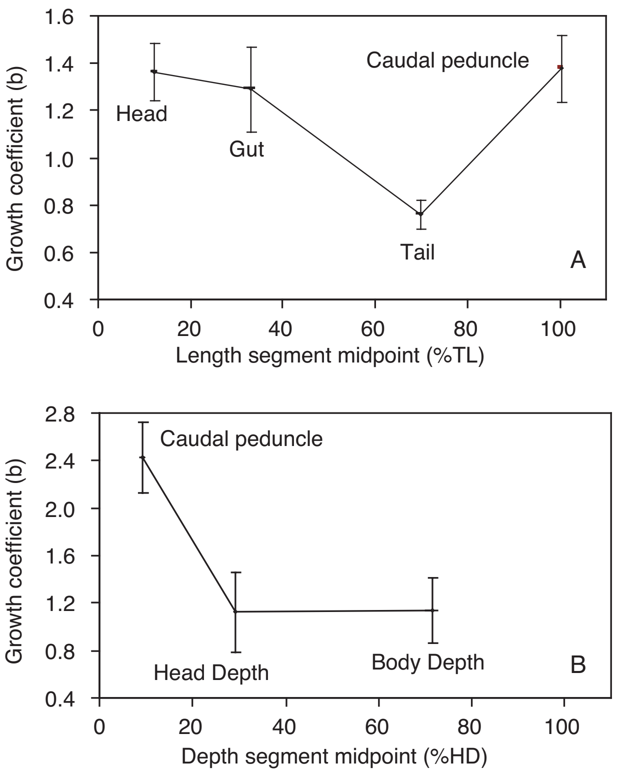

FIG. 2. – Growth profiles for A) longitudinally measured segment lengths and B) body depths in *Merluccius merluccius* larvae. Vertical lines indicate confidence intervals at 95%.

magnification (X1,000) to be discerned near the core. The core (small central part) appears as a dark spot surrounded by a check ring 16.3 μm (SD: 1.56) in diameter. We assumed that increment deposition began from that check, supposedly corresponding to hatching (Fig. 3). Another check is formed after 4-5 days. Larval sizes of larvae used for otolith analysis ranged from 2.6 to 9.1 mm (SL) and their estimated ages from 6 to 26 days after hatching (Table 2).

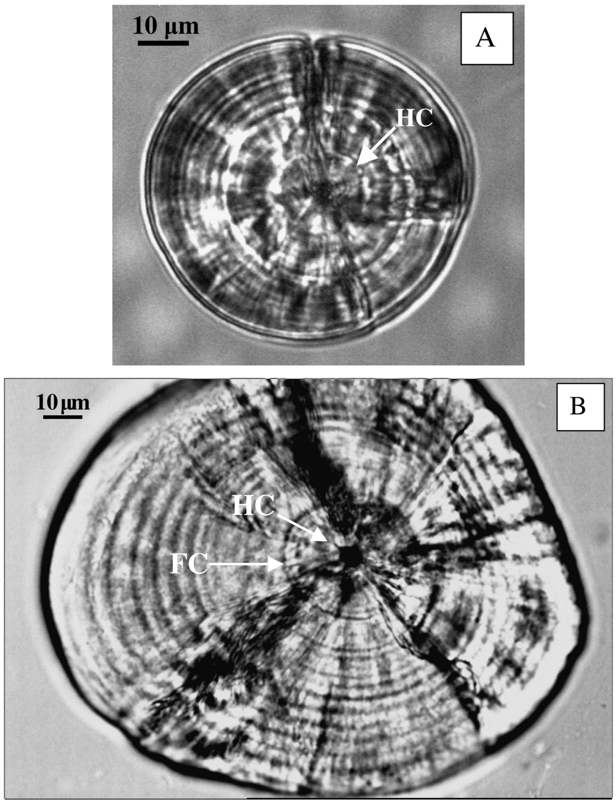

FIG. 3. – Transmitted light pictures showing sagittal otoliths of European hake larvae: A) 4.2 mm SL and B) 6.0 mm SL. Hatch check (HC) and first feeding check (FC) are indicated by an arrow.

Sagitta otoliths are disk-shaped in small larvae (2.5-4 mm SL) but their shape becomes asymmetric as the otolith grows (Fig. 3), increment widths being wider at the rostral edge. The biggest larva analysed, 11.7 mm TL (9.1 mm SL), did not yet show any sign of accessory primordium formation.

The maximum diameter of hake sagitta otoliths ranged from 18.9 to 221.1 μm. Significant relationships between SL and OD were observed for the three cruises analysed, indicating that otolith size reflects larval size in hake larvae. The slopes of the regression lines were not significantly different

TABLE 2. – Data concerning the larvae used for otolith analysis in the three cruises.

