



Larval growth of hake (*Merluccius hubbsi*) in the Patagonian shelf: Analysis of two reproductive seasons



Paola Betti^{a,b}, Daniel R. Brown^{a,*}, Brenda Temperoni^{a,b}, Laura Machinandiarena^{a,c}, Martín D. Ehrlich^{a,c}

^a Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), Paseo Victoria Ocampo N° 1, Escollera Norte, Mar del Plata, Argentina

^b Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina

^c Departamento de Ecología Genética y Evolución, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires (UBA), Intendente Güiraldes 2160, Ciudad Universitaria, Buenos Aires, Argentina

ARTICLE INFO

Article history:

Received 10 July 2013

Received in revised form 17 February 2014

Accepted 18 February 2014

Available online 26 March 2014

Keywords:

Age

Growth

Hake larvae

Merluccius hubbsi

ABSTRACT

The Argentine hake (*Merluccius hubbsi*) represents the most abundant fish resource in the Southwest Atlantic Ocean. Larval age, daily growth, and temporal distribution of birthdates of individuals collected throughout two reproductive seasons (2004–2005 and 2009) were studied by analyzing daily growth increments in their sagittae otoliths. Samples were obtained in the Northern Patagonian shelf, which constitutes the main spawning area reported for this species. A total of 365 hake larvae sampled with different types of gears was used in this study. Back-calculated hatching periods extended from mid November to the end of March and several larval cohorts were identified. Length-at-age relationships were best described by exponential models: $TL = 2.227 \exp(0.032t)$ and $TL = 2.581 \exp(0.035t)$ (for 2004–2005 and 2009, respectively). Growth rates obtained by deriving the models ranged from 0.07 to 0.48 mm day⁻¹ in 2004–2005, and from 0.09 to 0.74 mm day⁻¹ in 2009. Differences in larval growth were detected between both periods and within them; differential growth would not be attributed to thermal effect since temperature values were quite similar along both seasons. Prey availability could explain the growth variation detected within the 2009 season.

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1. Introduction

The Argentine hake (*Merluccius hubbsi*) is the most abundant demersal species in the Southwest Atlantic Ocean. It occurs from Cabo Frío in Brazil (22° S) to the south of Argentina (55° S) at depths between 50 and 500 m (Cousseau and Perrotta, 2000). This species represents the most important fish resource in the Argentine Sea, with reported landings of 281,715 t in 2010 (MAGyP, 2012).

Two stocks have been identified in the Argentine shelf: the northern stock (between 34° and 41°) and the southern one, also known as the Patagonian stock (between 41° and 55° S). The latter represents the most abundant population (Renzi and Irusta, 2007). The reproductive activity of this group occurs throughout austral spring and summer in the Northern Patagonian shelf (42–47° S

(Ehrlich, 1998; Macchi et al., 2007, 2010), which constitutes the main spawning area reported for this species in the Argentine Sea.

The Patagonian stock has been intensively overexploited (Cordo, 2006) and due to the declining tendency in catches during the last years there is an increasing interest to determine life history parameters such as age and growth through larval stages. Knowledge of the dynamics of mechanisms operating during the egg and larval stages of fish is important to the understanding of the inter-annual recruitment variability (Houde, 1987). Predation and starvation are the highest sources of mortality during the larval phase of fish (Bailey and Houde, 1989). As larvae grow, they are less vulnerable to predation, according to the “bigger is better” and the “stage duration” hypotheses (Houde, 2008; Legget and Deblois, 1994). Moreover, feeding success may also affect larval survival (Hunter, 1981). Thus, variability in growth rates would be a function of biological conditions (Pepin, 1991).

Since Pannella (1971), the analysis of daily increments in otoliths has been applied to study age in larvae and juveniles of fishes, estimating growth rates and survival patterns during early life stages (Houde, 2008). Several works regarding juvenile growth of hake species have been published (Morales-Nin, 1987; Belcari

* Corresponding author. Tel.: +54 223 4862586; fax: +54 223 4861830.

E-mail addresses: paolabetti@inidep.edu.ar (P. Betti), dbrown@inidep.edu.ar (D.R. Brown), lauram@inidep.edu.ar (L. Machinandiarena), mehrllich@inidep.edu.ar (M.D. Ehrlich).

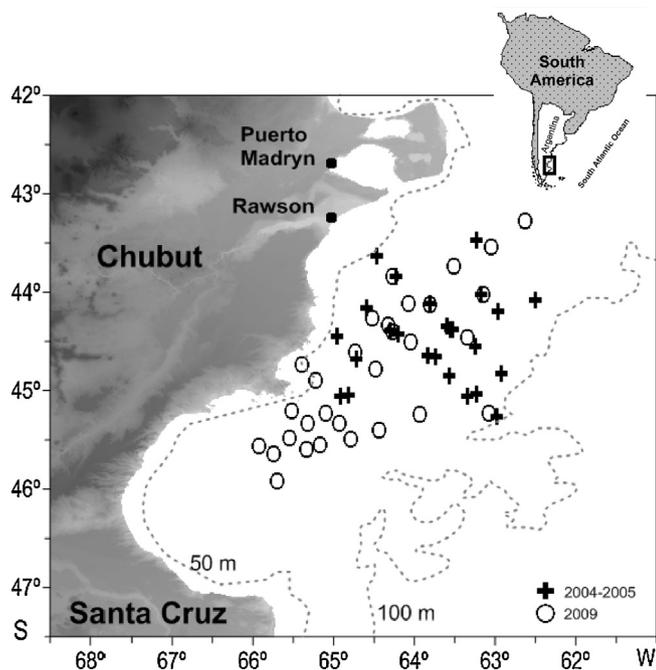


Fig. 1. Study area and sampling stations of the two reproductive periods (2004–2005 and 2009).

et al., 2006; Piñeiro et al., 2008; Otxotorena et al., 2010). Specific studies on larval stages analyzed larval growth of *M. merluccius* in relation to larval development (Palomera et al., 2005) and growth and condition of field-caught larvae and juveniles of *M. productus* and *M. capensis* (Grote et al., 2012).

