

# Anchovy stocks (*Engraulis anchoita*) and larval growth in the SW Atlantic

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## Abstract

Growth rates of anchovy larvae were estimated from samples collected in the Brazilian Southeastern Bight (BSEB) in June/July and November/December, 1995. Horizontal distribution and abundance of the larvae were determined. The rate of ring formation on the otolith was related to the marginal increments and time of day. The Laird–Gompertz growth model was adjusted to the data and instantaneous growth rates were compared for anchovy larvae of other habitats in the SW Atlantic. Larval growth rates for several stocks were shown to be dependent on environmental conditions and the calculated size at first feeding on the temperature, producing geographical variation of larval growth rate throughout the distribution range of the species. The results suggest that *E. anchoita* from the BSEB may form a population distinct from stocks already known in more southerly regions.

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## 1. Introduction

Small pelagic fish populations tend to be distributed over extensive areas, where no clear geographical and oceanographic barriers are present. Stocks are distributed over a continuum of environmental conditions, as they migrate and mature at different sizes, spawn at more than one location and period, recruit at different periods and sizes, feed, growth and survive (Begg et al., 1999).

The number of recruits is determined by the size of the parent stock as well as a diversity of factors acting during pre-recruitment, particularly in the egg and larval stages, which are characterized by high

mortality rates (Houde, 1989). The survival success of larvae is determined by a group of biotic and abiotic interdependent factors: (a) starvation (survival success would be largely dependent on food availability); (b) predation (survival is mainly influenced by predation of planktonic invertebrates and planktivorous fish); and (c) advection (influence of oceanic currents in the distribution of the larvae and its food) (Vasconcellos and Castello, 1996).

Bakun and Parrish (1982) suggested four categories of physical agents that influence the survival of larvae: processes related to stability of the water column; processes involved in horizontal transport; processes of convergence and divergence; and temperature.

*Engraulis anchoita* is the most important pelagic fish species found over the shelf area of the SW Atlantic. It is distributed between 47°S off Patagonia, Argentina and 23°S off Cape Frio, Brazil (Whitehead et al., 1988). As a

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secondary consumer, it is the prevailing forage species for many other fishes and marine birds and mammals (Castello, 1997a; Odebrecht and Castello, 2001).

Studies on anchovy larvae and juveniles in the southeastern and south region of Brazil, Argentina and Uruguay, reviewed by Castello and Vasconcellos (1995), Castello (1997a,b), Ekau, 1998 and Acha et al. (1999) presented a relatively clear view of the first stages of the anchovy (*E. anchoita*) biology in the wide area of distribution of that species.

A small commercial fishery is located off Argentina and Uruguay, but it is an unexploited resource in Brazilian waters. Off Uruguay and north and central Argentina, three stocks have been recognized (Castello, 1997a). In winter, the adult stock migrates from Uruguayan and Argentinean waters off Rio de La Plata (35–34°S) to Brazilian waters (34–29°S) where favorable spawning and feeding conditions prevail (Lima and Castello, 1995) and returns southward in late spring. In contrast, larval, post-larval and young-of-the-year of *E. anchoita* stay in coastal waters off the Rio Grande do Sul region of Brazil throughout the year (Castello, 1997b). Anchovy that move north of Santa Marta Grande Cape (29°S), up to Cape Frio (23°S) in the Brazilian Southeastern Bight (BSEB), differ from those to the south of Santa Marta Grande Cape. They reach sexual maturity at a smaller size, population is composed of smaller individuals, and age groups older than 4 years old are lacking (Castello, 1997a).

Because fish larval growth is controlled by the environment, it is the stage when a fish is more susceptible to oceanographic conditions. Thus fish larval growth studies show the influence of habitat on species development. This study presents data on growth of larval anchovy (*E. anchoita* Marini, 1935) collected in the BSEB and compares with larval growth rates for other stocks of anchovy of the south west Atlantic.

## 2. Materials and methods

### 2.1. Study area

Sample locations were distributed over the continental shelf between Macaé (RJ), 23°S, and Santa Marta Grande Cape (SC), 28°S (Fig. 1a and b), and along 28 transects perpendicular to the coast. Most

stations were separated by approximately 20 nm. The ECOSAR II cruise (06/11–07/02/95; austral winter) covered the continental shelf and the upper slope area, reaching 500 m deep regions, with a total of 130 ichthyoplankton samples. The ECOSAR III cruise (11/16–12/02/95; austral spring) collected 87 samples in waters between 20 and 100 m.

### 2.2. Sampling

At each station an oblique trawl using a Bongo net (300 µm mesh size) was performed at a constant speed of two knots. Water volume filtered by the net was calculated by the average readings of two calibrated flow meters. Sampling depth was estimated using an inclinometer. Sea surface temperature (SST) was determined with a calibrated CTD. Samples were preserved in alcohol. Anchovy larval density was estimated and standardized for 10 m<sup>2</sup> of surface: number of larvae/10 m<sup>2</sup> = (number of larvae × depth/volume × 10).

### 2.3. Larvae identification and otolith preparation

Anchovy larvae were identified following Phonlor (1984). Standard lengths (SLs) were measured to the nearest millimeter. To correct for shrinking, the Theilacker (1980) expression was applied. Sagittae were dissected out with a needle after dissolving the larvae's head in a drop of 4% sodium hypochloride for 5 min. Otoliths were washed in a drop of distilled water to remove sodium hypochloride crystals. The otolith was glued to a labeled glass slide using cyanoacrylate cement.