Cruise	Date of collection	Number of larvae	Standard length (mm)	Age (DGI)	Otolith diameter (μm)
LLUCET 1	November 1998	16	2.6-5.7	6-22	27.1-164.6
LLUCET 2	September 1999	35	2.6-6	3-22	33.2-123.2
LLUCET 3	November 1998	38	2.5-9.1	5-26	30.3-201.1

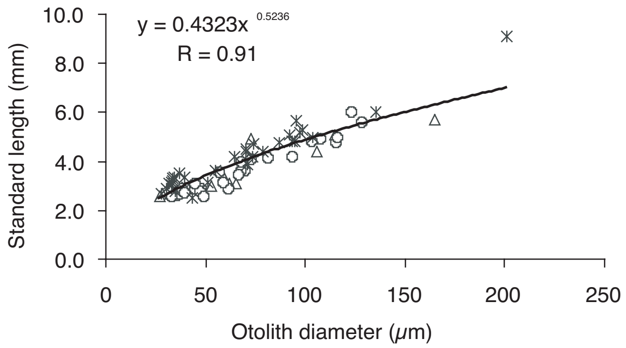

FIG. 4. – Relationship between larval size (SL mm) and otolith diameter for the three cruises combined.

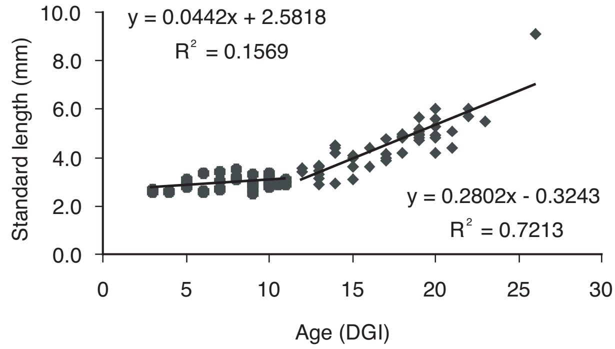

FIG. 5. – Relationship between larval size (SL mm) and age (days after hatching) showing the two growth periods.

between cruises (t-test, $p<0.01$), so the data were analysed by pooling the three cruises (Fig. 4).

The relationship between age and length was analysed by fitting the number of increments and the standard length using linear, Gompertz and exponential functions. High correlation coefficients were obtained in all cases and the estimated size at age and the absolute growth rate were fairly similar (Table 3). In this paper we used the parameters of linear function for further description of hake larval growth, to facilitate comparisons with other studies. Growth rates were not significantly different between cruises (t-test, $p<0.01$), so we analysed growth by joining the data of all the cruises (Table 3). The hake growth rates (0.15-0.19 mm d^{-1}) obtained by fitting all the larval size (SL) range are very close to those reported for larvae of the other species of the genus *Merluccius* at sea (Table 4). Although we analysed growth patterns over all the larval size range, looking at the size-at-age distribution points (Fig. 5), two subsets of data are clearly apparent. Canonical Discriminant Analysis showed clear separation into two groups. Discriminant scores from CDA results are shown by analysed individuals in Figure 6. The percentage of cases correctly classified was 97.5%, giving an age at transition point of 12 days. Growth rate for larvae below this age is very low ($y=0.04x+2.58$, $r=0.40$, but the

TABLE 3. – Estimations of the parameters of the three models applied to the relationship between size (standard length) and age (daily growth increments). R: correlation coefficient.

Date		Linear	Exponential	Gompertz
November 1998		$L = 0.157t + 1.489$	$L = 2.0488e^{0.038t}$	$L = 1.721e^{13.79(1-e^{-0.031t})}$
	R	0.89	0.92	0.92
	Growth rate (mm d^{-1}) t= 10 days	0.16	0.12	0.14
November 1999		$L = 0.152t + 1.744$	$L = 2.118e^{0.04t}$	$L = 1.794e^{14.42(1-e^{-0.032t})}$
	R	0.89	0.92	0.90
	Growth rate (mm d^{-1}) t= 10 days	0.15	0.13	0.15
September 1999		$L = 0.193t + 1.478$	$L = 2.170e^{0.04t}$	$L = 1.6521e^{16.43(1-e^{-0.036t})}$
	R	0.86	0.91	0.88
	Growth rate (mm d^{-1}) t= 10 days	0.19	0.15	0.19
Pooled data		$L = 0.175t + 1.545$	$L = 2.092e^{0.04t}$	$L = 1.9042e^{13.76(1-e^{-0.004t})}$
	R	0.87	0.91	0.90
	Growth rate (mm d^{-1}) t = 10 days	0.17	0.14	0.19

TABLE 4. – Larval growth rates of four different *Merluccius* species. Temperature refers to temperature experienced by larvae, as well in experimental conditions or in the field.

