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Models describing mackerel (*Scomber scombrus*) early life growth in the North and Northwest of the Iberian Peninsula in 2000*

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SUMMARY: Mackerel (*Scomber scombrus*) in early life stages were captured in 2000 in the north and northwest of the Iberian Peninsula (ICES Divisions VIIIc and IXa North). Daily rings on their otolith sagittae were identified. Otoliths from 377 larvae and post-larvae caught in April and May 2000, ranging in length from 2.3 to 23.7 mm L_S (Standard length) and ranging in age from 7 to 38 days after hatching were analysed. Additionally, 68 otoliths from juveniles and pre-recruits caught between July and October 2000 with a length range of 121-202 mm L_S and aged between 65-186 days after hatching were analysed. Gompertz and Logistic growth models were fitted to the pooled length at age data of the larvae-postlarvae and juveniles-pre-recruits. As length at hatch is assumed in the literature to be 3.0 mm, the models were applied in two ways; not forced to pass through L_0=3.0 mm and forced to pass through L_0=3.0 mm. The unforced logistic growth curve appeared to be the most suitable for describing growth during the first year of life of mackerel (L_∞ = 191.6 mm; K= 0.070; t_0= 66.7 d).

Key words: early growth, daily growth, mackerel, North East Atlantic, *Scomber scombrus*

RESUMEN: MODELOS QUE DESCRIBEN EL CRECIMIENTO EN LAS ETAPAS TEMPRANAS DE LA CABALLA (*SCOMBER SCOMBRUS*) EN EL NORTE Y NOROESTE DE LA PENINSULA IBÉRICA EN EL 2000. – Se han capturado caballas (*Scomber scombrus*) en las etapas tempranas de su ciclo de vida en el Norte y Noroeste de la Península Ibérica (Divisiones VIIIc y IXa Norte del ICES) en el año 2000. Los anillos diarios se han identificado en el otolito sagitta. Se ha analizado un total de 377 otolitos de larvas y post-larvas, capturadas en abril y mayo de 2000, con un rango de tallas entre 2.3 y 23.7 mm L_S (Talla estándar) y con edades comprendidas entre 7 y 38 días después de la eclosión. Además se han analizado 68 otolitos de juveniles y pre-reclutas, capturados entre julio y octubre de 2000, con un rango de tallas entre 121 y 202 mm L_S y edades comprendidas entre 65 y 186 días después de eclosionar. Se han ajustado los modelos de crecimiento Gompertz y logístico a los datos de las tallas por edad de las larvas, post-larvas, juveniles y pre-reclutas. Como se asume que la talla al eclosionar es de 3.0 mm, los modelos fueron aplicados de dos maneras; no forzados a pasar por L_0=3.0 mm, y forzados a pasar por L_0=3.0 mm. La curva de crecimiento logística no forzada a pasar por L_0=3.0 mm parece ser la más adecuada para describir el crecimiento de la caballa durante su primer año de vida (L_∞ = 191.6 mm; K= 0.070; t_0= 66.7 d).

Palabras clave: crecimiento temprano, crecimiento diario, caballa, Atlántico Nordeste, *Scomber scombrus*

INTRODUCTION

Northeast Atlantic mackerel (*Scomber scombrus* Linnaeus, 1758) (NEAM) is widely distributed

along European coasts and its migratory routes in this area are well known (Rankine and Walsh, 1982; Iversen and Skagen, 1989; Uriarte and Lucio, 2001; Uriarte *et al*., 2001). Since 1995, ICES (1996) has considered NEAM to be a single stock for assessment and management purposes, and has assumed

that there are three spawning components (ICES, 2000): the Western component, composed of individuals spawning in western European waters (ICES Areas VI, VII and VIIIabde); the Southern component, composed of individuals that do so in southern European waters (ICES Divisions VIIIc and IXa); and the North Sea component, composed of those spawning in the North Sea and Skagerrak (ICES Division IIIa and Subarea IV).

Mackerel are abundant in the Southern area (Division VIIIc and IXa) in spring, the season in which they come to the area to spawn, and after spawning they migrate towards northern Europe (Uriarte *et. al.*, 2001; Uriarte and Lucio, 2001). The Cantabrian Sea (Division VIIIc) contains the largest spawning ground (ICES, 2002) of the Southern component of mackerel. Spawning takes place in this area in spring, from February to June, reaching its peak in April (Solá *et al.*, 1990). The most important areas of distribution of juveniles (age 0) are Division IXa, mainly the area between the northern limit of the north of Portugal and Galicia, and the western region of the Cantabrian Sea (Villamor *et al.*, 1997).

Whereas the egg and recruit distributions are quite well known, the same cannot be said of the stages between them, particularly larval growth. Numerous studies have examined age and growth of mackerel adults in the northeast Atlantic using otoliths (e.g. Eltink and Gerritsen, 1982; Skagen, 1989; Villamor *et al.*, 2001). Nevertheless, the literature on growth during the early life stages of the northeast Atlantic stock of mackerel is limited. Some studies exist which deal with age and growth of larvae and post-larvae (Röpke, 1989; Iversen and Moksness, 1990; Kloppman *et al.*, 2001), but there is no information on the growth characteristics of juveniles. There is only one reference to somatic growth during the first year of life of the northeast Atlantic mackerel that includes juvenile growth characteristics (Cotano and Alvarez, 2003), although the area sampled was restricted to a small area in the inner Bay of Biscay. Most growth observations on Atlantic mackerel during the first year are from the western Atlantic, along the east coast of North America (Ware and Lambert, 1985; D'Amours *et al.*, 1990; Simard *et al.*, 1992)

The discovery of daily increments in fish otoliths (Pannella, 1971 and 1974) has made the interpretation of otolith microstructure one of the best tools for estimating age and growth of fish larvae and juveniles (Campana and Neilson, 1985; Jones, 1986;

Stevenson and Campana, 1992). Estimating age by counting otolith growth increments provides a direct measurement of length at age for the calculation of growth curves and may also reveal information on individual age and growth rates.

The aims of our study were to age mackerel larvae, postlarvae, juveniles and pre-recruits (0-year) in order to model their somatic growth, taking into account a wider geographical area than the studies previously cited for the Southern component of the NEAM, to compare different growth models and to determine which is the most appropriate model for mackerel early life stages.

MATERIAL AND METHODS

Otolith sampling

During the two consecutive surveys carried out in April and May 2000 along the coast of the Cantabrian Sea, a total of 1126 (446 in April and 680 in May) mackerel larvae (Standard Length (L_S) < 10 mm) and post-larvae (L_S =10-30 mm) were collected. Mackerel larvae were sampled by oblique tows from 200 m (or 5 m above the bottom at shallow stations) to the surface using a BONGO-50 net equipped with a 250 μm mesh. The net was lowered at a rate of 5 m / 6 sec., remained at the maximum depth for 20 to 30 sec. for stabilisation and then raised at 1 m / 3 sec. Postlarvae were sampled using neuston MIK (Method of Isaac Kidd) and rectangular mid-trawl (RMT) nets with a 1 mm mesh size.