### 2.4. Otolith ageing

Otolith ageing was undertaken under transmitted light with a stereomicroscope to which a mini-television camera was attached producing an image of constant optical magnification of 400× on a video screen. A ring was considered to be formed by a band of hyaline and opaque material (Beamish and Mcfarlane, 1983). Because of light microscopy limitations (refraction of transmitted light), countings of rings and measurements were repeated at least twice (Neilson, 1992). The number of daily rings was registered independently for each otolith by both authors without knowing size data of the larvae

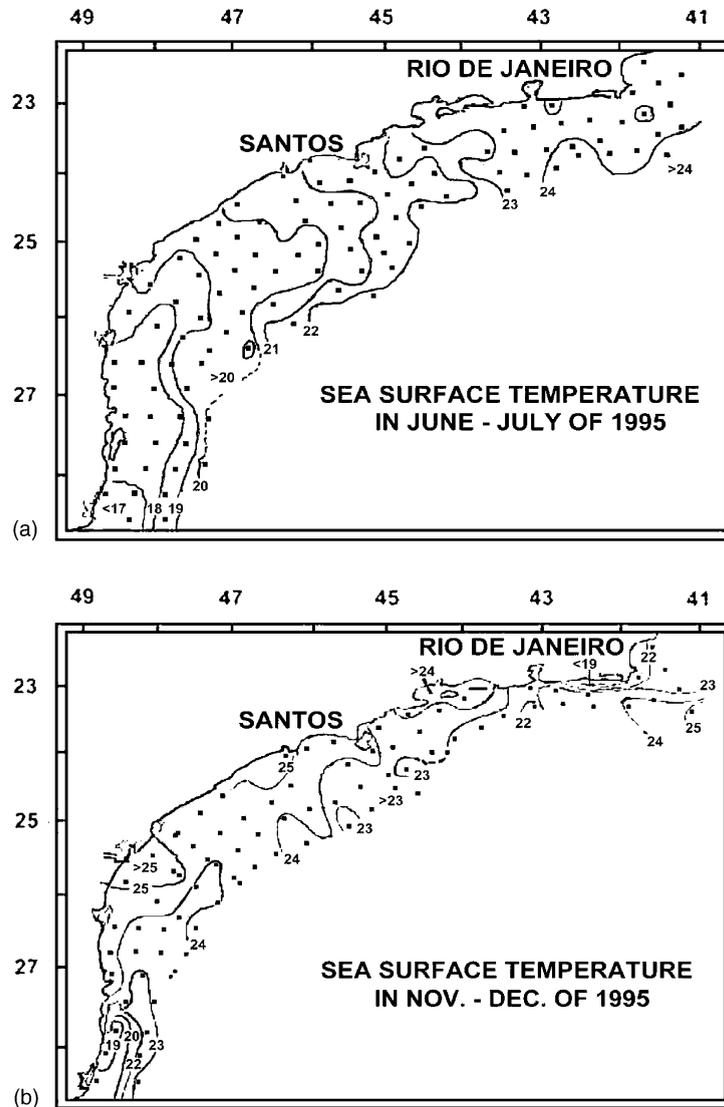


Fig. 1. Sampling station positions and SST ( $^{\circ}\text{C}$ ) in the BSEB (a) during June/July, 1995 and (b) during November/December, 1995.

(“blind” reading). If a persistent disagreement occurred, that otolith was rejected. Approximately 44% of the otoliths were not used due to errors in the preparation process and/or because of rejections. Altogether, 146 individuals were examined.

### 2.5. Validation

The relationship between percentage of marginal increment (MI) (defined as the percentage ratio between the last and previous increment) and time

of day when larvae were caught, grouped in 2 h intervals, was tested to validate ring counting into daily age.

### 2.6. Back-calculation

To allow for length back-calculation, procedures described by Castello and Vasconcellos (1995) were followed. Measures were taken from the nucleus to the last three rings and to the border of the otolith on the video screen with a graded transparent scale (Fig. 2).

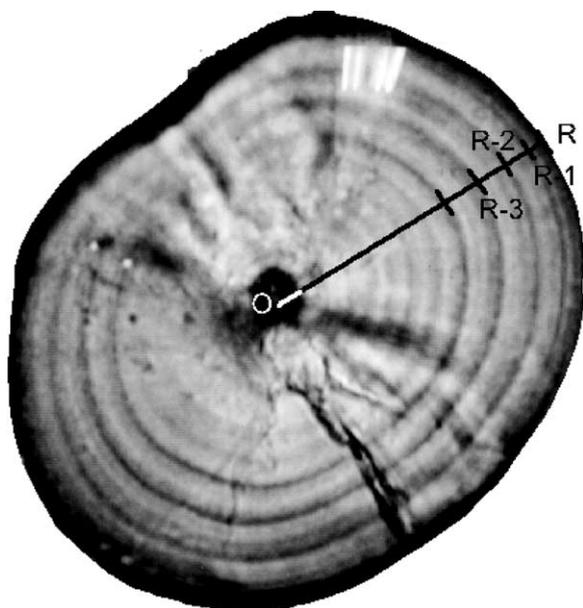


Fig. 2. Anchovy larval otolith (sagitta) showing measurements along the longest axis. OR: otolith radius; OR-1: distance from nucleus to first penultimate ring; OR-2: distance from nucleus to second penultimate ring and OR-3: distance from nucleus to third penultimate ring.