Although several studies regarding growth of adult specimens of *M. hubbsi* have been performed (Lorenzo, 2003; Norbis et al., 1999; Renzi et al., 1999; Vaz-dos-Santos and Rossi-Wongtschowski, 2007), little information is available with reference to growth of *M. hubbsi* during early life stages. Santos et al. (2005) studied growth of Argentine hake during its juvenile stage (26–190 mm total length) and Buratti and Santos (2010) determined the settlement time. Brown et al. (2004) determined the larval growth of hake for the first time but the authors considered a narrow size range (2–11 mm TL). Therefore, a combination of different nets was used in this work to cover a broader body size range in order to gain new information and increase the knowledge on hake larval growth. The objectives of this work were: (1) estimate *M. hubbsi* larval growth rates, covering a broader body size range than previous studies and (2) analyze growth rates of specimens collected throughout two reproductive seasons (2004–2005 and 2009), allowing a temporal analysis of growth variations in the main spawning area of the species. This study was performed on the North-Patagonian shelf which constitutes the main spawning area for *M. hubbsi* (Macchi et al., 2007, 2010).

2. Materials and methods

2.1. Data collection

Hake larvae were collected during six research cruises conducted by INIDEP (Instituto Nacional de Investigación y Desarrollo Pesquero) in the Northern Patagonian shelf on board the R/Vs “Dr. Eduardo L. Holmberg” and “Capitán Oca Balda”. Sampling included two reproductive seasons, from December 2004 to February 2005, and from January to April 2009. All samples were collected between 42 and 47° S, from near the coast to the 100 m isobath approximately (Fig. 1). A total of 346 ichthyoplankton samples was

acquired using a Bongo net (60 cm mouth diameter and 300 μm mesh-size), an Epibenthic sampler (MEB, 0.125 m² mouth area and 500 μm mesh-size) and a Rectangular Mid-water Trawl (RMT, 1 m² mouth area and 1000 μm mesh-size) (Table 1). Trawls were made obliquely, integrating the water column from near the bottom to the surface. Gears were fitted with a SCANMAR depth sensor. Samples were sorted on board and fixed in 96% ethanol which was changed several times to assure preservation. Hydrological data were vertically recorded by a self-recording conductivity-temperature-depth (CTD). According to previous reports on vertical migration, hake larvae are mainly found near the bottom during the day (Álvarez-Colombo et al., 2011). Since sampling took place from 7:00 to 17:00 hs approximately, bottom temperatures were considered as representative of hake larval habitat.

To analyze prey availability for *M. hubbsi* larvae, additional zooplankton samplings were performed along the 2009 season. Samples ($n = 13$ in January, $n = 10$ in March and $n = 4$ in April 2009) were obtained by oblique tows (from near the bottom to the surface) with a Minibongo net (20 cm mouth diameter and 67 μm mesh-size), equipped with a flowmeter to estimate the volume of filtered water. After collection, samples were immediately preserved in 4% buffered formalin until analysis in the laboratory.

2.2. Laboratory procedures

Each larva was measured to the nearest 0.1 mm total length (TL) under a dissecting microscope. Sagittal otoliths were removed from the head, placed on a glass slide, and included in a drop of transparent thermoplastic glue (Pro-texx®). When the mounting medium was completely dry (after two days), otoliths were polished using 12, 9, and 3 μm lapping film paper. For each individual, the number and width of increments in both otoliths were registered from nucleus to border along the longest axis to determine age, under a transmitted light microscope at 400–1000 \times magnification connected to an image analysis system (Kontron software) with a digital camera. Increments were counted in both otolith of the pair and, when the counts agreed in at least 90% (e.g. 22 and 20 increments) between left and right otolith, the information provided from either of them was considered as the larval age. If the difference between both otoliths was greater than 10% neither of them was considered. When only one otolith from the pair was available due to the loss of the other during the extraction procedures, such information was used.

Because the daily deposition of increments in otoliths has not been experimentally validated for this species up to date, the process was assumed according to the observations performed in other *Merluccius* species like *M. productus* (Bailey, 1982) and *M. merluccius* (Arneri and Morales-Nin, 2000; Morales-Nin et al., 2005). Zooplankton samples were inspected under a Wild M5 stereoscopic microscope, in order to enumerate and identify the different stages of copepods, which represent the main prey of *M. hubbsi* larvae (Temperoni and Viñas, 2013). Sample components were classified as eggs, nauplii, copepods < 1 mm (total length) and copepods > 1 mm. Sub-samples were obtained from each sample, and the volume was determined according to the density of organisms in the original sample, to count at least 100 individuals of the dominant stage. Abundances were expressed as individuals m⁻³ and derived from raw counts using sub-sample fraction and the filtered water volume.

2.3. Data processing

Hatching dates were determined by subtracting the number of daily increments from the dates of capture of the specimens, and analyzed for both reproductive seasons (2004–2005 and 2009); they were grouped in ten days intervals (1–10, 11–20, 21–30) to

Table 1
Sample data collected during the 6 cruises analyzed.

| Cruise | Ship | Dates | Gear | N° of plankton samples | N° of larvae | Size range (mm) |
|----------|-------------------------|---------------------------|---------------------|------------------------|--------------|-----------------|
| EH-10/04 | Dr. Eduardo L. Holmberg | 08–18 December 2004 | Bongo | 51 | 19 | 2–7.6 |
| EH-01/05 | Dr. Eduardo L. Holmberg | 14–29 January 2005 | Bongo | 24 | 77 | 3.9–15.8 |
| OB-02/05 | Capitán Oca Balda | 18–28 February 2005 | Bongo | 42 | 94 | 2.1–18.6 |
| EH-01/09 | Dr. Eduardo L. Holmberg | 10–27 January 2009 | Bongo MEB NCK | 54 | 11 | 4.3–6.2 |
| | | | | 6 | 67 | 3.3–11.5 |
| | | | | 5 | 1 | 6.20 |
| OB-02/09 | Capitán Oca Balda | 26 February–12 March 2009 | Bongo RMT MEB | 51 | 16 | 5.5–22 |
| | | | | 10 | 32 | 3.5–17 |
| | | | | 15 | 2 | 23–24 |
| OB-05/09 | Capitán Oca Balda | 09–21 April 2009 | Bongo RMT MEB | 5 | 1 | 16 |
| | | | | 75 | 2 | 18–24 |
| | | | | 22 | 44 | 4.5–24 |

visualize the hatching periods at the beginning, middle, and end of each month, respectively. Size-at-age data of larvae were represented as exponential functions of age: $TL = a \exp(b t)$, where: TL was the total length (mm), a and b were regression parameters, and t represented the number of increments in the otoliths. The fitted exponential functions were compared between both seasons or between cruises to detect inter-seasonal or within seasonal differences in size-at-age. Growth rates were determined by deriving the exponential models.

Power relationships between TL and otolith radius (OR, μm) were established for each season as $TL = aOR^b$, where a and b represented regression parameters.