The larvae and postlarvae were preserved in 80% buffered ethanol. The pH of the ethanol was monitored every 24 hours to ensure that a pH of 8 was maintained in order to prevent any corrosion of otoliths. In addition, a sample of 161 larvae and post-larvae were measured in a fresh state prior to their conservation in ethanol in order to obtain the conversion factor from conserved length to fresh length (length measured immediately after the catch), which is necessary due to the shrinkage individuals undergo when preserved in ethanol.

For the analysis of growth data, a representative sub-sample by length range and by area was taken in each survey (Table 1). The areas considered were those used for the general aims of the surveys: Galicia, Cape Ortegal, the Cantabrian and the interior of the Bay of Biscay (Fig. 1). A total of 1544 otoliths (*sagittae* and *lapilli*) were extracted from 386 specimens.

TABLE 1. – Mackerel larvae-postlarvae samples in the north and northwest of the Iberian Peninsula in 2000, including dates, locations, standard length (L_S) in mm (corrected for shrinkage) and age in days.

| Survey and Sampling date	Area	Number of Larvae-postlarvae		L_S Interval		Mean L_S		Age	
		Sampled	Aged	Sampled	Aged	Sampled	Aged	Range	Mean
SEAMAR 0400	Galicia	5	0	-	-	-	-	-	-
28 March	Ortegal	248	122	3.8-18.1	4.9-18.1	9.2	9.4	10-38	24
-14 April	Cantabrico	149	80	4.3-18.2	4.3-18.2	9.0	9.3	16-36	25
	Biscay	44	38	6.3-23.7	6.3-23.7	9.4	9.4	15-38	23
	Total Area	446	240	3.8-23.7	4.3-23.7	9.0	9.4	10-38	24
SEAMAR 0500	Galicia	0	0	-	-	-	-	-	-
24 April	Ortegal	21	14	3.9-7.1	4.1-7.1	5.3	5.4	12-24	17
- 15 May	Cantabrico	83	38	2.6-8.1	2.6-8.1	4.9	5.0	7-32	17
	Biscay	576	85	2.3-38.4	2.3-13.9	5.9	6.0	8-30	17
	Total Area	680	137	2.3-38.4	2.3-13.9	5.5	5.7	7-32	17
TOTAL	Galicia	5	0	-	-	-	-	-	-
	Ortegal	269	136	3.8-18.1	4.1-18.1	8.9	9.0	10-38	23
	Cantabrico	232	118	2.6-18.2	2.6-18.2	7.8	7.9	7-36	23
	Biscay	620	123	2.3-38.4	2.3-23.7	7.0	6.5	8-38	18
	Total Area	1126	377	2.3-38.4	2.3-23.7	8.1	8.0	7-38	22
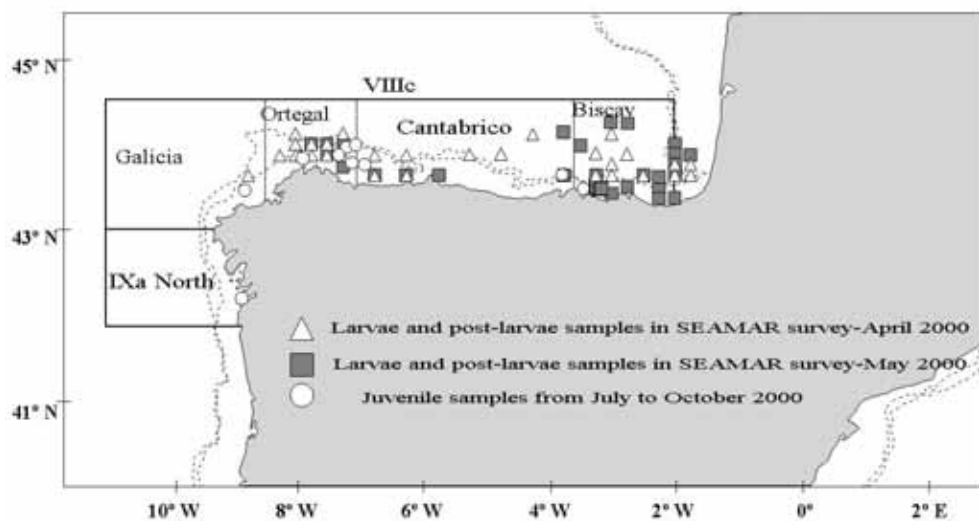
FIG. 1. – Map of the study area showing the location of otolith samples of mackerel larvae, postlarvae and juveniles-prerecruits in 2000: Samples of larvae and post-larvae come from the April survey; larvae and post-larvae samples come from the May survey; juvenile and pre-recruit samples were obtained on the 2nd half of the year.

Standard length (L_S) was measured for the entire sample of preserved larvae and postlarvae from each survey. The length range of individuals from the otolith sub-sample from the April survey was 4.3-23.7 mm L_S and that from the May survey was 2.3-13.9 mm L_S, coinciding with the length range of the whole sample. This length was corrected by a constant conversion factor (1.10) obtained using a regression performed on the sample of 161 specimens measured both in fresh state and after preservation. The regression led to this conversion factor. The fitted model was:

$$\text{Length (fresh)} = \text{Length (preserved)} \times 1.098$$
$$(R^2 = 0.98)$$

380 otolith samples were obtained from mackerel juveniles (L_S = 31-150 mm SL) and pre-recruits (L_S > 150 mm SL) in the second half of 2000. Of these samples, 160 were obtained in July from the commercial purse seine fleet with length ranging between 119 and 173 mm L_S, 40 were taken in August with length ranging between 158 and 196 mm L_S, and 180 samples came from the bottom trawl survey in October with length ranging between 177 and 207 mm L_S (Table 2). The samples from July and October came from ICES Division VIIIc, 171 from the Ortegal area and 169 from the Bay of Biscay area, and the August samples came from Sub-division IXa North (Fig. 1). Otoliths were extracted from fresh fish in 2000 and were dry-stored until they were mounted in 2001.

TABLE 2. – Mackerel juveniles-pre-recruit samples in the north and northwest of the Iberian Peninsula in 2000, including dates, locations, standard length (L_S) in mm and age in days.

Area and Sampling date	Number of juvenile		L_S Interval		Mean L_S aged		Age	
	Sampled	Aged	Sampled	Aged	Sampled	Aged	Range	Mean
Biscay (VIIIc East)								
26-27 July	160	28	119-161	121-156	138	132	65-100	80
26 October	11	2	184-207	202-204	196	203	156-170	163
Ortegal (VIIIc West)								
8-16 October	167	24	183-208	183-202	195	195	136-186	155
Galicia (IXa North)								
18 August	40	14	158-196	164-194	179	179	91-123	104
Total	378	68	119-208	121-204	169	166	65-186	114

Otolith processing

The otolith sagittae were extracted from larvae and postlarvae using fine dissection needles under a binocular microscope 3-5 months after having been preserved. They were then washed in distilled water, dried and mounted on glass slides within transparent synthetic enamel (Secor *et al*., 1992). Larvae and postlarvae otoliths were mounted as a whole and with the concave side upwards.