Larvae length at 1–3 days before being caught was calculated through:

$$\frac{OR}{LSL} = \frac{OR_n}{LSL_n}$$

$$LSL_n = \frac{OR_n}{OR} LSL$$

where OR is the otolith radius (mm), LSL the larvae's SL (mm),  $OR_n$  the otolith radius at age "n" (mm),  $LSL_n$  the larvae's SL at age "n" (mm).

Otolith radius and the larval SL were plotted in a scatter diagram and the correlation coefficient was calculated. It was assumed that otolith size increase is

directly proportional to larvae length increase, thus MI in otolith is proportional to the larval growth in size.

The daily growth rates in the last 3 days before capture were calculated as increments in the median of back-calculated SL (Methot, 1981) between successive days for winter and spring samples (Table 1).

### 3. Growth

Growth of larvae was calculated applying the Laird–Gompertz model (Zweifel and Lasker, 1976):

$$SL_t = SL_0 \exp K(1 - \exp(-\alpha t))$$

where  $t$  is the age in days,  $SL_t$  the SL at age ( $t$ ),  $SL_0$  the SL of the larvae at the beginning of formation of the first increment,  $K$  the specific growth rate,  $\alpha$  the decay rate.

The model was adjusted to the data through the non-linear regression of the least square routine available in the FISHPARM (Prager et al., 1987) software.

Instantaneous growth rates of the larvae ( $G'$ ) were calculated from the first derivative of the Laird–Gompertz growth equation (Sanchez et al., 1991).

$$G' = \alpha SL_t \left[ \ln \left( \frac{SL_t}{SL_0} \right) - K \right]$$

A linear mean of the medians was calculated from the back-calculated size distributions for 1–3 days before capture (Table 1). It was considered as linear growth rate.

### 4. Results

#### 4.1. SST, distribution and abundance of *E. anchoita* larvae

SST, during the winter cruise, varied between 17 and 24 °C. During the spring cruise, SST ranged from

Table 1

Daily growth rates (mm/day) for June–July (winter) and November–December (spring) samples calculated between size (SL) at capture and back-calculated sizes at 1–3 days before capture

	Size, mm (increment, mm/day)			
	Catch	1 day before	2 days before	3 days before
June–July	13.46	13.05 (0.42)	12.40 (0.65)	11.99 (0.42)
November–December	10.18	9.94 (0.24)	9.44 (0.51)	8.99 (0.44)

