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Age, growth and mortality of hake larvae (*Merluccius hubbsi*) in the north Patagonian shelf*

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SUMMARY: Age and growth and mortality rates were estimated in Argentinean hake (*Merlucius hubbsi*) larvae by counting and measuring otolith daily increments. Larvae were captured with a Bongo net in January and February 2001. Length-at-age data were represented by a linear model whose fitted expression was: L(t) = 0.156 t + 1.7. Slope represented mean the daily growth rate (0.156 mm/day). This value was quite similar to the values recorded by other authors for larvae of other Merluccius species. Individual growth rates were not significantly different between January and February. This homogeneity in the larval growth was coincident with the great thermal homogeneity recorded between months. Statistical analysis of the larval growth rates from different areas did not show significant differences. Daily mortality coefficients derived from the exponential decline models were 0.27 and 0.12 for January and February respectively. The difference between the two mortality coefficients could be attributable to the patchinnes, or larval recruitment pulses of distinct intensity between the two months.

Key words: hake, *Merluccius hubbsi*, larvae, age, growth, mortality, otoliths.

RESUMEN: EDAD, CRECIMIENTO Y MORTALIDAD DE LARVAS DE MERLUZA (MERLUCCIUS HUBBSI) EN EL NORTE DE LA PLATAFORMA PATAGÓNICA. – Se determinaron las edades y las tasas de crecimiento y mortalidad en larvas de la merluza argentina (*Merlucius hubbsi*) contando y midiendo incrementos diarios en los otolitos. Las larvas se capturaron con una red Bongo durante Enero y Febrero de 2001. Los datos largo-edad se representaron en un modelo lineal cuya expresión ajustada fue: L(t) = 0.156 t + 1.7. La pendiente representó la tasa de crecimiento diario (0.156 mm/día). Este valor fue bastante similar a los valores registrados por otros autores en larvas de otras especies del género *Merluccius*. Las tasas de crecimiento individuales no fueron significativamente distintas entre Enero y Febrero. Esta homogeneidad en el crecimiento larval resultó coincidente con la gran homogeneidad térmica registrada entre ambos meses. El análisis estadístico de las tasas de crecimiento de larvas provenientes de distintas áreas no mostró diferencias significativas. Los coeficientes diarios de mortalidad derivados de los modelos de disminución exponencial fueron 0.27 y 0.12 para enero y febrero, respectivamente. La diferencia entre ambos coeficientes de mortalidad podría deberse a la agregación o a pulsos de reclutamiento larval de distinta intensidad entre ambos meses.

Palabras clave: merluza, *Merluccius hubbsi,* larvas, crecimiento, mortalidad, otolitos.

INTRODUCTION

The Argentine hake *Merluccius hubbsi* is a demersal Gadiform species inhabiting the southwest Atlantic Ocean. It ranges from the proximity of Cabo Frío in Brazil (22°S) to the south of Argentina (55°S), at depths of between 50 and 500 m (Cousseau and Perrotta, 2000). In 2001, hake landing reached 240,000 t, corresponding to 29% of the total fishing captures.

Due to the declining tendency in catches during the last years (Pérez *et al.,* 2000), there is increasing

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interest in determining vital parameters through the larval stage. The success of the recruitment of marine fish is closely related to survival during the initial stages of ontogeny (Cushing, 1975). In addition, survival is related to growth (Houde, 1996), and small changes in growth rates may have a significant effect on recruitment by extending the stage duration over which high mortality could operate (Bailey and Houde, 1989). The studies of these parameters throughout the reproductive season contribute to the knowledge of recruitment of this species.

Since Panella (1971), the analysis of daily growth increments in otoliths has been broadly applied to ageing several larvae and juvenile of fishes, contributing to the knowledge of age, growth and mortality. Daily increments in at least 50 families and 300 species have been recognised (Secor *et al.*, 1992). This technique records the daily events consistently during the early life history of fishes, and the information remains unaltered over time (Jones, 1992).

Although several papers have dealt with growth and mortality of larvae and early juveniles of the *Merluccius* species (Bailey, 1982; Hollowed, 1992; Butler and Nishimoto, 1997; Jeffrey and Taggart, 2000), only Santos and Renzi, (1999) have studied these parameters in Argentine hake juveniles.

Hake spawns throughout the year with two more intensive periods, winter (May-July) in the Northern zone of its distribution (35°-38°S), and spring-summer (October-March) in the North Patagonian coastal zone (43°-45°S) (Louge and Christiansen 1992; Louge, 1996; Ehrlich, 1998). In the North Patagonian area hake larvae were also captured throughout the year but their densities were higher from November to January (Ehrlich and Ciechomski, 1994; Ehrlich, 1998).

The hydrography of the Northern Patagonian shelf is characterised by the formation of frontal systems produced as a consequence of tidal dynamics. Shelf-sea fronts separate totally homogenised areas from those with a stratified water structure (Glorioso, 1987). These frontal structures are non-permanent, beginning their formation in spring and summer. Characteristics of these systems are the high availability of nitrates associated with high biological production (phytoplankton blooms) (Carreto and Benavídez, 1990), and high aggregations of copepods (Ramírez *et. al.* 1990). This scenario creates a diversity of spawning habitats for the adult fish and different breeding conditions for eggs and larvae (Sánchez and Ciechomski, 1995).