The otolith sagittae extracted from juveniles and pre-recruits were cut into sections for growth ring interpretation. Each otolith section was processed on the sagittal plane with respect to the fish. The methodology applied to make the cuts is that described by Secor *et al*. (1992). The otoliths were embedded in polyester resin in silicon moulds. These moulds were allowed to dry at room temperature for 24 h before proceeding with sanding and polishing. Both sides of the otoliths were sanded and polished until very fine otolith sections were obtained, after which they were mounted on glass slides. The grades of sandpaper used were 180, 220, 600, 1200 and 1500 and the grades of diamond dust for polishing were 15, 6 and 1 micra. These were processed along the short axis, and the count of growth increments was made along the dorsal-ventral axis, as described by D'Amours *et al*. (1990). The numbering of growth rings on the otoliths was carried out within two triangular surfaces pointing towards the core on the dorsal-ventral axis relative to the fish; these two surfaces were defined as the standard reading fields, which correspond to the short axis of the otolith.

Age determination

Otoliths were examined at 1000x magnification through a microscope connected to a personal computer (PC) via a video camera. Counts and measurements of increments were made with the help of image analysis software (VISILOG/TNPC 3.1). In order to read the growth rings of both larvae and juveniles the objective (x100) was used with immersion oil. Each otolith was read at least 2 or 3 times until a consistent increment count was obtained. The number of growth increments was counted and otolith radius and size of each increment were measured. Numbering of otolith growth increments commenced from the hatch check and the last ring was omitted. The last ring is considered incomplete since it does not represent a full day. The deposition of daily growth rings in mackerel larvae, post-larvae and juveniles has been validated by Migoya (1989) and D'Amours *et al*. (1990) and the direct transformation of number of rings to age in days is justified, although it must be noted that these validations were made for mackerel from a different area, in the northwest Atlantic. Migoya (1989) incubated mackerel eggs in the laboratory at three temperatures and followed the growth of larvae to 13 and 21 days after hatching. She showed that the deposit of the first increment occurred on the day of hatching and that the increments were formed daily. In addition, D'Amours *et al*. (1990) performed a validation experiment on mackerel juveniles in captivity in which otoliths were marked with a fluorescent substance. The analysis of the otoliths showed that increments were deposited similarly on a daily basis.

The microstructure analysis was obtained using otoliths from 377 larvae-postlarvae and 68 juveniles-pre-recruits.

Data analysis

For the identification of possible differences in growth between larvae and postlarvae surviving until

juvenile stages, and those in which survival is not known (i.e. those caught at larvae-postlarvae stages), the following analysis was carried out. The size of standardised increments was obtained from 68 larvae-postlarvae taken at random and from 68 juveniles-pre-recruits up to increment 41 (i.e. in their larval state). The mean incremental width of these 136 individuals was estimated (larval/post-larval and juvenile/pre-recruit) as well as the corresponding standard deviation. The standardised incremental width is estimated for each increment as follows

$$x_{ij_{st}} = \frac{x_{ij} - \overline{x_i}}{s_i}$$

where x_{ij} is the width of the i-th increment in the j-th individual, x_i is the mean width of the i-th increment and s_i its standard deviation, i, j = 1, 2, ……,n

The Gompertz and logistic growth models were fitted to the 2000 pooled length at age data of the larvae-postlarvae and juveniles-pre-recruits. As length at hatch in the literature is assumed to be 3mm at t = 0 (Ehrenbaum, 1905-1909; Russell, 1976), the models were applied in two ways; not forced to pass through L_0 = 3 mm and forced to pass through L_0 = 3 mm. The Gompertz and logistic curves (Ricker, 1979) were fitted to the length at age data following the SPSS 10.1 non-linear regression procedure using the Marquard option.

The Models used were:
- Not forced to pass through L_0 = 3 mm:

Gompertz: $\qquad L_t = L_\infty e^{-e^{-k(t-t_0)}}$ (1)

Logistic: $\qquad L_t = \dfrac{L_\infty}{1 + e^{-k(t-t_0)}}$ (2)

where: L_t is L_S (mm) at age t (days from hatching), L_∞ is the asymptotic L_S (mm) at the end of the first growing season, k is the instantaneous growth rate at $t = t_0$, and t_0 is the abscissa of the inflection point (the age of maximum growth).
- Forced to pass through L_0 = 3 mm:

As length at hatching is assumed to be 3 mm at t = 0, the pair (t = 0, L_0 = 3) is used to derive a formula for t_0 from the above equations:

Rearranging the Gompertz model (Eq. 1) we obtain:

$$\ln\left(\ln\left(\frac{L_\infty}{L_0}\right)\right) = -k\left(t - t_0\right)$$

and by substituting the pair (t = 0, L_0 = 3);

$$t_0 = \frac{1}{k}\ln\left(\ln\left(\frac{L_\infty}{3}\right)\right)$$

If we now substitute t_0 in the original Gompertz model (Eq. 1), we derive the forced model with one parameter less than the original formula, as t_0 is now a function of the other parameters of the model.

Forced Gompertz:

$$L_t = L_\infty \times \left(e^{-e^{-k\left(t-\left[\frac{1}{k}\ln\left(\ln\left(\frac{L_\infty}{3}\right)\right)\right]\right)}}\right) \qquad (3)$$

For the case of the logistic model (Eq. 2), the rearrangement is:

$$\ln\left(1 - \frac{L_t}{L_\infty}\right) = k\left(t - t_0\right)$$

substituting the pair (t = 0, L_0 = 3) we derive

$$t_0 = \frac{\ln\left(\left(\frac{L_\infty}{3}\right) - 1\right)}{k}$$

and then substituting t_0 in the original logistic model (Eq. 2), as in the case of the Gompertz model.

Forced logistic:

$$L_t = \frac{L_\infty}{1 + e^{\left(-k\left(t - \left[\frac{\ln\left(\left(\frac{L_\infty}{3}\right) - 1\right)}{k}\right]\right)\right)}} \qquad (4)$$

RESULTS

A total of 377 larval and postlarval mackerel otoliths were analysed. Fresh length (corrected for shrinkage) of larvae and post-larvae of the otoliths analysed was 2.3-23.7 mm L_S and their ages ranged between 7 and 38 days after hatching. In the April survey, mean length of mackerel was 9.4 mm L_S, lengths ranged from 4.3 to 23.7 mm L_S (individuals of <13 mm were predominant in samples) and ages between 10 and 38 days after hatching. In the May survey mean length was 5.7 mm L_S with a length range of 2.3-13.9 mm L_S (lengths of <8mm L_S were predominant in samples) and ages were between 7 and 32 days after hatching. (Table 1)
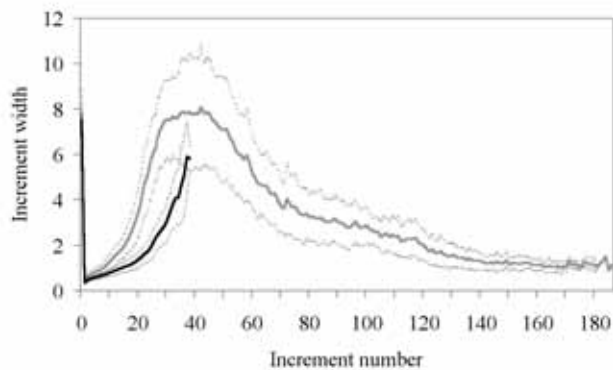
FIG. 2. – Mean increment width (μm, solid line) +/- 1 SD (dotted lines) at age (days) of larvae-postlarvae (black lines) and juvenile-pre-recruit (grey lines) mackerel in Divisions VIIIc and IXa North, in 2000.