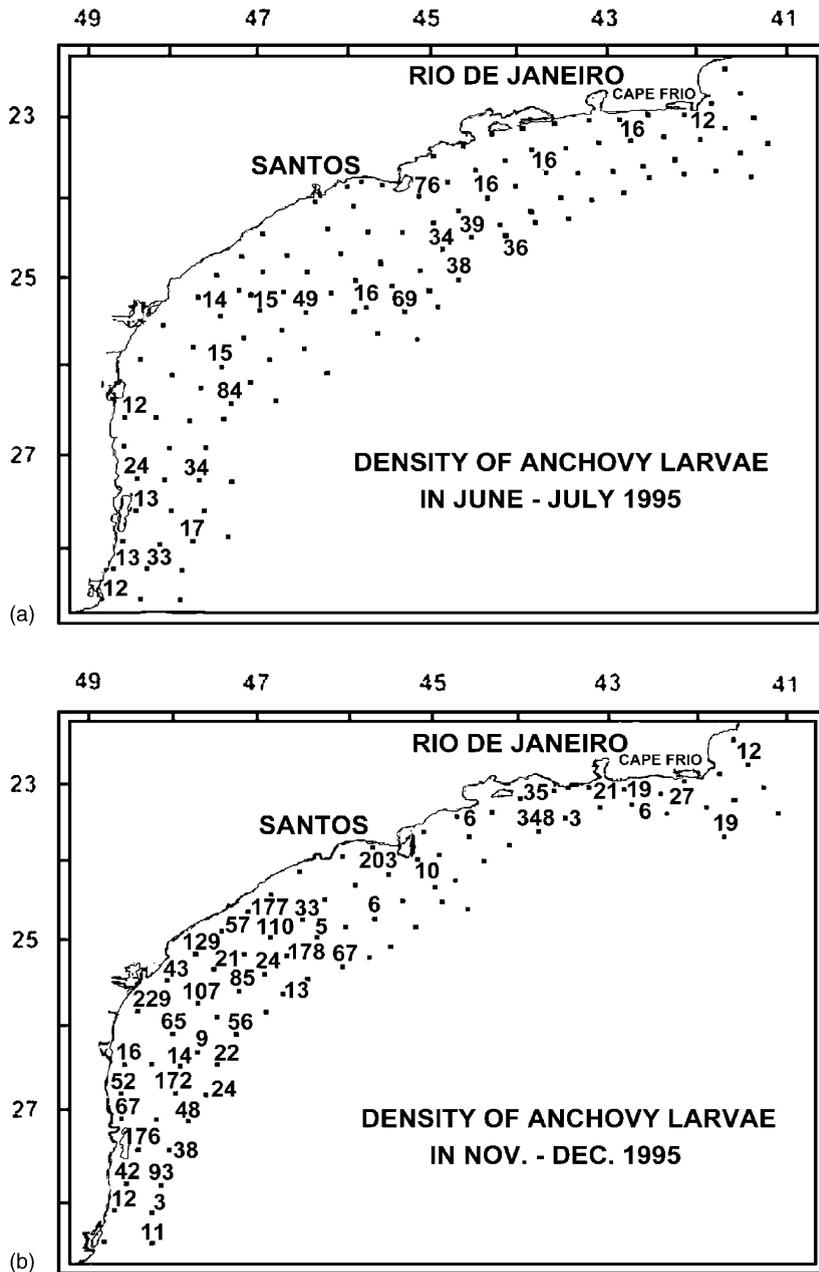


Fig. 3. Anchovy larvae distribution and density (No. of larvae/10 m<sup>2</sup>) in the BSEB during (a) June/July, 1995 and (b) during November/December, 1995.

18 to 25 °C, but most of the larvae were collected in 22–25 °C waters (Fig. 1a and b).

In winter (June/July, 1995), only 34 from a total of 130 samples contained anchovy larvae ( $\Sigma n = 67$ )

(Fig. 3a). Larval size ranged between 10 and 19 mm SL; 12 mm SL was the most abundant class (Fig. 4).

In spring (November/December, 1995), 47 from a total of 87 samples yielded 293 anchovy larvae. The

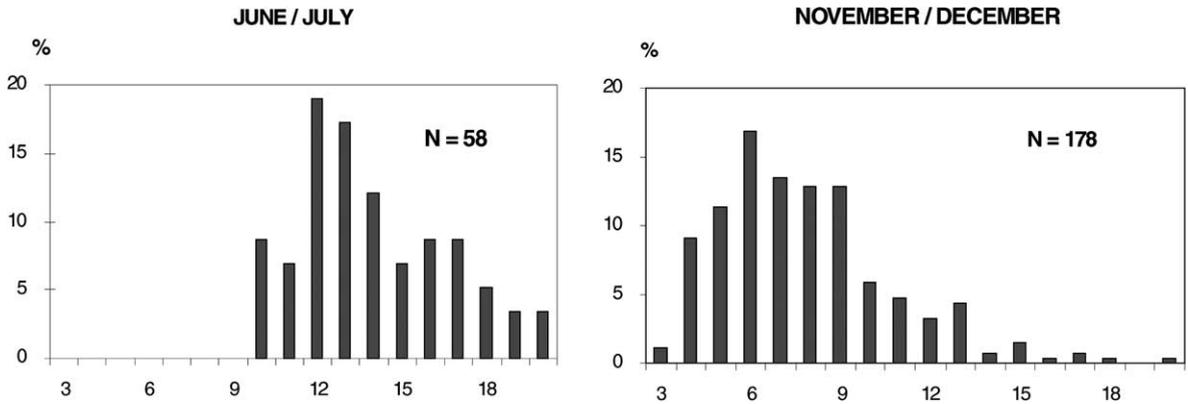


Fig. 4. Size distribution of anchovy larvae sampled in the BSEB during June/July and November/December, 1995.

most abundant classes were between 7 and 16 mm SL, with a mode at 8 mm.

Following Moser and Ahlstrom (1970), larvae were grouped into: pre-flexion (<8 mm SL), flexion (8–12.9 mm SL), post-flexion (13–19.9 mm SL) and metamorphic (20–33.3 mm SL). In spring pre-flexion and flexion stages were dominant, whereas in winter, flexion and post-flexion were more abundant (Fig. 5).

4.2. Size back-calculation

The relationship between otolith radius and standard larvae length was adjusted by a linear equation (Fig. 6).

$$OR = 1.8812 SL - 8.9158 (N = 146, r^2 = 0.768)$$

The size of larvae at age 0 (SL<sub>0</sub>) must be discounted to avoid the introduction of errors in the estimates of