Additionally to the fitted models, larval growth was analyzed by back-calculation of past sizes at previous ages (growth trajectories). In order to obtain past size values the methodology described by Watanabe and Kuroki (1997) and Watanabe and Nakamura (1998) was utilized. After fitting TL and OR in a power relationship, the relationship of the i th otolith increment radius (OR_i) and total length (TL) on the day of the i th increment formation (TL_i) was considered to be expressed by a power formula, $TL_i = aOR_i^b$, for individual larvae. The solution of the following two equations was necessary to obtain the values a and b . $TL_1 = aOR_1^b$ and $TL_{\text{captured}} = aOR_{\text{captured}}^b$ where TL_1 = total length at first increment deposition (2 mm); OR_1 = the measured radius of the first daily increment (μ); TL_{capture} = the measured total length at capture (mm); and OR_{captured} = otolith radius (μ) at capture.

2.4. Statistical analysis

Differences in size-at-age (between and within seasons) and size-otolith radius were tested by slope comparison (Zar, 1996). Previously, the equations were linearized using natural logarithms (\ln) and age and $\ln(\text{OR})$ were considered as covariates. To compare larval growth between both seasons we considered both the complete range of ages and the same age interval (10–50 days), to address the fact that individuals of both seasons had different sizes and ages and larval growth should be strongly linked to size. Such comparison was performed by slope comparison test.

Differences in back-calculated total lengths were examined between months within each season (2004–2005 and 2009) by MANOVA. Probability level ($p = 0.017$) was determined by using a Bonferroni correction.

3. Results

3.1. Thermal characterization

As a general trend, a longitudinal bottom thermal gradient was observed in all cruises, with warmer waters registered near the

coast. Thermal values varied from 7 to 16 °C approximately (Fig. 2). These values were quite similar among months and between both reproductive seasons. In 2004–2005 water temperatures increased from December to February (Fig. 2a–c), and the same pattern was observed from January to March 2009, while they were relatively constant between March and April 2009 (Fig. 2d–f).

3.2. Growth analysis

Smaller larvae were more abundant in December 2004 and January 2009 and they were collected with Bongo net whereas larger ones were captured in February 2005 with Bongo net, and April 2009 with MEB and RMT (Table 1). A typical pattern of successive clear and dark bands delimiting the daily increments was observed in all the otoliths. For larvae captured in the 2004–2005 reproductive season, 0–74 daily increments were counted (2.00–18.60 mm TL), while 10–75 increments (3.50–28.00 mm TL) were recorded for individuals collected in 2009.

The hatching period of hake larvae collected in 2004–2005 extended from 11–20 November to 11–20 February. Three hatching monthly peaks were detected within this season: 21–30 November, 21–31 December and 21–31 January (Fig. 3A). The hatching period of hake larvae collected in 2009 extended from 11 to 20 December to 21–30 March; three hatching monthly peaks were detected: 21–31 December, 11–20 February, and 21–31 March (Fig. 3B). The maximum peaks of both seasons coincided at the end of December (21–31 December).

Length-at-age data of larvae from both reproductive seasons were fitted in two exponential models. Both relationships were statistically different ($p < 0.01$), even when the same age intervals were compared (Fig. 4A). Registers in 2009 showed larger sizes at the same age than data recorded in 2004–2005. Instantaneous growth rates were determined by deriving the equations (Fig. 4B). Within seasonal differences in length-at-age were detected between specimens captured in January and February 2005 (Table 2). Slopes values of January and February 2005 were quite similar (0.038 and 0.033 respectively).

Power relationships between TL and otolith radius for hake larvae of both seasons (Fig. 5) were statistically distinct ($p < 0.001$). This fact should be interpreted as higher larval sizes at the same otolith radii for the 2009 series in comparison with the 2004–2005 season.

Growth rates derived from the exponential models showed a trend of increasing exponentially with respect to age (Fig. 6). To facilitate the interpretation, growth rates values were grouped by age and size intervals (Table 3).