A total of 68 juvenile and pre-recruit otoliths caught from July to October 2000 were analysed. Mackerel length ranged from 121 to 202 mm L_S and age from 65 to 186 days after hatching. The smallest fish were caught first, in July, and the largest later in the season, in October. 28 otoliths from July were read, among which lengths ranged from 121 to 156 mm L_S and age from 65 to 100 days. 14 otoliths from August were read, mackerel length ranging from 164 to 194 mm L_S and age from 91 to 123 days, and 26 otoliths from October were analysed with a mackerel length ranging from 183 to 204 mm L_S and ages from 136 to 186 days (Table 2).

The mean distance from the nucleus to the hatch check was 7.83 μm (SD=1.04) in juveniles-pre-recruits, which is similar to that measured in otoliths of larvae and postlarvae captured in April and May (7.38μm, SD=0.66) of the same year (Fig. 2). The mean width of the first 10 increments was 0.87 μm (SD=0.30) for juveniles-pre-recruits and 0.61 μm (SD=0.17) for larvae-postlarvae. The differences in the width of increments between larvae-postlarvae and juveniles-pre-recruits increase from increment
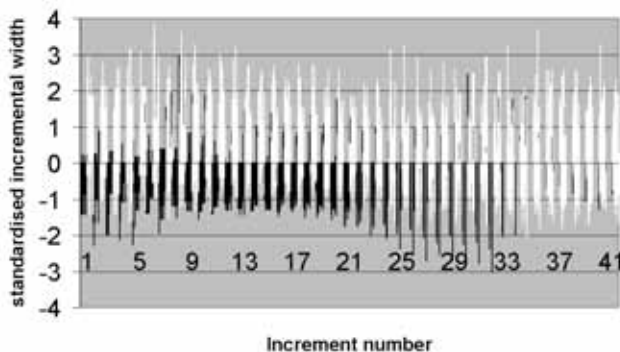

FIG. 3. – Standardised incremental width comparison of larvae-post-larvae (black lines) and juvenile-pre-recruit (white lines) mackerel in Divisions VIIIc and IXa North, in 2000.

10, with increments of juveniles-pre-recruits always larger than those of larvae-postlarvae. The greatest means of increment widths in juveniles-pre-recruits were found between 30 and 40 days (7.69 μm; SD=2.14) and between 40 and 50 days (7.58 μm; SD=2.35). From this point the width of increments of juveniles-pre-recruits descended progressively until it reached a mean of 1.13 μm (SD=0.25) between 150 and 180 days. When comparing the size of standardised increments (Fig. 3) of a random sample of 68 larvae-post-larvae with one of 68 juveniles-pre-recruits in the larval stage (up to increment 41), it was observed that the size of the increments in most of the larvae-postlarvae have a negative
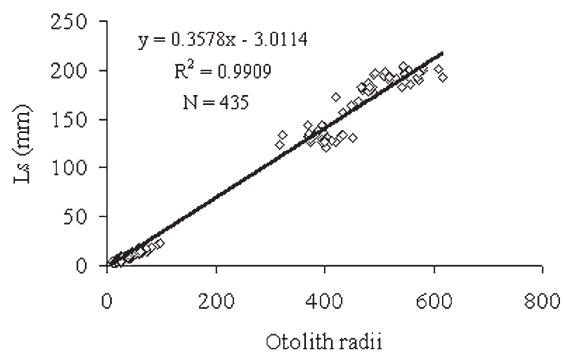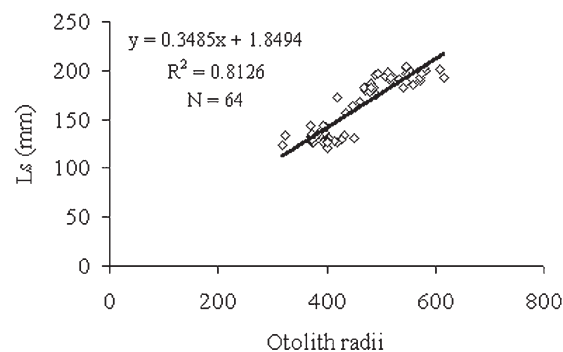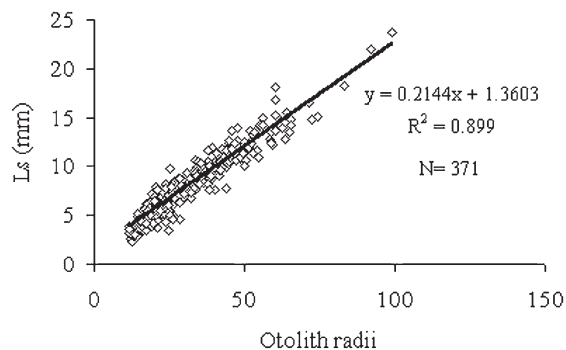

FIG. 4. – Regressions between standard length (L_S, mm) and otolith radii (μm) of larvae-postlarvae (upper figure) and juvenile-pre recruit (upper figure) mackerel in Divisions VIIIc and IXa North. Pooled set of larvae and juvenile in lower figure.

deviation with respect to the mean. Very few larvae-postlarvae have a positive deviation in any increments (only 5 larvae with over 5 increments larger than the mean), while 37 specimens have negative deviation in all their increments. On the other hand, most of the survivors (i.e. those samples at juvenile-pre-recruits stage), have a general positive deviation from the mean increment size (all specimens with more than 5 increments larger than the mean). There is no single juvenile-pre-recruits specimen in which increments were all negative, indicating that individuals with those characteristics did not survive until juvenile-pre-recruit stage.

Otolith radius correlated very well with standard length, both for the pooled set of larvae and juveniles (R^2= 0.99, N= 435) and for larvae and juveniles separately (Fig. 4). This demonstrates that fish growth and otolith growth are closely related.

The growth curves are based on the length at age data of 445 individuals with a length range of between 2.3 and 204 mm L_S and aged between 7 and 186 days.

For the unforced models (Table 3), both the logistic and Gompertz curves adequately represent the data with large correlation coefficients (R^2=

TABLE 3. – Parameters of Gompertz and Logistic curves fitted to length at age with upper and lower 95% confidence intervals. L_∞ = asymptotic standard length (mm), k=growth coefficient, t_0=inflection point (in days of age). Parameters obtained with pooled length at age data from larvae-postlarvae and juveniles-pre-recruits caught in 2000 in Divisions VIIIc and IXa North.