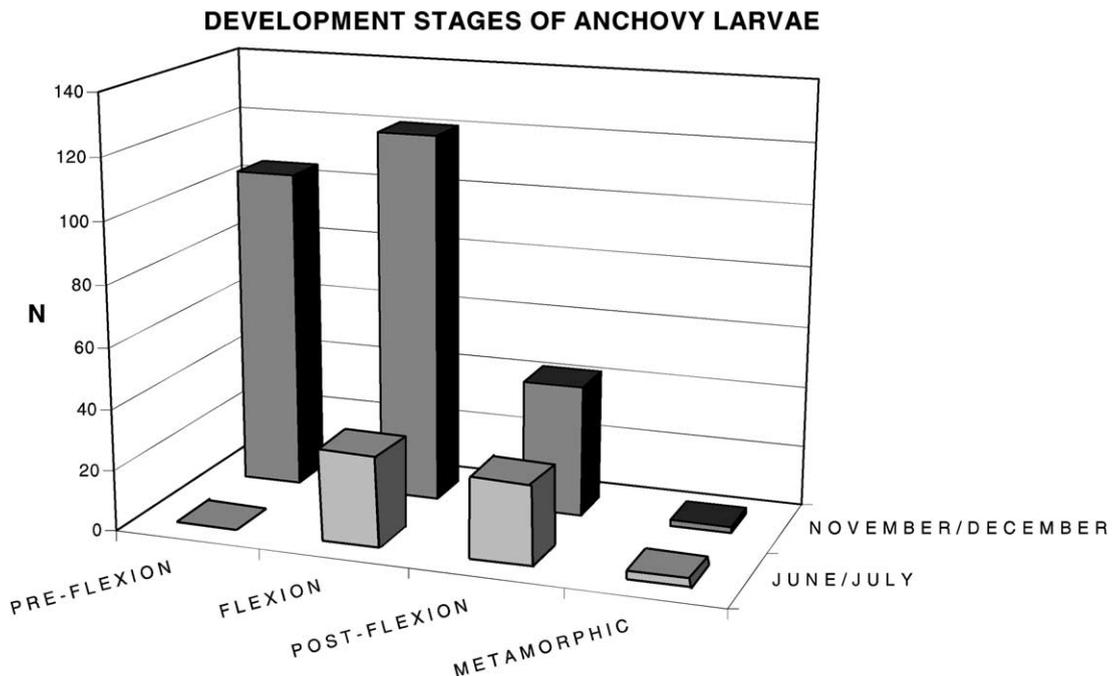


Fig. 5. Larval stage distribution according to notocord flexion (Moser and Alhstrom, 1970) in June/July and November/December, 1995.

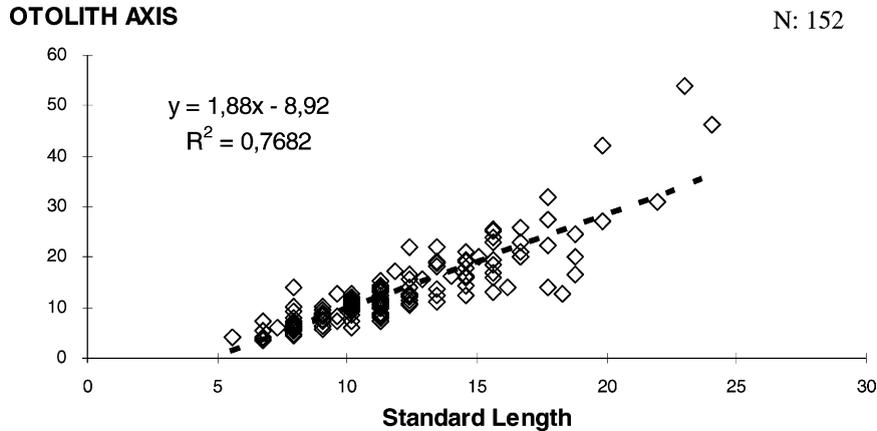


Fig. 6. Relationship between longest otolith axis ( $\mu\text{m}$ ) and SL of anchovy larvae (mm).

back-calculated sizes (Carlander, 1981).  $SL_0$  is found for  $OR = 0$  and subtracted from both terms of proportionality ( $SL_0 = 4.739$ ). Larvae sizes were calculated for 1–3 days before capture.

#### 4.3. Validation

The results of this analysis suggest that in a 24 h period there is a maximum and a minimum of MI. The highest mean percentages of MI were found in samples collected during daytime (Fig. 7). The lowest mean growth percentages are from larvae collected at night.

#### 4.4. Age determination

When anchovy larval otoliths are observed with transmitted light, rings are viewed as formed by a wide band of hyaline appearance followed by a thinner, opaque band. Because validation results suggested a one ring–one day relationship, number of counted rings was transformed in post-yolk absorption days (Table 2). Determined ages range from a minimum of 2 days and a maximum of 38 days. Most ages concentrated between 10 and 17 days for the winter samples and between 2 and 16 days for the spring larvae (Table 2).

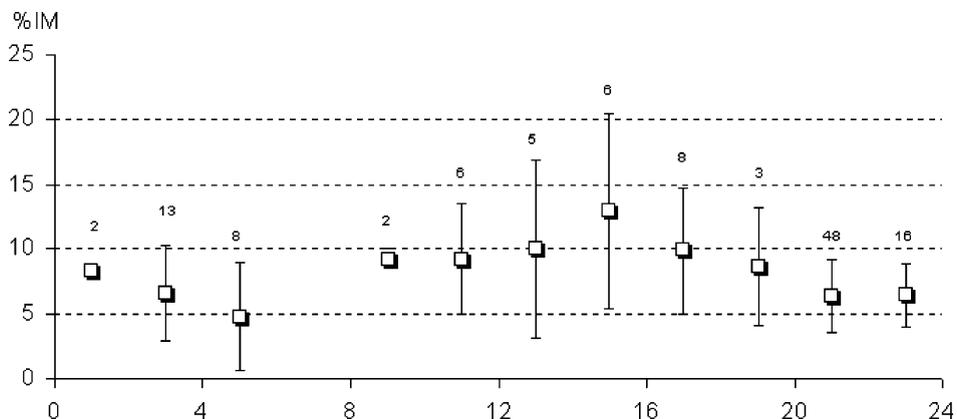


Fig. 7. Distribution of MI during the last day of larval life grouped in 2 h intervals. Mean MI, range,  $\pm 1$  standard deviation and number of observations are shown.