This study was made in order to obtain growth and mortality rates of *M. hubbsi* larvae by analysing microstructures of daily deposition in sagittal otoliths. As larvae were captured on the northern Patagonian coast during the period of main reproductive activity (January and February 2001), within-seasonal differences in growth and mortality estimations were analysed.

MATERIALS AND METHODS

Collection of samples

Fish larvae were collected during two research cruises conducted by INIDEP (the National Institute for Fisheries Research and Development) in January and February 2001. The sampling area is shown in Figure 1A. A total of 66 ichthyoplankton samples were analysed. A considerably greater amount of larvae was captured in January at a small number of positive stations (Table 1).

Ichthyoplankton sampling was carried out with a Bongo net fitted with 300 µm mesh and a flowmeter. A SCANMAR depth sensor mounted on the sampler determined the sampling depth. The net was towed obliquely from 5 m above bottom to surface at 2.5 knots. All the samples were taken during light hours between approximately 8 am and 7 pm. Hake larvae were identified, sorted and fixed on board in 80% ethanol. The alcohol was changed after 15 days to assure the preservation.

At all stations, the surface and bottom temperature was measured with a Sea-Bird CTD.

Laboratory procedures

Total length of larvae was measured to the nearest 0.1 mm with an ocular micrometer fitted to a Wild M8 dissecting microscope and the sagittal otoliths were identified by dissolving the heads in a concentrated sodium hypochlorite solution. Length measurements were not corrected for shrinkage. When the otoliths became visible, they were washed with distilled water. After drying, they were removed using fine dissecting needles and placed onto a glass slide covering with Pro-texx (a transparent mounting medium). When all increments were not easily identifiable in the same plane (larvae larger than approximately 4 mm), the embedded otoliths were polished using 12, 9, and 3 µm lapping film paper to enhance the visibility. Otolith incre-

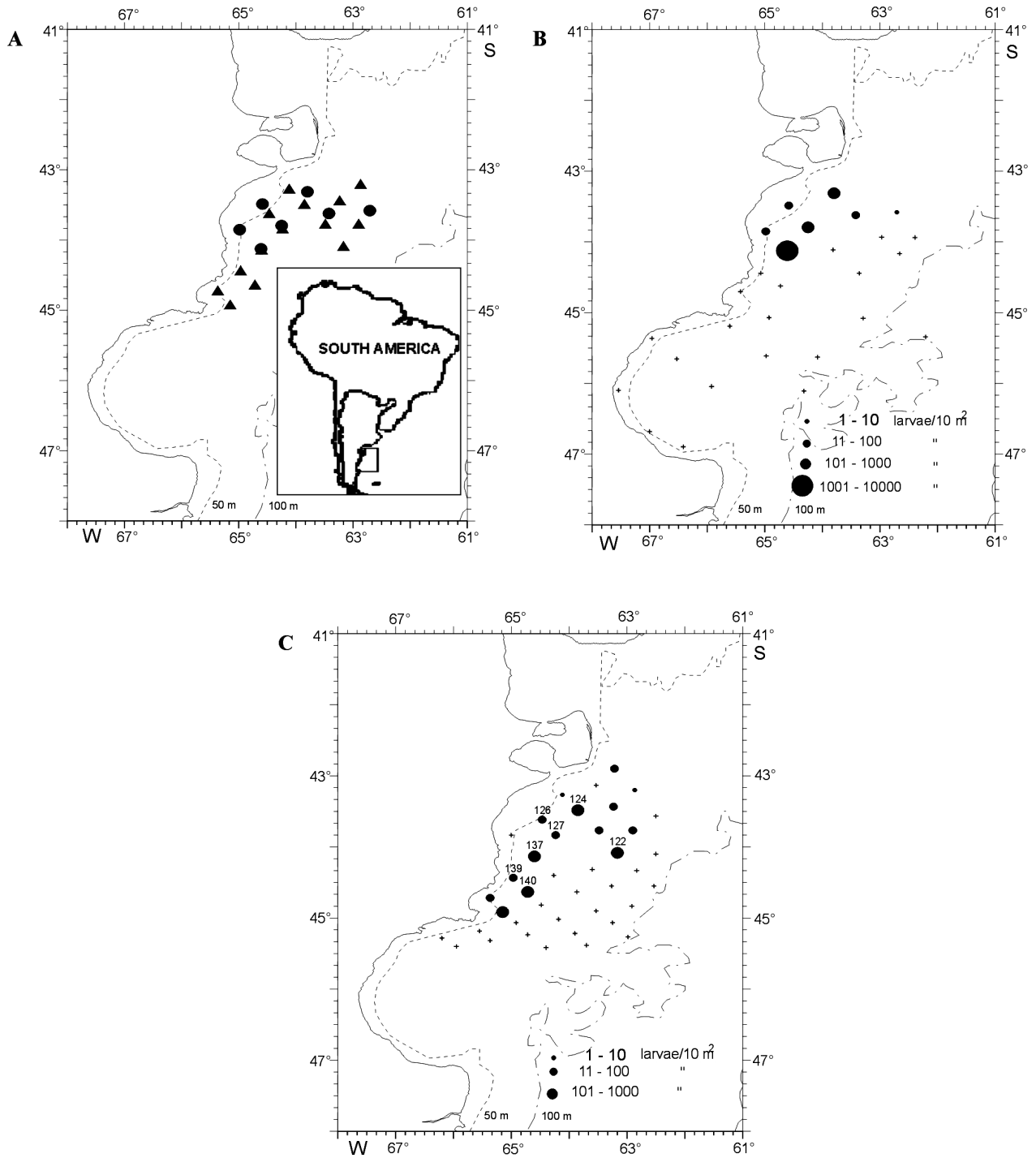

FIG. 1. – Study area and sampling sites for hake larvae on January and February cruises (A). Abundance of hake larvae collected in January (B) and February (C). Numbers in 1C are plankton positions where larval growth was analysed (see Table III).