Growth Models	Parameter	Estimate	95% Confidence Intervals	
			Lower	Upper
Unforced Gompertz	L_∞	200.2	197.7	202.7
R^2=0.990	k	0.038	0.037	0.039
	t_0	55.2	54.4	56.1
Unforced Logistic	L_∞	191.6	189.5	193.7
R^2=0.989	k	0.070	0.068	0.072
	t_0	66.7	65.9	67.6
Forced Gompertz	L_∞	234.8	226.7	242.9
R^2=0.956	k	0.023	0.022	0.024
	t_0	64.9	-	-
Forced Logistic	L_∞	195.6	193.1	198.0
R^2=0.986	K	0.061	0.060	0.062
	t_0	67.9	-	-

0.99). Estimated length at hatching (age = 0) for the Gompertz (L_0= 0.06 mm) and the logistic (Lo= 1.79 mm) models are lower than the one described in the literature and used in the forced models described in this paper (L_0 = 3 mm). In any case, no data of fish
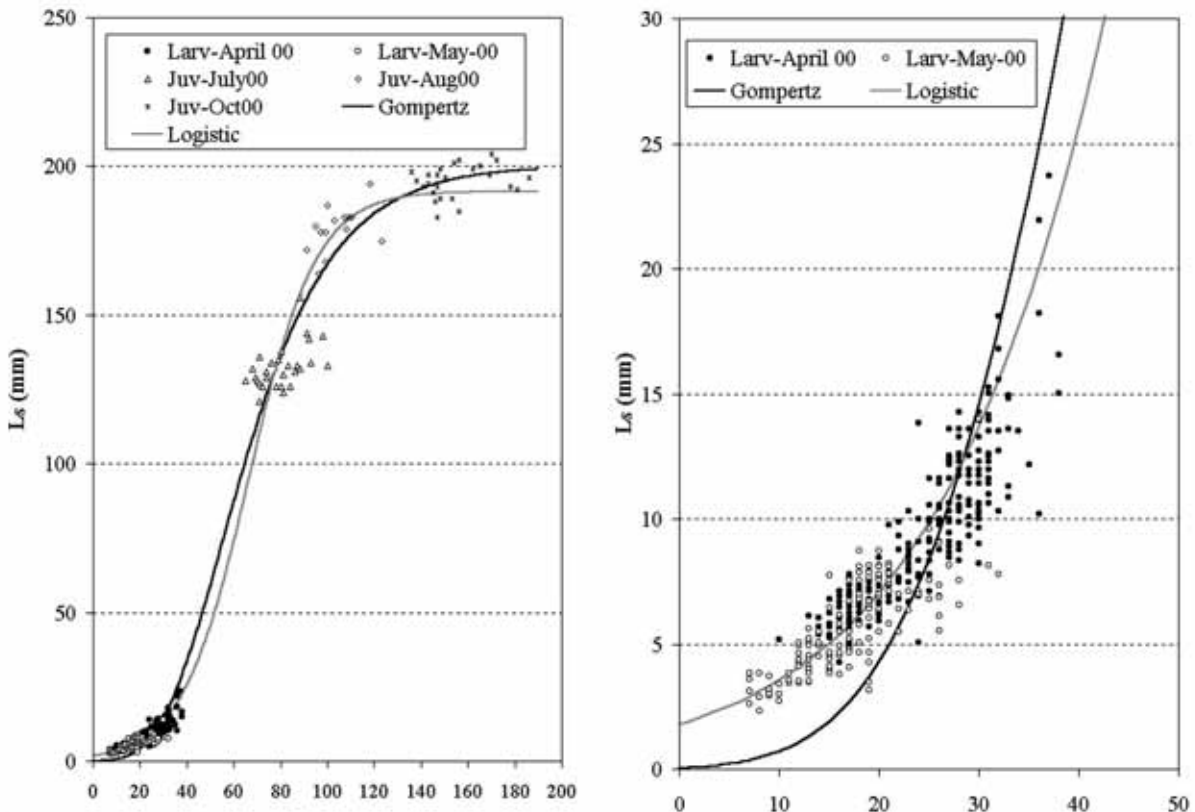