Table 2  
Age/length key<sup>a</sup>

Age (days)	Mean SL (mm)	Standard deviation	N	CV (%)
<i>Winter</i>				
2				
3				
4				
5	11.3		1	
6				
7				
8	9.6		1	
9				
10	12.7	1.66	3	13.0
11	11.3		1	
12	11.3		1	
13	12.0	1.26	3	10.5
14	12.7	1.66	4	13.0
15	13.4		2	
16				
17	15.4	2.53	3	16.4
18	15.6		1	
19				
20				
21	11.3		1	
22				
23	16.7		1	
24	16.7		1	
25	17.7		1	
26				
27	20.4		1	
28				
29				
30				
31	18.8		1	
32				
33				
34				
35				
36				
37				
38				
<i>Spring</i>				
2	9.1		2	
3	8.0	0.71	14	8.8
4	8.4	0.62	5	7.4
5	9.0	2.97	3	32.9
6	10.4	3.19	4	30.6
7	9.7	2.26	14	23.2
8	11.3	2.78	14	24.7
9	10.1	2.06	16	20.3
10	10.2	1.58	8	15.5
11	12.4	2.13	11	17.3
12	12.9	2.40	14	18.6
13	15.4	2.76	3	17.9

Table 2 (Continued)

Age (days)	Mean SL (mm)	Standard deviation	N	CV (%)
14	13.4	2.88	3	21.4
15	13.5	1.88	3	14.0
16	14.0		1	
17				
18				
19				
20	16.2	4.53	4	27.9
21				
22	15.1		2	
23	12.4		1	
24				
25				
26				
27				
28				
29				
30				
31				
32				
33	7.9		1	
34				
35				
36				
37	21.4		2	
38				

<sup>a</sup> N: number of observations; and CV (%): percentage of variation.

#### 4.5. Growth

Winter and spring Laird–Gompertz growth curves were calculated for larvae collected in the BSEB (Fig. 8):

Winter :

$$SL_t = 8.648 \exp(1.732)[1 - \exp(-0.020t)],$$

$$N = 26, R^2 = 0.726$$

Spring :

$$SL_t = 6.512 \exp(1.374)[1 - \exp(-0.052t)],$$

$$N = 120, R^2 = 0.828$$

Back-calculated SL 1–3 days before capture were compared between successive days and a daily linear growth rate was estimated (Table 1). On an average, winter larvae showed a higher daily growth rate of 0.50 mm/day whereas spring larvae had a rate of 0.40 mm/day. In both the cases, these rates are

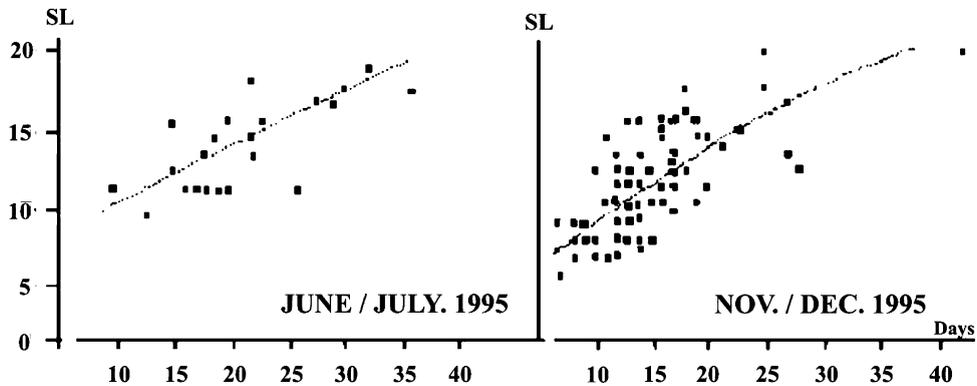


Fig. 8. Laird–Gompertz growth curves determined for June/July, and November/December, 1995 (SL in mm and age in days).

less than expected from theoretical calculations of Laird–Gompertz equations (0.72 and 0.84 mm/day, respectively).

## 5. Discussion

### 5.1. Abundance and size composition

Our results show higher abundance of anchovy larvae during spring, although Matsuura and Kitahara (1995) reported higher abundance during winter and early spring. Smaller larval sizes (pre-flexion and flexion stages) observed in November/December, are probably due to a recent spawning (Fig. 5). In June/July, flexion and post-flexion stages were predominant.

### 5.2. Spatial distribution

Anchovy larvae in June/July were scattered and isolated in rather small groups (Fig. 3a) without continuity. In November/December two distinct groups of larvae were observed, which in comparison to the June–July distribution, are more continuous and denser. At Cape Frio and its western surroundings an upwelling occurs, denoted by lower surface temperatures (Fig. 1b). A group of anchovy larvae extends westward to Sepetiba Bay (23°S, 44°W) avoiding the upwelling area, thus attenuating the negative effects of dispersion generated by the divergence (Bakun and Parrish, 1982). The group with higher densities showed a more extended and continuous distribution

and smaller larvae sizes, between Ilha Bela (24°S) and Santa Marta Grande Cape (29°S) in an area with warmer waters.

Anchovy spawning occurs during the whole year in the BSEB (Matsuura et al., 1992; Matsuura and Kitahara, 1995). In summer, it is mainly associated with the upwelled colder waters, and in winter it occurs mainly offshore in the neritic region, when a mid-water stability zone is formed (Bakun and Parrish, 1991). Thus, displacement of the spawning area seems to be related to water column stability (Matsuura and Kitahara, 1995).