TABLE 1. – Sampling data, number of hake larvae captured, and number of otoliths analysed.

Cruise	R/V	Date	Positive bongo stations N°	(%)	Number of larvae captured	Number of otoliths analysed
EH-01/01	Dr. Holmberg	January 2001	7	25	2343	94
OB-02/01	Cap. Oca Balda	February 2001	14	37	305	86

ments were observed under an Zeiss Axioscop binocular microscope fitted with an image analysis system. Image enhancement and analysis was conducted using Kontron software. The number, widths of each increment and otolith radius were recorded. All measurements were taken along the longest axis of the otolith. When the number of increments between right and left otolith agreed at least in 90%, the information provided from one of them was randomly considered; if this difference was greater, they were discarded. When only one otolith was available, we considered this information.

The identification of the daily deposition pattern was made following the recommendations of Campana (1992), and daily deposition of increments was assumed according to the observations in other hake species like *Merluccius bilinearis* and *M. productus* (Pannella, 1971; Bailey, 1982; Morales Nin, 1987). Back-calculation by counting daily increments has been used to determine the temporal distribution of birth dates during the spawning season. Considering the period during which the larvae do not deposit the first prominent daily increment, to calculate the true larval age two days were added to the number of increments, as Bailey observed (1982) in *Merluccius productus* larvae.

Age and integrated growth of all larvae were estimated from the slope of a linear regression between body size and the number of increments enumerated:

$$L(t) = bt + a,$$

where: L(t) = total length (mm) at age t; t = age in days (number of increments +2); b = slope (mean growth rate, mm/day); a = intercept. Represents estimated length (mm) at hatching.

A power relationship between larval size and otolith radius was fitted:

$$TL = a\ OR^b,$$

where: TL = total length (mm); a, b = regression parameters; OR = otolith radius (µm).

Individual growth rates were determined for each larva according to:

$$\frac{\sum_{1=0}^{n} TL_i - TL_{i-1}}{n},$$

where n: number of increments in the otolith; TL_i: total length back-calculated at i increments from the power relationship $TL_i = a\ OR_i^b$; OR_i: otolith radius measured at i increments.

For the instantaneous mortality coefficient determination, fish larvae were grouped into 0.5 mm size categories (2-2.5; 2.5-3...). For each size interval we established the mean length which was converted to mean age in days according to the L(t)-age relationship. Mean densities by age, expressed as number of larvae per 10 m^2, were calculated at the positive stations using a mean estimator based on delta distribution, which is a more efficient estimator than the ordinary sample mean (Pennington, 1983). Instantaneous daily mortality rates of larvae were estimated from exponential models of decline in abundance (mean density) with respect to age:

$$N(t) = N_0\ e^{-zt},$$

where N(t) = abundance at age t (number 10/m^2); N_0 = estimated abundance at hatching (*y* intercept of regression, number/10 m^2); Z = instantaneous mortality coefficient; t = age in days (increments enumerated in the otoliths +2).

Two mortality models were fitted independently to determine mortality rates during each cruise. Daily mortality percentages were expressed as:

$$M = [(1-\exp(-Z)]*100$$

Statistical analysis

L(t)-age, TL-OR and mortality relationships were compared between cruises (months) in analysis of covariance (ANCOVA). Previously to the comparisons, the data of TL-OR and mortality were linearly transformed using $\log_e$. The average increment widths at age were compared between cruises by t-test. Differences in individual mean growth rates were tested between month using t-test, and differences between stations by Tukey post-hoc pairwise comparison of probabilities.

RESULTS

Distribution of larvae

In January hake larvae were concentrated in a reduced area. The highest larval concentration was detected in the southernmost positive station with a maximum of 4100 larvae/10 m^2. In February it was observed an eastward and south-westward displacement of nursery areas, in a wider geographic range (Fig. 1 B, C).