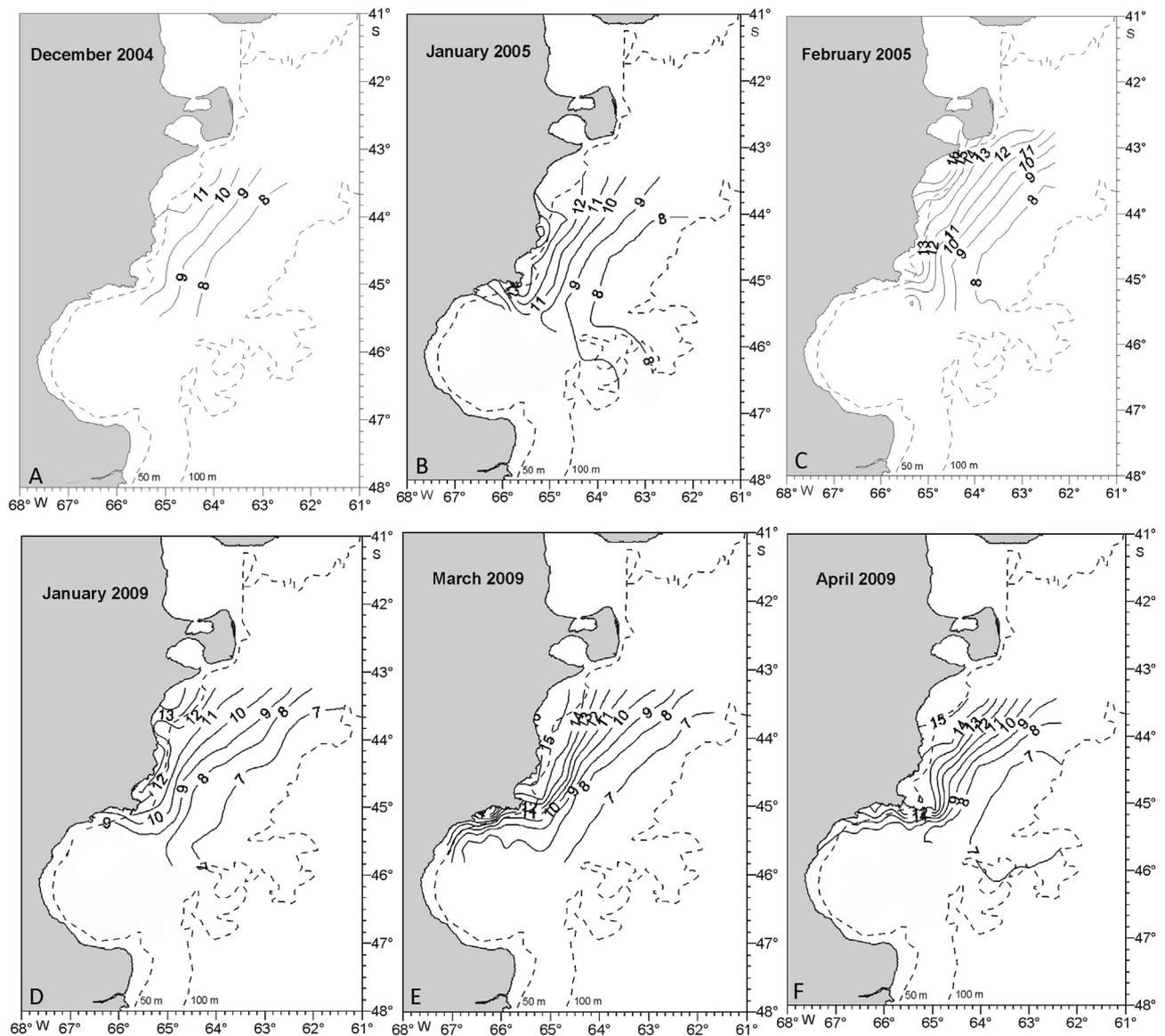


Fig. 2. Sea bottom temperatures in Northern Patagonian coast during the reproductive periods 2004–2005 and 2009. (A) December 2004; (B) January 2005; (C) February 2005; (D) January 2009; (E) March 2009; (F) April 2009.

Table 2

Slopes, intercepts and results of pairwise comparison of slopes between months within each season (two last columns).

| | Slope | Intercept | <i>n</i> | January 2005 | February 2005 |
|---------------|-------|-----------|----------|--------------|---------------|
| December 2004 | 0.038 | 2.083 | 19 | 0.96 | 0.16 |
| January 2005 | 0.038 | 2.055 | 77 | | 0.01* |
| February 2005 | 0.033 | 2.055 | 95 | | |
| | Slope | Intercept | <i>n</i> | March 2009 | April 2009 |
| January 2009 | 0.040 | 2.147 | 79 | 0.08 | 0.03 |
| March 2009 | 0.034 | 2.662 | 50 | | 0.20 |
| April 2009 | 0.030 | 3.537 | 47 | | |

Table 3

Growth rates derived from the exponential models for hake larvae collected in each cruise.

| | Growth rate (mm days ⁻¹) | Age (days) | Size ranges (mm) | <i>N</i> |
|---------------|--------------------------------------|------------|------------------|----------|
| December 2004 | 0.06–0.25 | 2–31 | 2.28–7.58 | 18 |
| January 2005 | 0.12–0.67 | 11–57 | 2.92–15.83 | 77 |
| February 2005 | 0.09–0.77 | 7–74 | 2.17–18.61 | 95 |
| January 2009 | 0.18–0.44 | 19–41 | 5.00–11.50 | 79 |
| March 2009 | 0.10–0.73 | 10–66 | 3.50–24.00 | 50 |
| April 2009 | 0.12–0.63 | 21–75 | 5.08–28.00 | 47 |

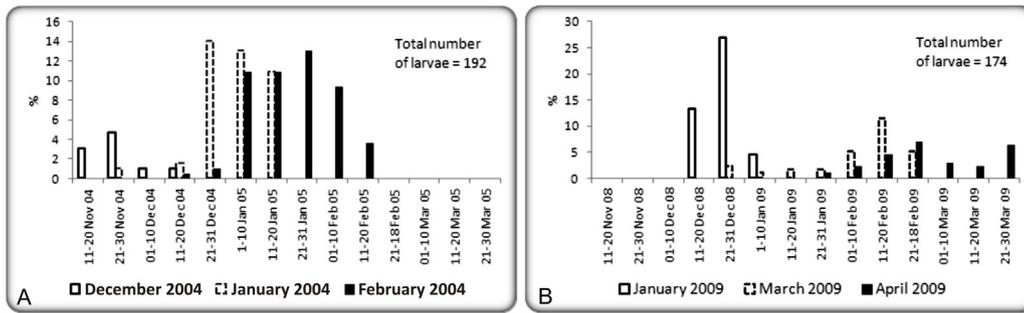


Fig. 3. Back-calculated hatching dates of hake larvae for 2004–2005 and 2009.

Individual back-calculated sizes (growth trajectories) of hake larvae were slightly exponential in shape (Fig. 7). Statistical differences in size at previous ages were detected between: December 2004 and February 2005 ($p=0.007$); January 2005 and February 2005 ($p=0.001$); January 2009 and April 2009 ($p=0.000$); March 2009–April 2009 ($p=0.002$). Significant differences were not observed between December 2004 and January 2005 ($p=0.731$); January 2009 and March 2009 ($p=0.043$).

3.3. Prey availability

Overall, mean total copepod abundances were higher in March while the lowest values of the season were recorded in January

2009 (Table 4). Copepods < 1 mm were the most abundant group in March 2009, while in January and April 2009 nauplii dominated the copepod community.

4. Discussion

Merluccius hubbsi is one of the most important and studied species in the Argentine Sea, but little information has been published regarding biological aspects during its early life history. This work constituted a good opportunity to study the larval growth in the main spawning area of the species with biological material from different reproductive periods.

Daily growth increment in otolith microstructure represents a strong tool for ageing larvae and juveniles of fish (Álvarez and Cotano, 2005). A central point in larval growth studies is the instant when the first increment is deposited (Brown et al., 2004). Bailey (1982) registered the first increment deposition one or two days after the yolk-sac absorption in larvae of *M. productus*. As such information was not available for larvae of *M. hubbsi*, we assumed the number of increments counted from first check to be the larval age.