### 5.3. Validation

Geffen (1992) stated that validation is an essential aspect of any age study and Jones (1986) demonstrated that different fish species larvae when developed under optimum conditions present a daily cycle in the formation of otolith increments. Age determination in larvae, based on the recognition of otolith increments, assumes that the beginning of the deposition process is constant among individuals and that daily ring formation is independent from growth rate, age, or season, in a manner that the number of rings can be related to the age of the larvae in days (Geffen, 1987). Microincrement periodicity and width are the two main aspects that determine otolith growth. The first one is obligatory and part of the daily and seasonal physiological cycles. The second one, width, may change according to temperature and diet (Morales-Nin, 2000).

Age validation was intended to relate MI of the otolith to time of day, divided in 2 h intervals. When

MI is at its minimum, the last ring is close to the otolith border. Fig. 7 does not show a clear and conclusive daily cycle in MI deposition, as one would expect from previous research (Jones, 1986). As pointed by Neilson (1992), when measurements are taken, light refraction at the border of the otolith may introduce errors. Nevertheless, the lowest MI rates were found in larvae caught at night as previously found by Castello and Vasconcellos (1995) who, working with larvae collected off Santa Marta Grande Cape, suggested that rings completed their formation between 08:00 p.m. and 08:00 a.m. In spite of our small sample size, our results seem to support a one-to-one ratio for rings and days of life after yolk absorption.

#### 5.4. Temperature effect

Sanchez (1986) experimentally demonstrated that formation of MIs does not begin until yolk absorption is over. Ciechomski (1966), Phonlor (1984) and Sanchez (1986) determined that larvae, at the yolk absorption stage, reach a size between 3.75 and 4.2 mm SL. The  $SL_0$  parameters of the Laird–Gompertz equations, 6.5 mm for larvae collected in November/December and 8.6 mm for June/July, were found to be larger than those already calculated by other authors for higher latitudes and colder temperatures. Temperature may be considered as one of the main factors controlling development rates of yolk stage larvae. After yolk absorption, development would be more

dependent on food availability. Time of embryonic development of *E. mordax* can be doubled when temperature decreases from 18 to 13 °C (Lasker, 1981). If a 5 °C difference can influence the development rate, then calculated lengths at first feeding seems to be consistent with values of other authors for other temperatures. Fig. 9 shows a scatter diagram and a possible line of tendency between size of larvae at first feeding ( $SL_0$ ) and SST for six set of larvae data collected in the SW Atlantic. In spite of differences in year and regions, this result suggests a positive relationship between both variables.

#### 5.5. Growth comparison

When our data are compared to other reported results for *E. anchoita* in the SW Atlantic, aspects as different as efficiency and selectivity of sampling gears and years of collection must be taken into consideration. The samples of this study were obtained with a Bongo net, whereas the others came from larvae caught with a rectangular mid-water trawl (RMT) or a BIOMOC (biological multiple opening/closing) net sampler. These gears tend to undersample the largest larvae, but at different size limits, the Bongo net provides the most size-selected samples. Therefore, growth models adjusted to this data will reflect such bias.

The average daily growth rates estimated from the Laird–Gompertz curves for larvae between 5 and

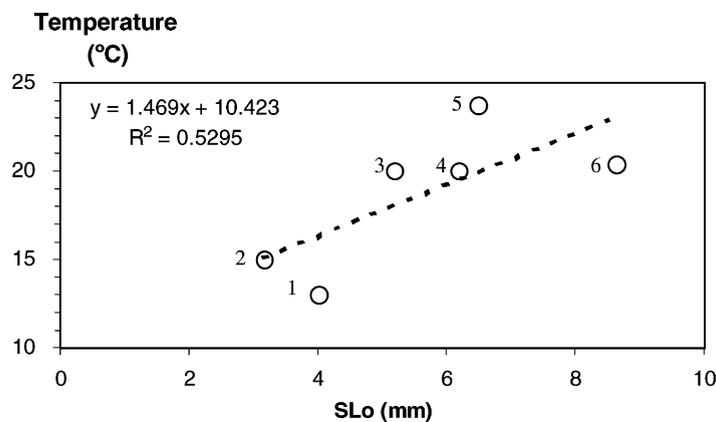


Fig. 9. Relationship between SST (°C) and SL at yolk absorption stage ( $SL_0$ ) for different larval growth curves of *E. anchoita* in the SW Atlantic (1 and 2: Off Patagonia and off Rio de la Plata, respectively, Sánchez and Martínez, in Castello and Vasconcellos (1995); 3: Off Sta. Marta Grande Cape (Castello and Vasconcellos, 1995); 4: Off Sta. Marta Grande Cape (Kitahara and Matsuura, 1995); 5: BSEB, spring (this study), 6: BSEB, winter (this study)).

20 mm are 0.75 mm/day (7.0%) for winter and 0.78 mm/day (8.1%) for spring samples. These rates were also estimated from daily increments of the median of back-calculated sizes in the last 3 days before capture (Table 1). Values obtained are lower, 0.497 mm/day (4.08%) and 0.397 mm/day (4.41%) for winter and spring samples, respectively. While the first estimations were derived from theoretical equations adjusted to data, the second ones resulted from back-calculations applied to observed data. Because of the size-selection problem, growth rates derived from the back-calculated sizes are thought to be more reliable.