	M. productus			*M. bilinearis*	*M. hubbsi*	*M. merluccius*
Growth Rate (mm day^{-1})	0.16	0.16	0.14-0.28	0.17-0.18	0.16	0.15-0.19
Temperature (ºC)	12	—	10.5-12.4	13-17	11-16	15
References	Bailey (1982)	Butler and Nishimoto (1997)	Cass-Calay (1997)	Jeffrey and Taggart (2000)	Brown *et al.* (2004)	This study

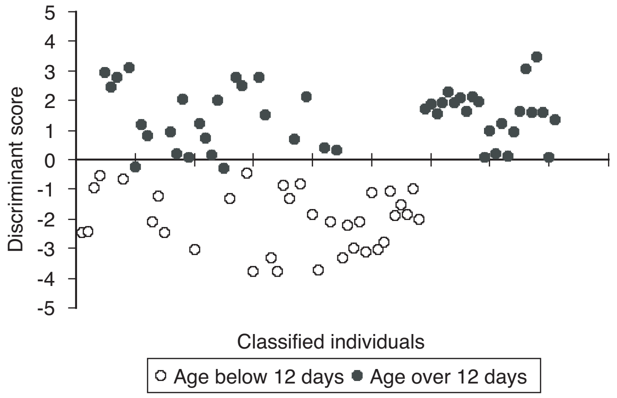

FIG. 6. – Discriminant scores from canonical discriminant analysis of pairs of size-age of all the hake larvae analysed.

slope was significantly different from zero: p =0.03, *t-test*), while for older larvae a slope significantly higher is evident (y=0.28x-0.32, r=0.85) (Fig.5).

DISCUSSION

Like most of the larvae that hatch from planktonic eggs, newly-hatched hake larvae are poorly developed (Kendall *et al.,* 1984). The growth pattern of the several body measurements in relation to body length indicated that body length growths at a slower rate than some particular portions of the body. The growth profiles, both in length and depth, highlight the strong development of the caudal peduncle. Growth intensity is also important for the head and gut regions, while the tail shows a slower development. The strong development of the caudal region must be related to the locomotor activity, as already observed in other fish larvae (Fuiman, 1983; Osse and van der Boogaart, 2004), while the intense growth of the anterior part of the body must be related to the feeding regime. A preliminary examination of gut content of some larvae from the present surveys indicated that adult copepods constitute their main prey item (G. Quílez, pers. comm.), similarly to observations for other hake species (Sumida and Moser, 1980). The ability to feed on adult stages of copepods requires a good swimming performance in order to capture prey and a well developed gut region to catch, swallow and digest them.

Otolith morphology also changes during development, being lentil-shaped at the start of the growth and changing to almond shaped in the largest specimens. No accessory growth centres were visible in any of the examined larvae, including the biggest one of 9.1 mm SL (11 mm TL). However, accessory growth centres have been described for a 16 mm TL individual that had completed its metamorphosis and had a shape similar to the adult *M. merluccius,* which was caught near the bottom (Arneri and Morales-Nin, 2000). The biggest larvae caught by us with the plankton gear at the pelagic domain still have the typical features of hake larvae. This suggests that *M. merluccius* begin to settle to the bottom at a size of between 11 and 16 mm that corresponds to an age of over one month. Steves and Cowen (2000) estimated the settlement of the silver hake *M. bilinearis* at a size of 15-20 mm SL, associated with the appearance of secondary growth centres in their otoliths.

Experimental studies (Coombs and Mitchell, 1982; Marrale *et al.,* 1996, Bjelland, 2001 and Morales-Nin *et al.*, in press) have shown that endogenous feeding (yolk sac period) extends from 4 to 6 days. The fact that otoliths of field larvae have two check rings with 4-5 daily rings between them reinforces our hypothesis that the second one is probably related to yolk sac absorption and the onset of external feeding. This also coincides with the findings of Bailey (1982) in *M. productus*.

The lack of significant differences between growth rates in length estimated for the three cruises was probably related to the vertical distribution of hake larvae, mainly below 50 m (Coombs and Mitchell, 1982; Sabatés, 2004). Due to the thermal characteristics of the hake spawning areas studied, with values ranging from 13 to 15ºC at this depth, we conclude that hake larvae develop under similar temperatures independently of the time of the year.

Larval growth analysis for other hake species of the same genus, *M. productus, M. bilinearis* and *M. hubbsi,* pooled all the larval stages (Bailey, 1982; Buttler and Nishimoto, 1997; Jeffrey and Taggart, 2000; Brown *et al.,* 2004). The present results on growth rates for *Merluccius merluccius* larvae using the same approach agree with those results. However, the information on development of *Merluccius merluccius* larvae reared in the laboratory (Bjelland, 2001) gives slow growth rates during the first 26 days after hatching, but a size of 10 mm is reached at 33 days, which is very close to the age of the 9.1 mm SL that we analysed (26 d). The two different growth periods evidenced by us for *M. merluccius* field larvae agree with the data of Bjelland (2001) and indicate that growth rate estimates using length-at-age over the entire larval period could give an erroneous perception of the growth pattern of this species. The almost null growth in length for larvae younger than 12 days indicates that length is probably not the best parameter for describing the growth of hake larvae in the first days of life. In fact, the ontogenic development of this species, with a positive allometric growth of the anterior part of the body in relation to standard length, indicates that larvae have a greater growth in thickness than in length. This may have implications in the analysis of the larval age-length relationship, because it shows that body length by itself may not always be the best indicator of growth for fish larvae.

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