All larvae were born within the spawning period which was previously reported based on the reproductive biology of adult specimens (Macchi et al., 2010). Even though hatching dates of both series were difficult to compare because the data were taken at different moments and with distinct gears, the analysis revealed

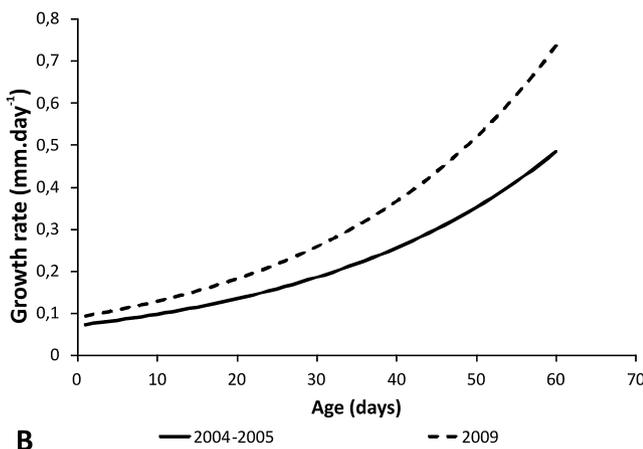
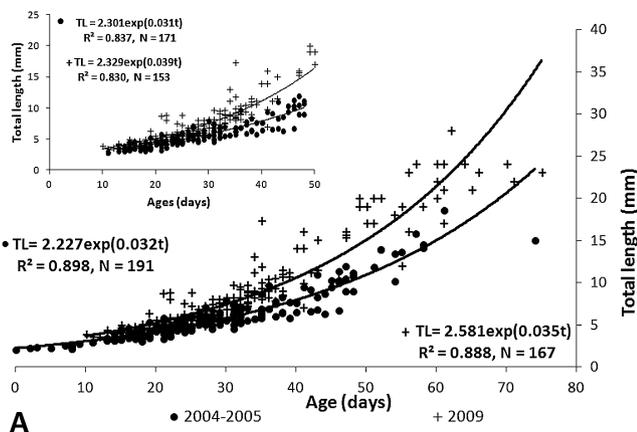


Fig. 4. Size-at-age relationships for *Merluccius hubbsi* larvae collected during the periods 2004–2005 and 2009. (A) Exponential model was fitted to each data set. TL: total length; t: larval age. The small graphic represents the models fitted to the length-at-age data at 10–50 days interval. (B) Growth rates were obtained by deriving the equations.

Table 4 Mean abundance (individuals m^{-3}) values of the North Patagonian copepod community along the 2009 season (January–April).

| Prey item | Abundance (ind m^{-3}) | | |
|----------------------------------|---------------------------|------------|------------|
| | January 2009 | March 2009 | April 2009 |
| Copepod eggs | 1119.35 | 1087.24 | 1091 |
| Copepod nauplius (<200 μm) | 2493.59 | 5107.39 | 5083.53 |
| Copepods <1 mm | 1595.32 | 12880.91 | 4980.47 |
| Copepods >1 mm | 8625 | 2444.8 | 1320.36 |
| Total | 1517.69 | 5380.09 | 3118.84 |

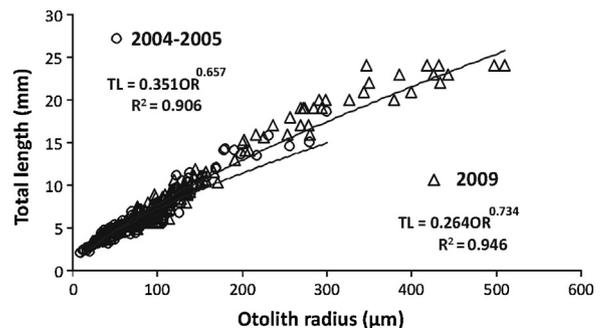


Fig. 5. Power relationships between total length (TL) and otolith radius (OR).

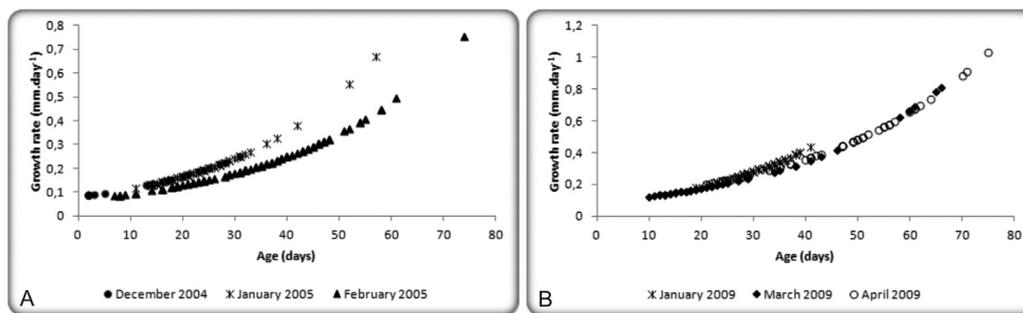


Fig. 6. Growth rate derived from exponential models. (A) 2004–2005 and (B) 2009 data.

a common pattern between them related to the temporal coincidence of maximum peaks at the end of December. The use of different gears allowed the capture of larvae in a broad size range. Under these circumstances, several larval cohorts were identified, and this was the methodological advantage of the 2009 sampling period. If several larval cohorts are being produced throughout a spawning period, each group could be subject to distinct environmental conditions, affecting their survival. Houde (2002) developed a methodology which relates the growth and mortality of fish larvae that can be used to compare survival potential of larval cohorts. Further studies will be required to advance in this field. An important aspect to consider in this section should be: what could be identified as a cohort? We grouped the hatching dates in ten days intervals to analyze the process at the beginning, middle and end of each month. At the same time, the cruises had a monthly resolution, and for this motive we have mentioned the main monthly peaks. Additionally, individuals that were born in two consecutive periods of ten days (e.g. 1–10 January, 11–20 January) could be considered as the same cohort in a species with a protracted reproductive period as *M. hubbsi*. Other probable mechanisms affecting the hatching dates could be the larval drift or advective losses. However, Álvarez-Colombo et al. (2011) have proposed a retention mechanism for hake larvae in the area, coupled to a horizontally or vertically stratified circulation.

For *M. hubbsi* larvae, the size-at-age data fitted an exponential model. Álvarez and Cotano (2005) also utilized an exponential relationship to describe the larval growth of *M. merluccius*, while Brown et al. (2004) fitted a linear growth model to *M. hubbsi* larvae from 2 to 12 mm TL. Working with larger individuals than the specimens analyzed here, Santos and Renzi (2006) utilized the Laird-Gompertz model to describe juvenile hake growth. The model considered an increasing growth phase and a decreasing one, both separated by an inflection point which corresponds to the maximum growth rate (Sánchez, 1995). Since larvae analyzed in this study appear to be positioned before the inflection point, in the ascending phase, fitting an exponential model might be adequate.

Considering the exponential trend, growth rate expressed as an instantaneous value will increase with age. Larval growth is probably being affected by the morphological changes that occur during first phases of ontogeny, allowing larger individuals to derive a higher amount of energy to growth. Several somatic changes as mouth opening, eye and digestive tract development occur in newly hatched hake larvae from 2.2 to 3.2 mm (Betti, 2011). Such important morphological modifications in a short period of time could reduce significantly the initial larval growth in length during the first days, in coincidence with the observations of Palomera et al. (2005) for *M. merluccius* larvae. At around 8 mm length the notochordal flexion has finished and all the meristic structures are present. At the same time, the muscle development is notoriously increased (Betti et al., 2009). At 15 mm another important mechanism that could affect larval growth could be the transition from pelagic to demersal habitat. For *M. hubbsi*, this habitat change starts around 15 mm TL and finishes at 30 mm TL (Buratti and Santos, 2010). Steves and Cowen (2000) detected that prior to settlement in the demersal habitat; larval growth of silver hake (*M. bilinearis*) was slower, suggesting that the transitional process increased their potential growth.