FIG. 5. – Gompertz and Logistic growth curves for larvae-postlarvae and juvenile-pre-recruits in Divisions VIIIc and IXa North in 2000. Curves not forced to pass through L_0 = 3 mm. On the left, the full data range and on the right, only larvae data range
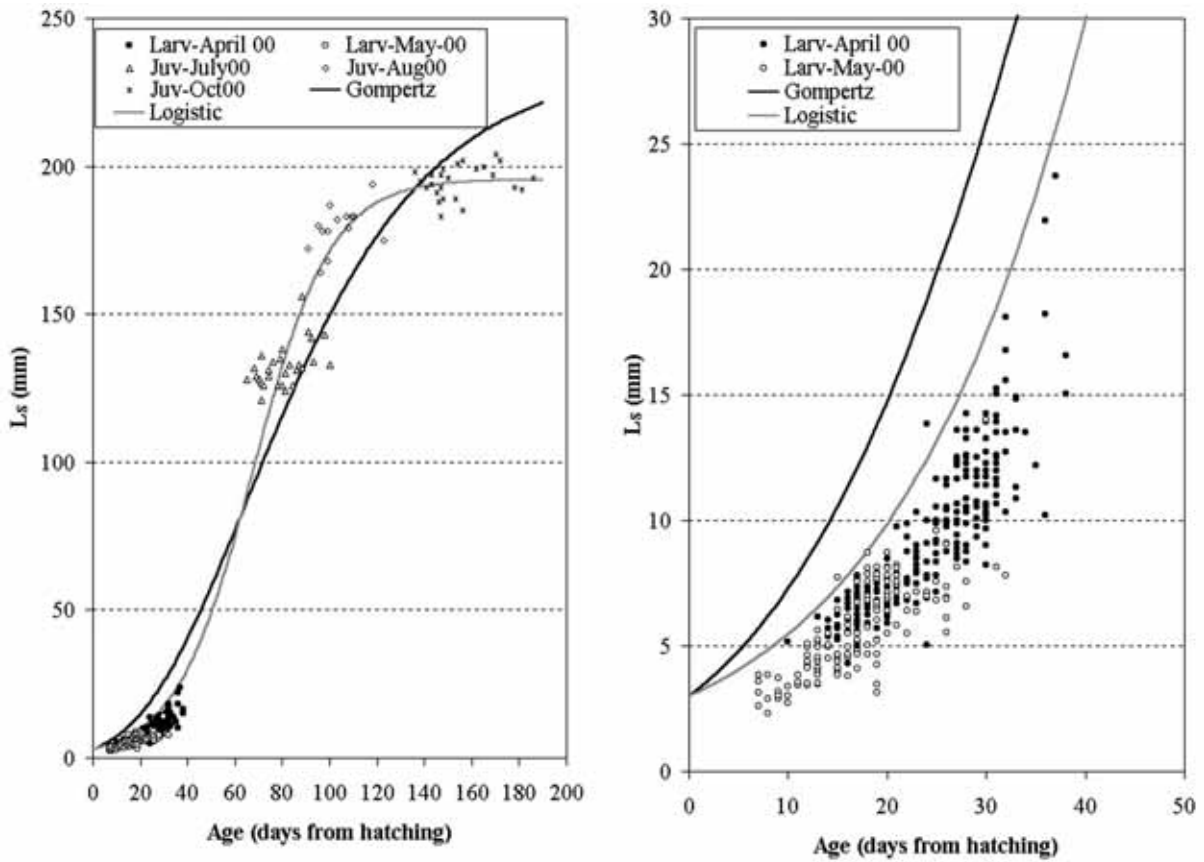
FIG. 6. – Gompertz and Logistic growth curves for larvae-postlarvae and juvenile-pre-recruits in Divisions VIIIc and IXa North in 2000. Curves forced to pass through $L_0 = 3$ mm. On the left, the full data range and, on the right, only larvae-postlarvae data range
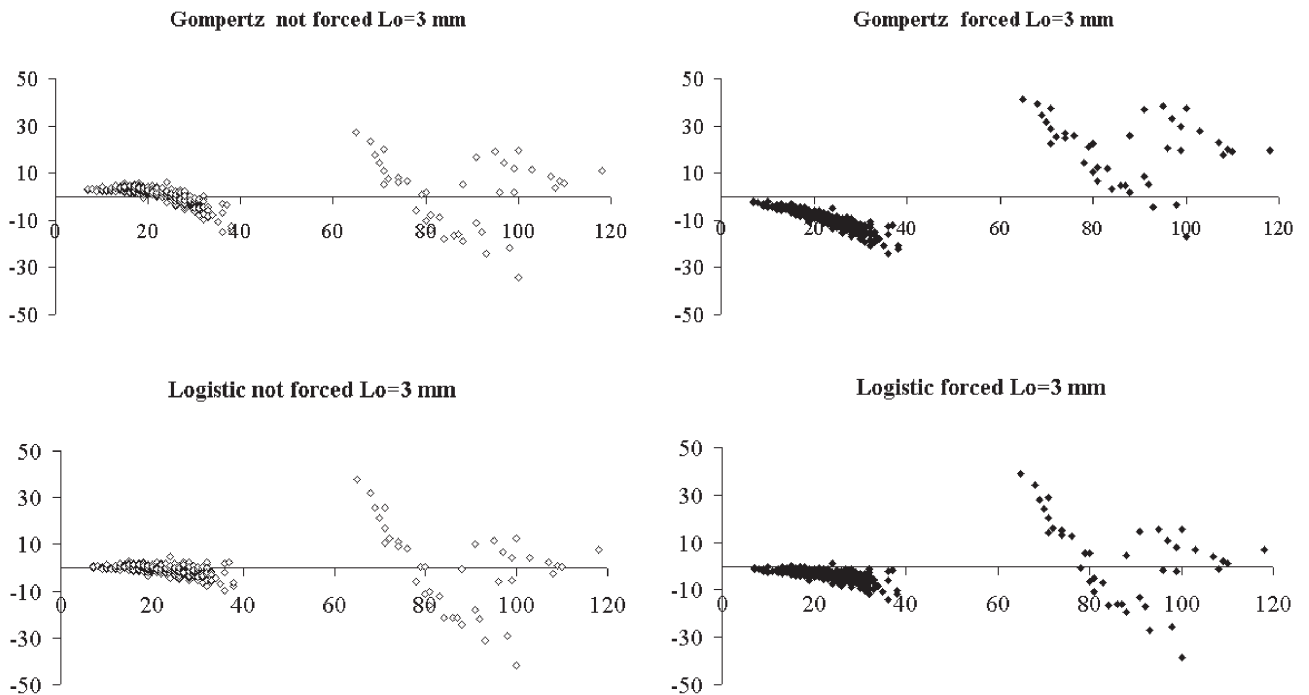

FIG. 7. – Distribution of residuals (for all data): On the left, curves not forced to pass through $L_0 = 3$ mm and on the right, curves forced to pass through $L_0 = 3$ mm.

Gompertz not forced Lo=3 mm

Gompertz forced Lo=3 mm

Logistic not forced Lo=3 mm
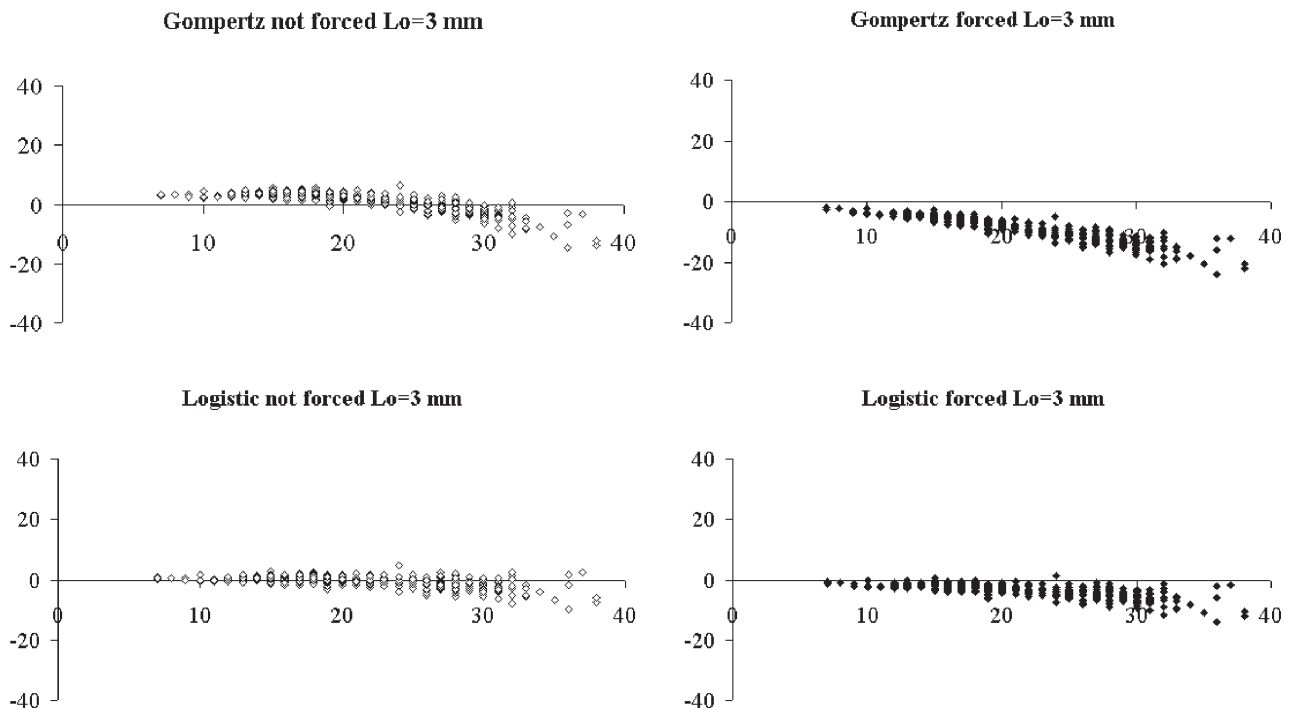
Logistic forced Lo=3 mm