Comparing the instantaneous growth rates ( $G'$ ) of *E. anchoita* larvae estimated by other authors and this work (Fig. 10), two groups of curves are observed. Three curves can be seen, two from Santa Marta Grande Cape (Kitahara and Matsuura, 1995; Castello

and Vasconcellos, 1995), and another from the BSEB in early winter (this work). The first two curves belong to larvae developed in waters characterized by upwelling and where water column stability is disturbed by a pulsing wind pattern. The third curve (early winter) is from larvae developed in well-mixed water columns. In these three cases, almost the same surface temperatures were observed (20.0–20.4 °C) with initial (SL = 5 mm) instant growth rates ( $G'$ ) between 0.2 and 0.28 mm/day lower than values observed for larger larvae (SL = 25 mm;  $G' > 0.3$  mm/day). The second group is also formed by a set of three growth curves. Larvae came from: a patagonic tidal front (Sánchez, personal communication; Castello and Vasconcellos, 1995), an estuarine front off Rio de La Plata (Martinez, personal communication; Castello and Vasconcellos, 1995), and the BSEB in the spring season (this work). The first three cases are related

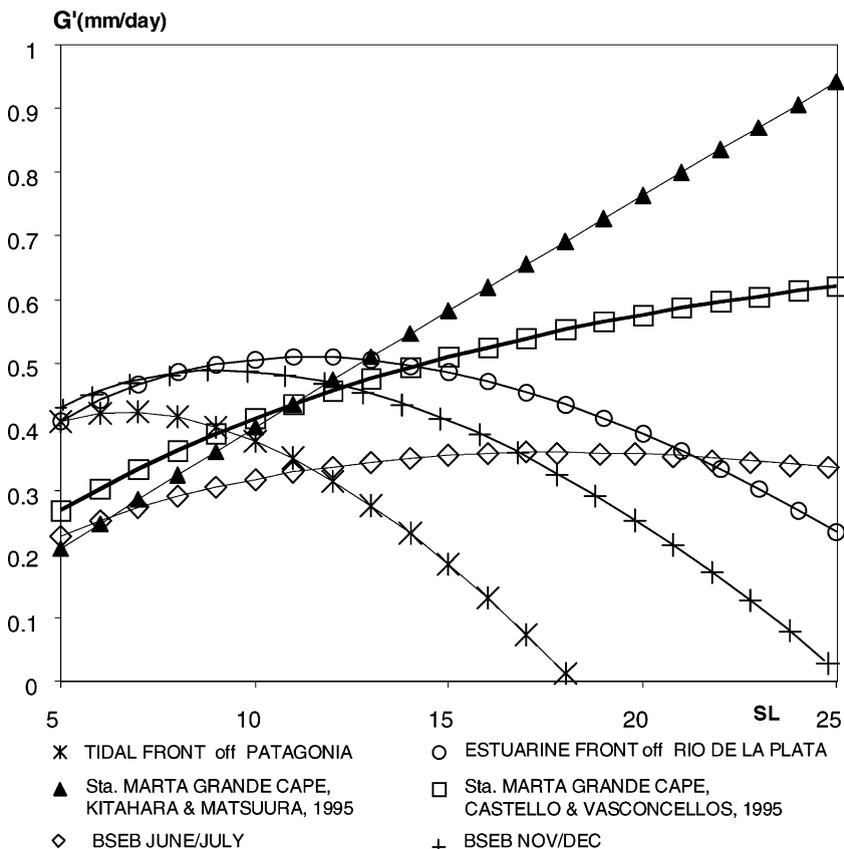


Fig. 10. Instant growth rates ( $G'$ ) comparison for anchovy larvae of the SW Atlantic (BSEB: winter and spring, this work; SMG: Santa Marta Grande Cape (two curves), a tidal front off Patagonia, an estuarine front off Rio de La Plata).

to upwelling environments, where the depth of the well-mixed layer reaches the nutricline (Wroblewski et al., 1989). The second three curves are related to larvae coming from stabilized water columns with initially high instant growth rates ( $G'$ , between 0.40 and 0.55 mm/day) independently of water temperature. Lasting conditions of water stabilization may result in unfavorable conditions for larval growth since nutrients in the euphotic layer are not replenished (Lasker, 1981).

Comparing  $G'$  rates of the first group (Fig. 10), there is a difference in the rates determined by studies in the upwelling of Santa Marta Grande Cape, where Kitahara and Matsuura (1995) found a value 50% higher than Castello and Vasconcellos (1995). Rates calculated for BSEB in the early winter (this work) are more constant than any other. In the second group (estuarine and tidal front and BSEB during spring), the instantaneous growth rates from the Patagonic tidal front are the lowest, possibly due to the low temperature (13 °C).

Larval growth curves refer to the initial phase of fish life, reflecting how fish species respond to early environmental conditions. The differences found are an indicator of how the habitat may mould individuals.

The comparison between growth curves (Fig. 10) shows the effects of different habitats on *E. anchoita* larvae, particularly the direct effect of temperature. The results shown here suggest that anchovy larvae from the BSEB may constitute a different stock from those already known in higher latitudes. *E. anchoita* is distributed on a very extensive shelf area of the SW Atlantic between central Patagonia (47°S) and Cape Frio (23°S), therefore, inhabiting waters under the domain of sub-Antarctic waters in the south (Brandhorst and Castello, 1971; Piola and Rivas, 1997) and the domain of sub-tropical waters in the north (Matsuura, 1986). For this to happen, the species must be able to spawn and its larvae develop under very different conditions, which explains its success.

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