Larval growth rates of *M. hubbsi* were close to the values previously registered for the same species and for other species of the genus *Merluccius*, principally when mean growth values are taken into account (Table 5). Therefore, similar growth rates during the larval stage might be interpreted as a common feature of the genus.

Differences in hake larval growth were detected in this study between the 2004–2005 and 2009 seasons, and within the 2009 season. An important aspect to consider in the comparison is the lack of larger larvae in 2004/5; this fact could lead to inconsistent results since larger individuals tend to exhibit faster growth. However, when both series were compared at the same observational range the individuals collected in 2009 evidenced a faster growth. Prey availability and temperature have been generally considered the most important sources of variability in growth (Dower et al., 2002). Trying to explain the observed growth differences between both seasons on the basis of thermal influence might be difficult,

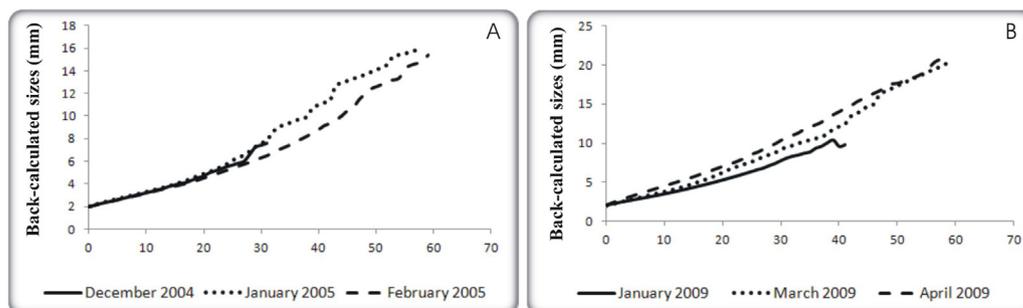


Fig. 7. Mean back-calculated sizes (growth trajectories) of the hake larvae. (A) Periods 2004–2005 and (B) 2009.

Table 5
Larval growth rates of different *Merluccius* species.

| Species | Size range (mm) | Age range (days) | Growth rates (mm day ⁻¹) | Temperature (°C) | Sources |
|------------------------------|-----------------|------------------|--------------------------------------|------------------|-----------------------------|
| <i>Merluccius merluccius</i> | 2.6–12.0 | | 0.14–0.15 | 10–13 | Álvarez and Cotano (2005) |
| <i>Merluccius merluccius</i> | 2.5–9.1 | | 0.15–0.19 | 15 | Palomera et al. (2005) |
| <i>Merluccius biliniaris</i> | | 3–47 | 0.17 | 13–17 | Jeffrey and Taggart (2000) |
| <i>Merluccius productus</i> | <20 | | 0.16 | 8–15 | Bailey (1982) |
| <i>Merluccius productus</i> | 2.0–25.0 | | 0.156 | – | Butler and Nishimoto (1997) |
| <i>Merluccius productus</i> | 4.0–11.0 | | 0.135–0.279 | 10.5–12.4 | Cass-Calay (1997) |
| <i>Merluccius hubbsi</i> | 2.0–11.0 | | 0.16 ± 0.03 | 14.5–18 | Brown et al. (2004) |
| <i>Merluccius paradoxus</i> | 2.0–7.0 | | 0.21 | – | Grote et al. (2012) |
| <i>Merluccius capensis</i> | 2.4–5.4 | | 0.21 | – | Grote et al. (2012) |
| <i>Merluccius hubbsi</i> | 2.0–18.6 | | 0.07–0.48 (0.22) | 14.5–18.5 | This work |
| <i>Merluccius hubbsi</i> | 3.5–28.0 | | 0.09–0.74 (0.31) | 14–19 | This work |

Mean values are indicated between parentheses.

because bottom temperatures were quite similar throughout these periods (Fig. 2), and constitute punctual observations while growth is a continuous process during the larval life. Furthermore, hake larvae are able to exert daily vertical migration, staying near the bottom during the day and ascending to the thermocline depth during the night, experiencing daily thermal differences of about 5 °C (Álvarez-Colombo et al., 2011). Additionally, since it inhabits a broad geographical range, the species is subject and adapted to different environmental changes (Cousseau and Perrotta, 2000); under these circumstances the influence of temperature on larval growth could not be easily identifiable. Other mechanisms such as maternal influences could be involved (Marteinsdottir and Steinarnsson, 1998).

In relation to analysis of growth differences within both seasons obtained from slopes comparisons, some observations must be taken into account. Despite the fact that slopes of January and February 2005 were significantly different, such difference was registered in the third decimal position, which seems unreasonable from a biological standpoint. Similarly, slopes resulted statistically identical between January 2009 and April 2009, while intercepts were considerably distinct (2.055 and 3.537 mm, respectively). The presence of larger larvae captured in April due to differential efficiency of gears could artificially diminish the value of the slope. It is known that hake larvae around 3.5 mm are several days old. From this point of view the analysis of growth trajectories results a more reliable method to detect differences in larval growth between both groups of hake larvae.

As it was mentioned before, the larval growth could also be affected by food availability. A positive relationship between the average growth rate of larvae and the average concentration of prey-sized particles has previously been reported for *M. productus* (Cass-Calay, 1997). In the Northern Patagonian shelf, where high zooplankton production has been documented (Sabatini and Martos, 2002; Santos and Ramírez, 1995; Viñas et al., 1992), *M. hubbsi* larvae are known to prey mainly on copepods (Ciechomski and Weiss, 1974; Moriondo, 2002; Viñas and Santos, 2000). As our data showed, copepod abundances were higher in March and April than in January 2009, providing a plausible explanation for growth differences observed within this season for both larval cohorts. Abundance data of the copepod community were not available in 2004–2005; additional studies considering prey availability might contribute to explain differences in hake larval growth.

This study reported larval growth characteristics of *Merluccius hubbsi* in the main spawning area of the species, which is the Northern Patagonian Shelf. Growth differences were detected between seasons (2004–2005 and 2009 periods) and within them. Differences observed in 2009 could be attributable to the zooplankton prey availability. Several larval cohorts were identified throughout both study periods. Future studies will be required to analyze the causes of differential growth in hake larvae and the probable impact on the recruitment of this species.