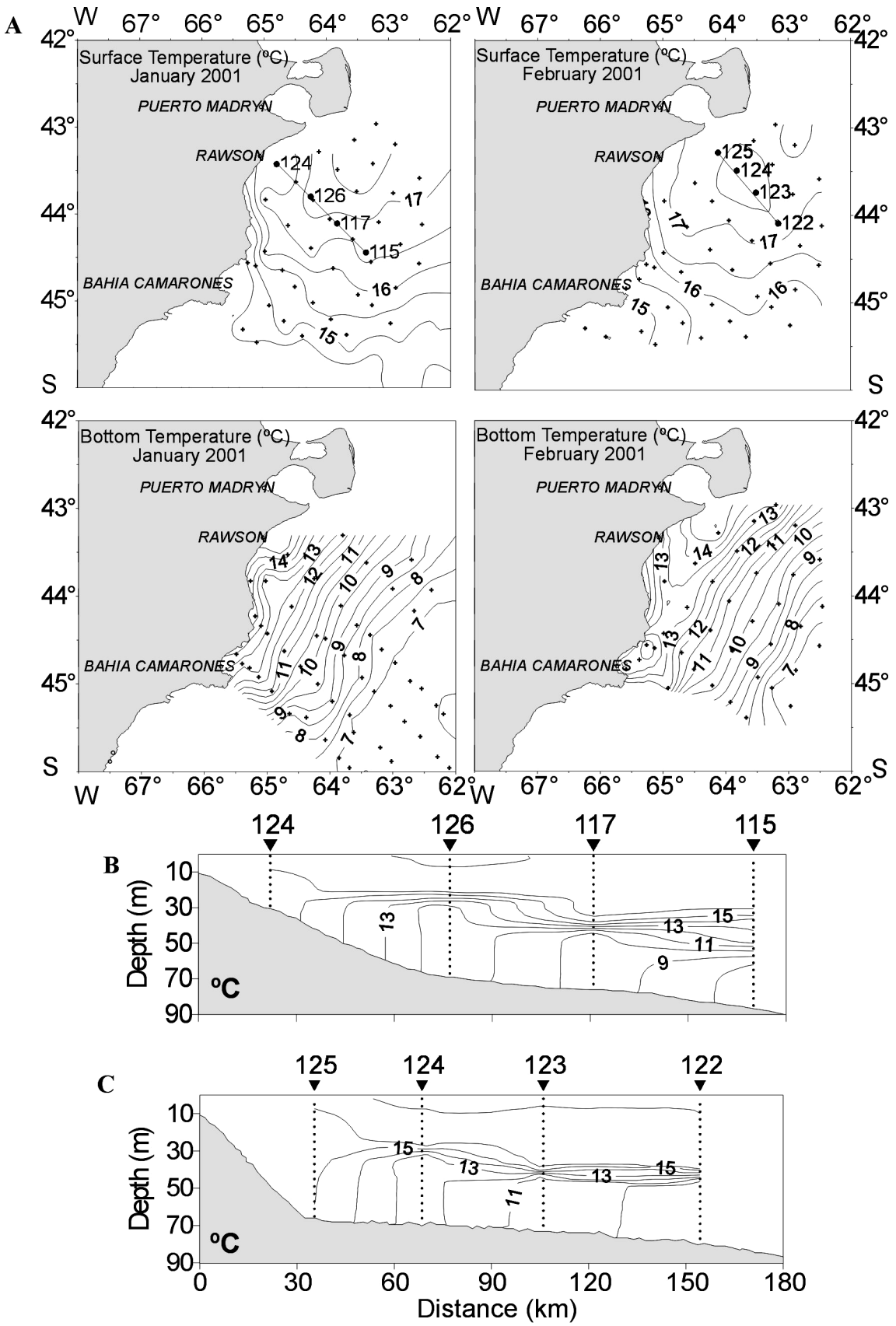

FIG. 2. – Sea surface and bottom temperature off northern Patagonia in January and February 2001 (A). Vertical distribution of temperature in January (B) and February (C). Positions of sampling stations along both transects are indicated by numbers (115, 117...).

Hydrography

According to the oceanographic data, temperature distribution patterns were quite similar between January and February. However, the temperature values were rather different between regions within the same month. Horizontal and vertical temperature distributions are shown in Figure 2. In the surface field a latitudinal thermal gradient was observed. Sea surface temperature ranged from 14.5 to 17.5°C and from 15 to 18°C in January and February respectively. A strong longitudinal temperature gradient at the bottom field was observed in both months, which was indicative of a frontal system. Bottom temperature ranged from 7 to 15ºC in January and from 7 to 14.5°C in February. Analysing vertical temperature distribution, the January profile (Fig. 2 B) showed a relatively wide stratified sector and only one onshore station (124) was located within the homogeneous sector. The February profile showed a wide stratified sector and one onshore station (125) was situated in the homogeneous zone (Fig. 2 C). The frontal area was quite close to the coast during January and February and most of the stations were situated within the stratified sector.

Variations in salinity in the study area were not considered because according to Guerrero and Piola (1997), salinity values are similar throughout the year, showing a vertically homogeneous field.

Age and growth

Hake larval size ranged from 2 to 6.5 mm and from 2.5 to 11 mm total length during January and February respectively (Fig. 3).

Otoliths were round and disc-shaped (Fig. 4). As larvae grew, the otoliths acquired an oval shape. From 0 to 54 increments were counted and measured for all larval sizes, and the first prominent increment was observed at larval sizes of approximately 2 mm. Sub-daily increments were rarely observed.

Hatching dates were estimated from December 19 to January 24 (peak January 14), and December 19 to February 17 (peak February 11) (Fig. 5). There was little superposition in the hatching dates between cruises, which means that both groups of larvae originated from different spawning times within the same reproductive season.

Length-at-age data of larvae collected on both cruises were fitted in two linear models and analysed separately. The regressions were: TL = 0.136 t + 1.76, R^2 = 0.86, for January; and TL = 0.153 t + 1.95, R^2 = 0.87 for February. Slopes were not statistically different (P>0.1), but the intercepts were distinct (ANCOVA, P<0.001). Because the difference between the intercepts was small and could be within the biological variability of hake larvae at hatching, the length-age data of both cruises were fitted in a single linear model (Fig. 6).