FIG. 8. – Distribution of residuals of larval and post-larval data only: on the left, curves not forced to pass through L_0=3 mm and on the right, curves forced to pass through L_0= 3 mm.

younger than 5 days are available, so the estimation of L_0 needs to be extrapolated from the models. The Gompertz model performs worse for larvae younger than 25-30 days, in which it underestimates observed lengths (see detail in Fig. 5), while the logistic model performs slightly worse for the older ages, underestimating observed lengths (Fig. 5)

When curves are forced to pass through $L_0 = 3$ mm (Table 3), the coefficients of determination of both models are still very large (R^2=0.95 for the Gompertz and R^2=0.98 for the Logistic curves), since the general growth trend from larvae to recruits can still be represented by the models. Nevertheless, none of the models adequately represents growth in any of the development phases individually (larvae, postlarvae, or juveniles-pre-recruits, Fig. 6). The problems are greater in the Gompertz model, which greatly overestimates length of larvae and older fishes, while underestimating the length of fish of intermediate age.

Examining the residual plots (Figs. 7 and 8), the logistic model generally shows fewer residual trends, particularly for the larval and old postlarval data. Also, the unforced models show better behaviour in relation to the larval-postlarval data, and the unforced Logistic model seems to show the best behaviour of all the models fitted to the data. Nevertheless, residuals are in general larger for juve-

nile/pre-recruit data and some residual trends can be seen for fish aged between 60 and 80 days. Larger residuals are expected as the fish grow older, as differences open up in individuals' life histories, increasing variability in the length to age relationship. For the age range of 60 to 80 days, fish length shows a lower correlation with age than that expected by the model, and this is reflected in the trend observed in the residual plots. Nevertheless, mean length for fish at these ages (129.73 mm, SE= 4.57) is similar to the length predicted by the models (L = 122.98 mm for the unforced Gompertz model and L = 119.72 mm for the unforced logistic model, both at age = 74 d). Juvenile and pre-recruit data is more sparse than larval and postlarval data, but residual plots for the unforced models do not show trends. Nevertheless, negative residuals are somewhat larger and fewer in number in the case of the unforced Logistic model (ages >85 d), and a larger number of positive residuals can be observed in the case of the unforced Gompertz model (ages >100 d).

Modelled growth rates varied between 0.02 mm immediately after hatching and 2.82 mm day^{-1} at the 55th day according to the unforced Gompertz model, and between 0.13 mm immediately after hatching and 3.34 mm day^{-1} at the 66th day according to the unforced Logistic model. The modelled
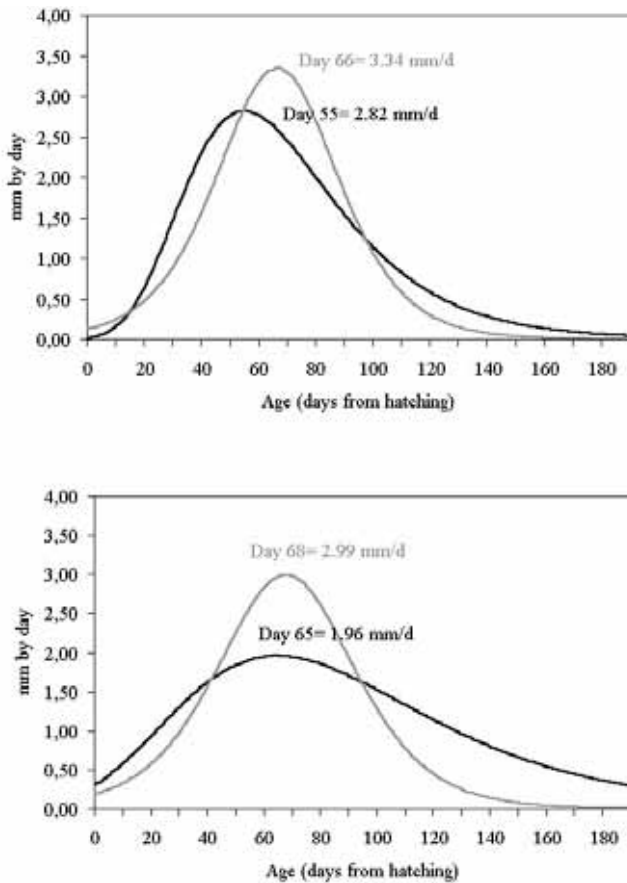
Fig. 9. – Modelled growth rate according to the Gompertz (black line) and logistic (grey line) models. Above, unforced models and below, forced models.

growth rate according to forced models varied between 0.31 mm after hatching and 1.96 mm at the 65th day according to the Gompertz model and between 0.19 mm after hatching, 2.99 mm at the 68th day and 0.01 mm between 180 and 190 days according to the Logistic model (Fig. 9).

DISCUSSION

The literature regarding growth studies in the first life stages of mackerel is limited, particularly for the northeast Atlantic stock. Previous studies on growth of mackerel larvae and juveniles showed growth curves fitted to the length at age data based on the count of daily increments on otoliths in the Gulf of St. Lawrence (e.g. Kendall and Gordon, 1981; D'Amours *et al.*, 1990; Simard *et al.*, 1992) and in a reduced area in the inner part of the Bay of Biscay (Cotano and Alvarez, 2003).

Distinct growth increments were visible on the sagittae of northeast Atlantic mackerel larvae-post-

larvae and juveniles-pre-recruits in the Southern Area, which were assumed to have been deposited daily (Migoya, 1989; D'Amours *et al.*, 1990). It was also assumed that increment formation started at hatching, following reports by Migoya (1989) for northwest Atlantic mackerel.

The comparison of mean width of increments between larvae-postlarvae and juvenile-pre-recruit survivors shows larger otolith increments in the latter. The difference may be due to the fact that the larvae and juveniles analysed did not originate from the same spawn or that the juvenile survivors enjoyed better environmental conditions for growth and survival, or both of these reasons. The standardised incremental width comparison shows that in the larval stage, juvenile-pre-recruit survivors had a higher growth rate than that observed in larvae-postlarvae samples. This comparison clearly indicates the selection for fast growing larvae.

It is generally accepted that mortality is high in the first life stages of fishes and that differential mortality due to environmental conditions during development is an important factor determining the strength of annual recruitment. Limitations to the availability of food and predation are believed to be the greatest causes of mortality in the larval phases and, as a direct result, in the subsequent recruitment (Cushing, 1981; Bailey and Houde, 1989). Nevertheless, the direct influence that the availability of food has on larval mortality is only evident at very low prey levels (Cushing, 1981), whereas its most important influence has its origin in the limits to larval growth. Fast growth in fish larvae seems to have greater importance in reducing mortality, either by reducing direct vulnerability to predation (Bailey and Houde, 1989; Leggett and Deblois, 1994) or in order to minimise cumulative mortality until recruitment (Chambers and Leggett, 1987). The case described in this paper provides evidence that fast growth in the larval stage gives rise to a high potential for survival.