Acknowledgments

We are indebted to the crew and technicians of the R/Vs “Eduardo Holmberg” and “Capitán Oca Balda” for their assistance during the cruises. We also would like to express our gratitude to two anonymous reviewers for their valuable comments on the draft. This work was partially supported by PIP CONICET 112 20080100815.

References

- Álvarez-Colombo, G., Dato, C., Macchi, G., Palma, E., Machinandiarena, L., Christiansen, E., Betti, P., Martos, P., Castro-Machado, F., Brown, D., Ehrlich, M., Mianzan, H., Acha, E.M., 2011. Distribution and behaviour of Argentine hake larvae: evidences of a biophysical mechanism for self-recruitment at the North Patagonian shelf waters. *Cienc. Mar.* 37 (4B), 633–657.
- Álvarez, P., Cotano, U., 2005. Growth, mortality and hatch-date distributions of European hake larvae *Merluccius merluccius* (L.), in the Bay of Biscay. *Fish. Res.* 76, 379–391.
- Arneri, E., Morales-Nin, B., 2000. Aspects of the early life history of European hake from the central Adriatic. *Journal of Fish. Biol.* 56, 1368–1380.
- Bailey, K.M., 1982. The early life history of the Pacific hake *Merluccius productus*. *Fish. Bull. U.S.* 80, 589–598.
- Bailey, K.M., Houde, E.D., 1989. Predation of eggs and larvae of marine fishes and the recruitment problem. *Adv. Mar. Biol.* 25, 1–67.
- Belcari, P., Ligas, A., Viva, C., 2006. Age determination and growth of juveniles of the European hake, *Merluccius merluccius* (L., 1758), in the northern Tyrrhenian Sea (NW Mediterranean). *Fish. Res.* 78 (2–3), 211–217.
- Betti, P., (Doctoral Thesis) 2011. Ecomorfología de larvas y prerreclutas de merluza (*Merluccius hubbsi*) como aporte a su conservación. Buenos Aires University, Argentina.
- Betti, P., Machinandiarena, L., Ehrlich, M., 2009. Larval development of hake (*Merluccius hubbsi*). *J. Fish Biol.* 74, 235–249.
- Brown, D.R., Leonarduzzi, E., Machinandiarena, L., 2004. Age, growth and mortality of hake larvae (*Merluccius hubbsi*) in the Patagonian shelf. *Sci Mar.* 68 (2), 273–283.
- Buratti, C.C., Santos, B.A., 2010. Otolith microstructure and pelagic larval duration in two stocks of the Argentine hake *Merluccius hubbsi*. *Fish. Res.* 106, 2–7.
- Butler, J.L., Nishimoto, R.N., 1997. Growth and cohort dynamics of larval Pacific hake (*Merluccius productus*). *CalCOFI Rep.* 38, 63–68.
- Cass-Calay, S., 1997. Relation of mean growth to concentration of prey-sized particles for larvae of Pacific hake (*Merluccius productus*). *CalCOFI Rep.* 38, 69–76.
- Ciechomski, J.D., Weiss, G., 1974. Estudios sobre la alimentación de larvas de la merluza, *Merluccius merluccius hubbsi* y de la anchoita, *Engraulis anchoita* en el mar. *Physis Secc. A Oceanos Org.* 33, 199–208.
- Cordo, H.D., 2006. Evaluación del estado del efectivo sur de 41° S de la merluza (*Merluccius hubbsi*) y estimación de la captura biológicamente aceptable correspondiente al año 2006. *Tech. Rep. INIDEP N° 34*, pp. 27.
- Cousseau, M.B., Perrotta, R.G., 2000. Peces marinos de Argentina. *Biología, distribución, pesca*. INIDEP, Mar del Plata.
- Dower, J.F., Pepin, P., Leggett, W.C., 2002. Using patch studies to link mesoscale patterns of feeding and growth in larval fish to environmental variability. *Fish. Oceanogr.* 11 (4), 219–232.
- Ehrlich, M.D., (Doctoral Thesis) 1998. Los primeros estadios de vida de la merluza *Merluccius hubbsi*, Marini 1933. en el Mar Argentino como aporte al conocimiento de su reclutamiento y estructura poblacional. Buenos Aires University, Argentina.
- Grote, B., Ekau, W., Stenevik, E.K., Clemmesen, C., Verheye, H.M., Lipinski, M.R., Hagen, W., 2012. Characteristics of survivors: growth and nutritional condition of early stages of the hake species *Merluccius paradoxus* and *M. capensis* in the southern Benguela ecosystem. *ICES J. Mar. Sci.* 69 (4), 553–562.
- Houde, E.D., 1987. Fish early life dynamics and recruitment variability. *Am. Fish. Soc. Symp.* 2, 17–29.