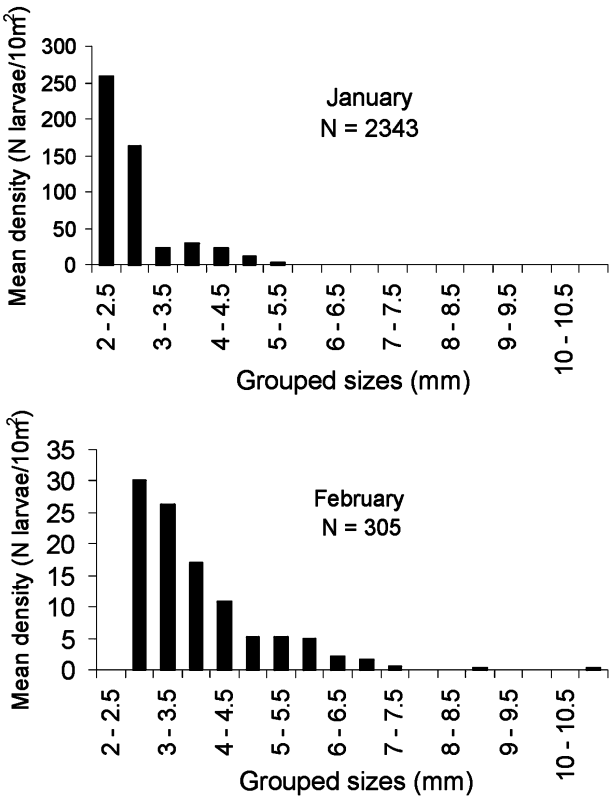

FIG. 3. – Length-frequency distributions of hake larvae captured on two cruises grouped by 0.5 mm intervals (N: number of larvae).

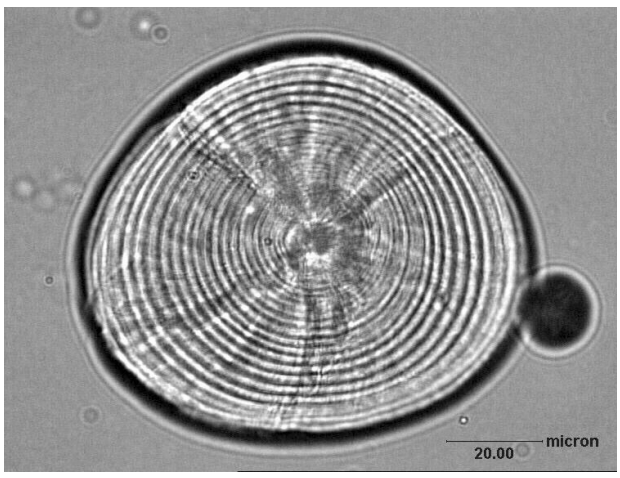

FIG. 4. – Larval otolith of hake (6.16 mm total length) showing 21 daily increments (1000 X).

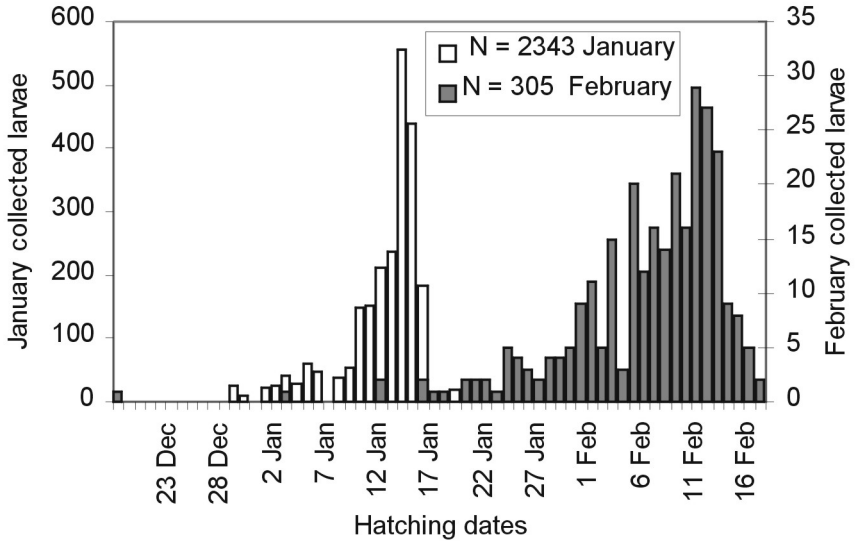

FIG. 5. – Back-calculated hatching dates of hake larvae.

Plots of total length (mm) and otolith radius (µm) were fitted for both cruises considering two power functions. The mathematical expressions were: $TL = 0.78\ OR^{0.46}$ for January and $TL = 0.76\ OR^{0.50}$ for February. To compare the equations, they were linearised using natural logarithms. Slopes were not significantly different (P>0.1). Nevertheless, the intercepts were different (ANCOVA P< 0.001). Because the variability in the intercepts could be biologically reasonable, TL-OR data from both cruises were fitted in a single power function (Fig. 7).

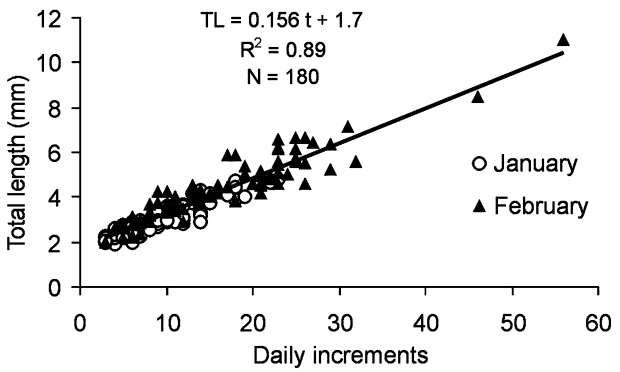

FIG. 6. – Linear regression between total length and the number of daily growth increments enumerated from the otoliths combining January and February larvae.