These differences found between the size of the increments in larvae-postlarvae and juveniles-pre-recruits may also be affected by sampling techniques. In the beginning of the April to May sampling period, young mackerel (larvae and post-larvae) were collected with a 250 μm and 1mm plankton net. The largest mackerel caught during this period were 38 mm long. When the sampling was carried out with the plankton net, fish of over 38 mm (early spawned fish, or faster growing fish) were not available to the net, and the proportion of slower

growing fish in the plankton samples may have been greater than it is for the whole population of 0-yr fish. When juvenile mackerel were collected with purse-seine and trawl gears, the smallest fish caught were 119 mm long. The proportion of early spawned or faster growing fish may have been greater in the purse-seine hauls than it is in the whole population of 0-yr fish. Also, the effect of obtaining the age of juveniles-pre-recruits from otolith sections instead of using the whole otolith may also have an influence on these differences and may affect the measurements of the increments.

There is very little information available on mackerel length at hatching, although it is assumed to average about 3.0 mm standard length (Ehrenbaum, 1905-1909; Russell, 1976) and individuals are assumed to have non-functional mouths and eyes. During yolk sac absorption, which normally takes between 3 and 4 days, mouth and eyes become functional and larvae start feeding. In this paper, different growth models were used to describe mackerel growth after hatching. When not forcing the growth curve to pass through the assumed length at hatch, the logistic model fits the observed data reasonably well , but results in a lower estimate of the length at hatching than that described in the literature. Nevertheless, the Gompertz model did not fit so well, even when the length at hatching assumption was not used. When forcing the curve to pass through the point (0,3), the Gompertz model does not represent any of the individual developmental phases well. The logistic model performs slightly better in general than the Gompertz model, even when the models are forced through a fixed length at hatching, but the data observed for larvae are mostly below the curve. Differences between the length at hatching estimated by the unforced models used in this paper and that found in the literature may be due to different reasons. If the assumed mean length at hatching of 3 mm is regarded as an appropriate assumption, it may either be that the larva grows very little at first or that there is a pause in its growth. Migoya (1989) describes areas of interrupted growth in northeast Atlantic mackerel otoliths associated with hatching, the absorption of the yolk sac and the change in feeding. In any case, no data of fish younger than 5 days old were available in this paper, so length at hatching is extrapolated by the model. Also, complex developmental changes may occur in this early phase as described above, and they may not be explained by a simple single growth model of the larvae-postlarvae-juveniles. This does

not affect the validity of the models to explain growth within the age range of the observed data, but prevents the length at hatching estimates from the unforced models from being considered as accurate.

Fitting growth curves to field length at age data is quite problematic. It assumes that length at age data taken from a large enough sub-sample of a population reflects mean individual growth within that particular population. Ricker (1979) indicated that while individual growth goes through different stanzas, which respond to different internal and external constraints, it is difficult to describe growth with a single equation. This is particularly true for the first year of mackerel growth, in which many transformations take place, e.g. from endogenous to exogenous feeding, metamorphosis, etc

Nevertheless, the unforced logistic growth curve provides a reasonably good description of the length-age relationship over the entire length range studied, which indicates that the model appropriately describes growth during the first year of life of mackerel. It did, however, underestimate length at age at hatching (1.79 mm) in relation to the estimate of 3.00 found in the literature and also tended to underestimate size at age at its higher end. This discrepancy for fish older than 150 days may be interpreted as the result of a possible underestimate of the age of the larger fish. The short axis of the otolith was used to estimate juvenile age and the counts of growth rings on the short axis of the otolith may underestimate the age of the fish (D'Amours *et al.*, 1990). This has also been described by Wild and Foreman (1980), who demonstrate that for yellowfin, the rate at which increments are deposited at the ventral edge is approximately 13 percent lower than the deposition rate on either the postrostrum or rostrum. Another potential source of bias in the calculation of growth rate may come from the fish having different histories of environmental conditions affecting growth. Growth in larval fish is predominantly determined by environmental temperature (Ricker, 1979; Blaxter, 1992) and food availability (see e.g. Brett, 1979). Wind forcing seems to be an important factor for incursions of warmer and saltier waters in the Bay of Biscay (the study area) (Anon., 2003). Although spring incursions induce less volume transport than those of autumn/winter (Cabanas *et al.*, 2003), it may be relevant to the growth rate of larvae in the study area. On the other hand, turbulent mixing brought about by wind may disrupt

food aggregation and so also affect the growth rate of larvae.

In comparison with other studies of growth carried out on the same component of the northeast Atlantic mackerel stock, there are some differences in the growth pattern. Mackerel grew faster in 2000 (our work) than in 2001 (Cotano and Álvarez, 2003). The unforced Gompertz growth curve derived from this study and the Gompertz growth curve presented by Cotano and Álvarez (2003) revealed that maximum growth was 2.8 mm d^{-1} at 55 days in 2000 and 2.0 mm d^{-1} at 62 days in 2001. These differences may be due to differences in growth conditions between the different years, as well as to differences in growth conditions due to spatial differences in temperature and food supply. The work presented here covers a larger area spanning the entire north Iberian coast, while the work of Cotano and Álvarez (2003) comes from a small sub-area in the inner part of the Bay of Biscay. This area has different oceanographic conditions to the rest of the north Iberian coast (Porteiro *et al.*, 1996), and thus growth in this area may not adequately represent growth for the whole north Iberian coast.

If we compare the growth rates of mackerel larvae and juveniles between the northwest and northeast Atlantic, substantial differences are found between them. Gompertz growth curves presented by D'Amours *et al.* (1990) and Simard *et al.* (1992) were compared with the unforced Gompertz curve derived from this study. This revealed that while maximum growth rates are comparable (maximum absolute growth rate of 2.8 mm d^{-1} from the eastern Atlantic and rates of 2.9 and 3.3 mm d^{-1} from the western area), larval growth rates, as well as the timing at which maximum growth is reached, differ conspicuously. Western Atlantic mackerel larvae reach growth rates >1.0 mm d^{-1} quite quickly, achieving maximum growth at ages between 36 and 40 days. The mackerel in the eastern Atlantic achieves its maximum growth only after the 55th day, about 15 to 20 days later. The differences in early growth may be due to much cooler sea surface temperatures in spring in the western Atlantic (Doyon and Ingram, 2000), and so the first growing season of mackerel is much shorter in the western Atlantic than in the east. A shorter growing season should be compensated by a higher growth rate in the western Atlantic. This is supported by the observation that, at the end of their first year, lengths of juvenile mackerel from both sides of the Atlantic are similar (D'Amours *et al*, 1990; Simard *et al.*, 1992;

Villamor *et al.*, 2001; ICES, 2001). This may reflect an adaptation of western Atlantic mackerel to the shorter production period of the west Atlantic coast, where annual variability in water temperature is much higher, with lower temperatures in the winter and spring but higher temperatures in the summer than in the east Atlantic (Kloppmann *et al.*, 2001)

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