- Houde, E.D., 2002. Mortality. In: Fiuman, L.A., Werner, R.G. (Eds.), *Fisheries Science. The Unique Contribution of Early Life Stages*. Blackwell Science Ltd., USA, pp. 64–87.
- Houde, E., 2008. Emerging from Hjort' Shadow. *J. Northw. Atl. Sci.* 41, 53–70.
- Hunter, J.R., 1981. Feeding ecology and predation of marine fish larvae. In: Lasker, R. (Ed.), *Marine Fish Larvae: Morphology, Ecology, and Relation to Fisheries*. Washington Sea Grant Program, Seattle, pp. 34–37.
- Jeffrey, A., Taggart, C.T., 2000. Growth variation and water mass associations of larval silver hake (*Merluccius bilinearis*) on the Scotian Shelf. *Can. J. Fish. Aquat. Sci.* 57, 1728–1738.
- Legget, W.C., Deblois, E., 1994. Recruitment in marine fishes: is it regulated by starvation and predation in the egg and larval stages? *Netherlands J. Sea Res.* 32, 119–134.
- Lorenzo, M.I., 2003. Crecimiento y mortalidad de la merluza en la Zona Común de Pesca Argentino-Uruguaya. *Fronte Marítimo* 19, 37–46.
- Macchi, G.J., Martos, P., Reta, R., Dato, C., 2010. Offshore spawning of the Argentine hake (*Merluccius hubbsi*) Patagonian stock. *PanamJAS* 5 (1), 22–35.
- Macchi, G.J., Pájaro, M., Dato, C., 2007. Spatial variations of the Argentine hake (*Merluccius hubbsi*) spawning shoals in the Patagonian area during a reproductive season. *Rev. Biol. Mar Oceanogr.* 42 (3), 345–356.
- MAGyP, 2012. Informe de Coyuntura Octubre 2012. República Argentina, Ministerio de Agricultura, Ganadería y Pesca., pp. 15. Available at http://www.minagri.gov.ar/site/pesca/pesca_maritima/04=informes/01informes_de_coyuntura/_archivos2012/121101_Informe%20de%20coyuntura%20-%20Noviembre%202012.pdf
- Marteinsdottir, G., Steinarsson, A., 1998. Maternal influence on the size and viability of Iceland cod *Gadus morhua* eggs and larvae. *J. Fish. Biol.* 52, 1241–1258.
- Morales-Nin, B., 1987. Influence of environmental factors on microstructure of otoliths of three demersal fish species caught off Namibia, in: Payne, A.I.L., Gulland, J.A., Brinkd, K.H. (Eds.), *The Benguela and comparable ecosystem*. S. Afr. J. Mar. Sci. 5, 255–262.
- Morales-Nin, B., Bjelland, R.M., Moksness, E., 2005. Otolith microstructure of a hatchery reared European hake (*Merluccius merluccius*). *Fish. Res.* 74, 300–305.
- Moriendo, P., 2002. Alimentación de larvas y juveniles de merluza (*Merluccius hubbsi*) en su área de cría norpatagónica. *Tech. Rep. INIDEP N 47.*, pp. 36.
- Norbis, W., Lorenzo, M.I., Torres, G.J., 1999. Intra-annual growth variations of young-of-the-year hake (*Merluccius hubbsi*) of the Uruguayan continental shelf based on otoliths analysis. *Fish. Res.* 44, 129–137.
- Otxotorena, U., Díez, G., López de Abechuco, E., Santurtún, M., Lucio, P., 2010. Estimation of age and growth of juvenile hake (*Merluccius merluccius* Linnaeus 1758) of the Bay of Biscay and Great Sole by means of the analysis of macro and microstructure of the otoliths. *Fish. Res.* 106, 337–343.
- Palomera, I., Olivar, M.P., Morales-Nin, B., 2005. Larval development and growth of the European hake *Merluccius merluccius* in the northwestern Mediterranean. *Sci Mar.* 69 (2), 251–258.
- Pannella, G., 1971. Fish otoliths: daily growth layers and periodical patterns. *Science* 173, 1124–1127.
- Pepin, P., 1991. Effect of temperature and size on development mortality, and survival rates of the pelagic early life history stages of marine fish. *Can. J. Fish. Aquat. Sci.* 48, 503–518.
- Piñeiro, C., Rey, J., de Pontual, H., García, A., 2008. Growth of Northwest Iberian juvenile hake estimated by combining sagittal and transversal otolith microstructure analyses. *Fish. Res.* 93, 173–178.
- Renzi, M., Irusta, C.G., 2007. Evaluación del estado del efectivo sur de 41° S de la merluza (*Merluccius hubbsi*) y estimación de la captura biológicamente aceptable correspondiente el año 2007. *Tech. Rep. INIDEP N° 47.*, pp. 34.
- Renzi, M., Santos, B., Simonazzi, M., 1999. Edad, crecimiento y estructura poblacional de merluza. In: INIDEP/JICA (Ed.), *Avances en métodos y tecnología aplicados a la investigación pesquera. Seminario final del Proyecto INIDEP-JICA sobre evaluación y monitoreo de recursos pesqueros 1994–1999*. INIDEP, Mar del Plata, pp. 107–110.
- Sabatini, M.E., Martos, P., 2002. Mesozooplankton features in a frontal area off northern Patagonia (Argentina) during spring 1995 and 1998. *Sci. Mar.* 66, 215–232.
- Sánchez, R.P., (Doctoral Thesis) 1995. Patrones de distribución espacio-temporales de los estadios embrionarios y larvales de *Engraulis anchoita* (Hubbs and Marini, 1935) a micro y macroescala. Su relación con la supervivencia y el reclutamiento. Buenos Aires University, Argentina.
- Santos, B.A., Buratti, C.C., Renzi, M.A., 2005. Estimación del crecimiento diario del grupo 0 de la merluza argentina, *Merluccius hubbsi*, al sur de 41° S. *Tech. Rep. INIDEP N° 124.*, pp. 10.
- Santos, B.A., Ramírez, F.C., 1995. Distribución y abundancia de copépodos en el sistema frontal de Península Valdés durante florecimientos fitoplanctónicos. *Thalassas* 11, 133–142.
- Santos, B.A., Renzi, M.A., 2006. Growth in the 0-group of Argentine hake *Merluccius hubbsi* from the Argentine-Uruguayan Common Fishing Zone. *Rev. Invest. Des. Pesq.* 18, 45–55.
- Steves, B.P., Cowen, R.K., 2000. Settlement, growth, and movement of silver hake *Merluccius bilinearis* in nursery habitat on New York Bight continental shelf. *Mar. Ecol. Prog. Ser.* 196, 279–290.
- Temperoni, B., Viñas, M.D., 2013. Food and feeding of Argentine hake (*Merluccius hubbsi*) larvae in the Patagonian nursery ground. *Fish. Res.* 148, 47–55.
- Vaz-dos-Santos, A.M., Rossi-Wongtschowski, C.L.D.B., 2007. Age and growth of the Argentine hake *Merluccius hubbsi* Marini, 1933 in the Brazilian South-Southeast Region during 1996–2001. *Neotrop Ichthyol.* 5 (3), 375–386.
- Viñas, M.D., Ramírez, F.C., Santos, B.A., Pérez Seijas, G.M., 1992. Zooplankton distribuido en el área de desove y crianza norpatagónica de la merluza (*Merluccius hubbsi*). *Fronte Marítimo* 11, 105–113.
- Viñas, M.D., Santos, B., 2000. First-feeding of hake (*Merluccius hubbsi*) larvae and prey availability in the North Patagonian spawning area – Comparison with anchovy. *Arch. Fish. Mar. Res.* 48 (3), 213–225.
- Watanabe, Y., Kuroki, T., 1997. Asymptotic growth trajectories of larval sardine (*Sardinops melanostictus*) in the coastal waters off western Japan. *Mar. Biol.* 127, 369–378.
- Watanabe, Y., Nakamura, M., 1998. Growth trajectory of the larval Japanese sardine *Sardinops melanostictus*, transported into the Pacific coastal waters off central Japan. *Fish. Bull.* 96, 900–907.
- Zar, J.H., 1996. *Biostatistical Analysis*. New Jersey, Prentice-Hall/EEUU, 662 pp.