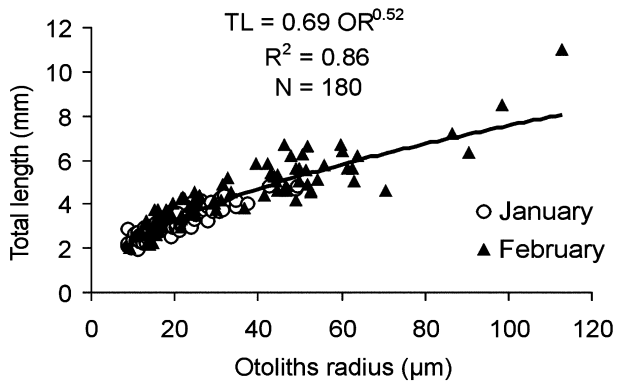

FIG. 7. – Allometric relationship of total length on maximum otolith radius combining January and February larvae.

Average increment widths at age showed the general tendency to increase with respect to age; moreover, from 1 to 5 increments the widths seemed to decline (Fig. 8). The mean width values ranged from 1.39 to 2.19 µm (January) and 1.50 to 2.70 µm (February). Increment widths were compared by analysing an identical increment interval (0-20) for both cruises. No significant differences in average increment width were detected at 5 and 10 increments (P>0.06). Evident differences seemed to be observed from 15 increments, but this was not statistically tested because there was a high difference in the data number between January and February (Table 2).

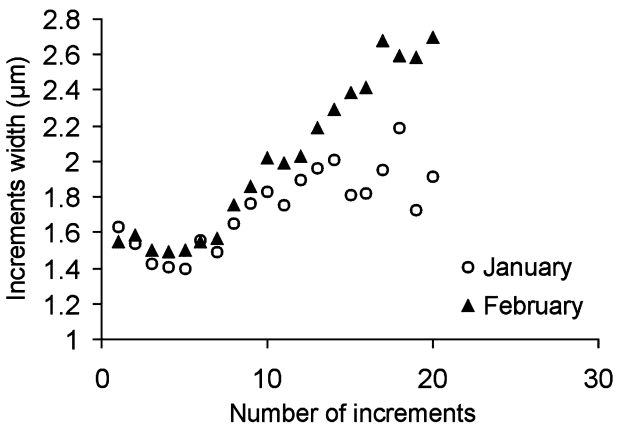

FIG. 8. – Average width of otolith increment measured in hake larvae captured on January and February cruises.

TABLE 2. – Average increment widths of hake larvae at 5, 10, 15 and 20 increments after hatching

Increments	5			10			15			20		
	Mean width (μm)	SD	N	Mean width (μm)	SD	N	Mean width (μm)	SD	N	Mean width (μm)	SD	N
January	1.39 *	0.32	63	1.83 *	0.41	32	1.81 **	0.33	8	1.91 **	0.59	4
February	1.50 *	0.41	75	2.02 *	0.44	54	2.38 **	0.70	40	2.70 **	0.87	32

* not significantly different (P>0.06); ** no statistically tested

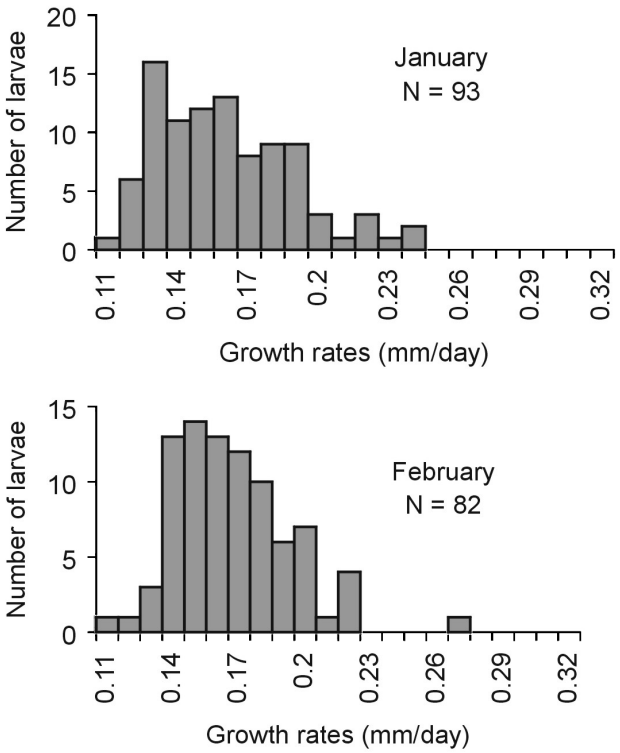

FIG. 9. – Growth rate frequencies of hake larvae collected in January and February. N: number of analysed larvae.

Individual mean growth rates of larvae were 0.160 (S.D.= 0.030) mm/day in January and 0.167 (S.D.= 0.027) mm/day in February (Fig. 9); the two groups were not significantly different (t-test, P> 0.1). These mean values of growth rates obtained individually were quite similar to the value obtained from the slope of linear regression integrating all the length-at-age data (0.156 mm/day).

Analysis of growth rates from different areas was performed for February (Fig. 1C). The average of individual growth rates in the seven stations analysed ranged from 0.145 to 0.195 mm/day and mean surface temperature values fluctuated between 15.8 and 17.6ºC (Table 3). The results of Tukey post-hoc pairwise comparisons showed significant differences in growth rates only between stations number 124 and 127 (P<0.05). All the other comparisons were not significantly different (P>0.1).

TABLE 3. – Mean individual growth rate of hake larvae and surface temperature per sampling station. Data correspond to February cruise.

Station number	Mean growth rate (mm/day)	SD	Sea surface temperature (ºC)	Number of larvae
122	0.157	0.019	17.0	16
124	0.145	0.023	17.6	5
126	0.167	0.028	16.7	7
127	0.195	0.015	16.9	7
137	0.180	0.035	16.7	18
139	0.179	0.021	15.9	9
140	0.163	0.025	15.8	18

Mortality

Mean densities observed in January and February ranged from 298 to 0.30 larvae/10 m^2 (2-6.5 mm) and from 30.2 to 0.32 larvae/10 m^2 (2.5-11 mm) respectively (Fig. 3). Larval size ranges were different between the two cruises. In January there was a greater abundance of early larvae (size range 2-2.5 mm). These larvae were not included in mortality estimates, because they were considered as a product of recent spawning and their abundance does not necessarily reflect larval mortality. In order to obtain comparative mortality between two months, the same larval size interval (2.5-6.5 mm) was considered. Total length intervals were converted to age in days by the growth model fitted in Figure 6. The slopes of the regression lines of log e transformed abundance plotted against age were estimates of mortality coefficients. Larval mortality coefficients were 0.27 and 0.12 for January and February respectively. The values differed significantly between months (ANCOVA, P<0.0001) (Fig. 10), and corresponded to a daily mortality percentage (M) of 23.67 and 11.3 for January and February respectively.

DISCUSSION

A central point in larval growth studies is the estimate of the starting length when the first incre-

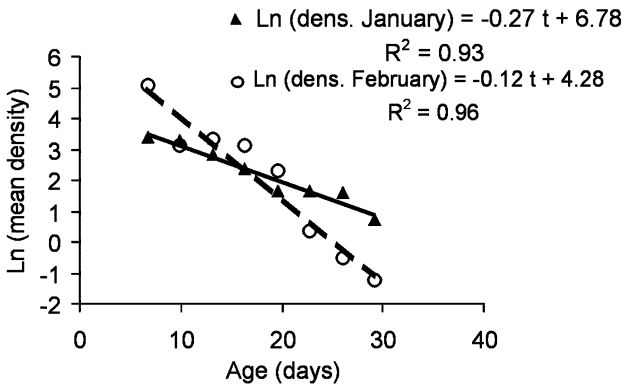

FIG. 10. – Exponential decline models (expressed linearly) fitted to the abundance by age of hake larvae. Size interval considered was the same for both cruises (2.5-6.5 mm).

ment is deposited. Of course, this parameter is not a fixed value and could have high variability. In *Merluccius productus* the deposition of the increments began one or two days after the complete absorption of yolk-sac, agreeing with the beginning of the exogenous feeding (Bailey, 1982). Larval size at first increment deposition (2 mm TL in this work) was slightly smaller than the exogenous first feeding larvae (2.25 mm TL) recorded by Viñas and Santos (2000).

Growth rate values obtained from the slope of the linear model fitted to the length-at-age data (0.156 mm/day) were quite similar to the values recorded by other authors for other *Merluccius* genus species. For *M. productus*, Bailey (1982) found a daily growth rate of 0.16 mm/day and Butler and Nishimoto (1997) one of 0.156 mm/day, while for *M. bilinearis*, Jeffrey and Taggart (2000) reecorded 0.17 mm/day (Fig. 11). None of the mentioned authors considered corrections for shrinkage. Slopes were similar and only differed from the intercept (L0) (size at hatching) values reported. Similar intercept values were reported in *M. bilinearis* (Jeffrey and Taggart, 2000). The higher intercept values reported in *M. productus* (Bailey, 1982; Butler and Nishimoto, 1997) could be attributed to greater egg diameters. *M. hubbsi* egg diameter ranged from 817 to 910 Bm (Ehrlich, 1998), while *M. bilinearis*, 880-950 Bm (Kuntz and Radcliffe, 1917) and *M. productus* ranged from 1070 to 1180 Bm (Ahlstrom and Counts, 1955).

Analysing the vertical distribution of *M. hubbsi* larvae in a thermal profile failed to reveal a defined pattern (Ehrlich, 1998). On the basis of a study performed in the same area, with data gathered in January during seven sampling years (1995-2001), Louge *et. al.* (2001) found that the surface temperature values were statistically equal to the ones recorded in the first 20 m of the water column. Therefore, the surface temperature could be assumed to be representative of the first 20 m of the water column. Ideally, instead of a bongo sampler, it would be better to work with opening-closing plankton gear with a temperature sensor.

The two main exogenous factors affecting the larval growth are temperature and food availability (Methot and Kramer, 1979; Sánchez, 1999). This study showed that the growth rates of hake larvae were not different between two consecutive months (January and February) within the reproductive season. This homogeneity in the larval growth is coincident with similar thermal regimes observed between months.

Though there is no significant difference, the higher growth rate obtained in February larvae (slope of fitted linear models or back-calculated growth rate, see results) than in January should be related to the widths of the increments. Although at 5 and 10 increments the mean widths were not significantly different between months, it would seem that as of approximately 15 increments, the widths were visually greater in February than in January.

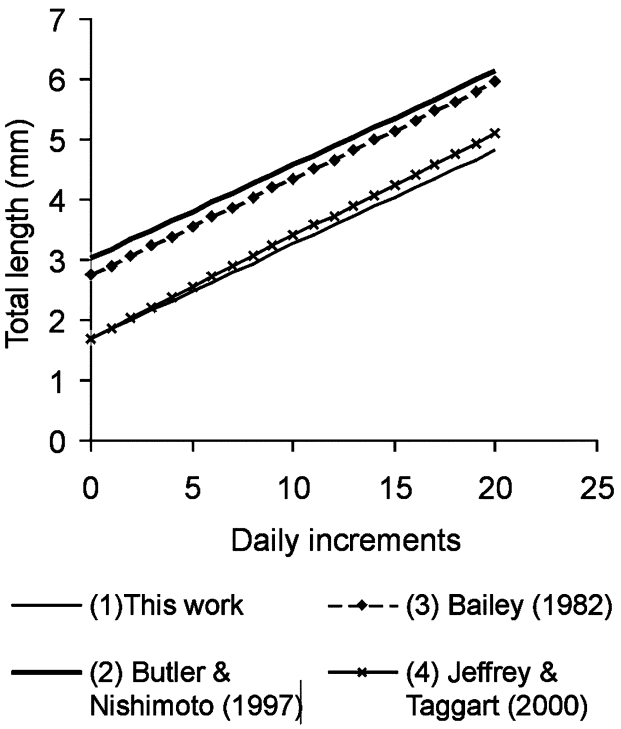

FIG. 11. – Comparison of linear growth models obtained by other authors in larvae of different species of *Merluccius* genus. 1: *M. hubssi* L(t) = 1.70 + 0.156 t; 2: *M. productus* L(t) = 3.02 + 0.156 t; 3: *M. productus* L(t) = 2.75 + 0.16 t; 4: *M. bilinearis* L(t) = 1.70 + 0.17 t.

Unfortunately, the difference could not be statistically tested for 15 and 20 increments because the number of data was quite unequal (Table 2).

There were no observed geographic differences in larval growth, probably because the thermal variations around 1-1.5ºC were insufficient to produce such differences. An exception was between the general stations 124 and 127 (see Table 2), which showed individual growth rates of 0.145 and 0.195 mm/day and surface temperature values of 17.6 and 16.9ºC respectively (Table 2). This difference cannot be explained on the basis of thermal influence, because higher larval growth was recorded at the station with the lower temperature. Obviously, other mechanisms such as endogenous causes must be involved.

Cass-Calay (1997) established a positive relation between the average growth rate of larval hake (*M. productus*) and the average concentration of prey-sized particles. In contrast, this author did not find a relation between the average growth rate and the average temperature. Further studies investigating the prey-sized particles in the plankton are required for a better understanding of the process affecting the larval growth of *M. hubbsi* larvae.

M. productus daily mortality coefficients ranged from 0.41 to 0.23 (average 0.31), from egg stages to 4.25 mm total length larvae (Hollowed, 1992). Mortality coefficients estimated in this study were smaller (0.27 and 0.12 in January and February respectively), because larval sizes were greater and egg abundance was not included in the estimations. Smith (1995) estimated for *M. productus* a larval mortality rate of 0.135 d^{-1} (size range 2.75-10.75 mm). This value fell within the range of our mortality estimates. Our values were quite similar to those obtained by Vargas *et. al.* (1996) for *M. gayi gayi* larvae from 4 to 11 mm standard length.

It is not easy to explain the difference between mortality coefficients obtained in January and February. In January the hake larvae were distributed at a smaller number of positive stations, being mainly concentrated in a single patch. The aggregation in patches could increase the larval mortality due to predation because predators feed intensively on the patches (McGurk, 1986). From this standpoint, higher mortality in January than in February could be related to patchiness. Another possibility for explaining the difference is to consider that larval recruitment was pulsed, not constant, between the two months. If a study is performed during a spawning pulse, the mortality values will be artificially increased, because the recruitment of young individuals will be more intensive (Sánchez, 1995). An indicator of the pulsed recruitment is the higher larval abundance in January than in February and the presence of earlier larvae in January ranging from 2 to 2.5 mm. (Fig. 3). Of course, these larval sizes were not included in the analysis. Another indicator could be the hake egg abundance. Hake eggs were gathered during the same cruises (EH-01/01, OB-02/01) and mean density values were 455.2 and 371.9 eggs/10 m^2 in January and February respectively (*unpubl. data*). From the point of view of a pulsed recruitment, the daily mortality coefficient in January larvae must be an overestimate.

Predation has been considered as the main cause of mortality in the early life of marine fishes (Bailey and Houde, 1989; Legget and DeBlois, 1994), and is a size-specific phenomenon. There is a close correlation between the size and mortality coefficient (Peterson and Wroblewski, 1984). Starvation at larval stages is well documented as an important cause of mortality among marine fish (Lasker, 1975; Owen *et. al.* 1989). Future studies will be necessary to detect the causes of larval mortality of the Argentine hake.

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