



Abundance, distribution and population dynamics of the short fin squid *Illex argentinus* in Southeastern and Southern Brazil



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ABSTRACT

Surveys and commercial fishing landings data of the short fin squid *Illex argentinus* were analyzed to address three related issues: the seasonal and spatial pattern of abundance; seasonal and regional variation of growth and maturation; and the interannual variation in the size at maturity and growth from Southern Brazil (SB, 28°–34°S) and Southeastern Brazil (SEB, 23°–28°S). Overall, 2455 specimens were examined for maturity and 337 specimens had their daily increments in the statoliths recorded. Aged specimens from SB ranged from 51 to 275 days, 55 to 354 mm ML and 2.4 to 1098 g. It was observed that (1) *I. argentinus* is a common component of the nekton on all the outer shelf and slope and appears to be more abundant south of Santa Marta Grande Cape, where the largest catches were obtained in the autumn survey. (2) Spawning and hatching occurs year round along all the region. (3) In SB growth was faster and maturity was attained at larger sizes in the cold season (June to November) and no differences between seasons were observed in the mean age of mature specimens. (4) In 2001/2002, growth was faster, mature squids were in mean 159 days old and most were under 210 days, in 2007/2008, growth was slower, mean mature age was 191 days and most were 250 days. (5) In SEB, maturity was attained at smaller sizes and it is likely that maturity is attained at a lower age and the lifespan is shorter. In the northern range of its distribution *I. argentinus* is characterized by a decreasing adult size toward lower latitudes, a short and variable lifespan with hatching and spawning in all seasons.

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1. Introduction

Ommastrephid squids sustain the most important cephalopods fisheries in the world, among which *Illex argentinus*, together with *Todarodes pacificus* were the main species landed in the last decade (FAO, 2012).

I. argentinus is distributed along more than 4000 km of the eastern coast of South America from Rio de Janeiro (22°S) to southern Argentina (52°S) (Jereb and Roper, 2010). Most catches occur in the southern range (35°S–52°S) of the species, along the outer shelf and slope under the influence of the cold Patagonian and Malvinas/Falkland Current responsible for the high productivity of the region (Brandini et al., 2000; Matano et al., 2010). Since the full development of fishery in that region in 1987, recorded landings fluctuated between 0.18 million tons and 1.15 million tons. Because of its ecological and fishing importance, the species in

its southern range has been intensely studied since exploratory fishing in the 1970'. Studies on its life cycle and migrations identified several spatial and seasonal spawning groups south of the Malvinas (Falklands) Brazil confluence (52°S–38°S) (Hatanaka et al., 1985; Brunetti, 1988; Arkhipkin, 1990, 1993; Haimovici and Perez, 1990; Laptikhovskiy and Nigmatullin, 1992; Crespi-Abril and Barón, 2012). Early studies, summarized in Haimovici et al. (1998), were based in the assumption of a one year long life cycle, supported by aging studies by counting the daily increments in the statoliths of specimens from Patagonian waters (Arkhipkin, 1990, 1993; Rodhouse and Hatfield, 1990; Uozumi and Shiba, 1993).

In its northern range of the species (22°–35°S), in the early 2000' a small bottom trawl fishery developed (Perez et al., 2009) with recorded landings annual fluctuating between 40 and 2600 t. Despite being far less important than the Patagonian fishery for fishing in the less productive waters of the warm Brazil Current (Castro and Miranda, 1998; Odebrecht and Castello, 2001; Gaeta and Brandini, 2006), *I. argentinus* is an important component of the trophic webs and the pelagial nekton of the shelf break and upper slope of Southern Brazil (Santos and Haimovici, 1998; Madureira et al., 2005a). Early research on distribution, feeding,

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trophic relations and reproduction of *I. argentinus* in its northern range was based data obtained in bottom trawl and plankton surveys (Haimovici and Perez, 1990, 1991; Haimovici et al., 1995; Santos and Haimovici, 1997, 1998, 2000). Recent studies have showed that *I. argentinus*, in the northern range of its distribution, has a lifespan shorter than one year (Schwarz and Perez, 2010, 2012; Baily and Haimovici, 2012).

The relationship between the spawning stocks in the southern and northern ranges of the distribution of *I. argentinus* is still nor clearly established. Several hypotheses have been raised ranging from “no connection” (Brunetti et al., 1998), to favoring the hypothesis that winter and spring spawners in Southern Brazil are a continuity of the BNPS (Arkhipkin, 1993; Santos and Haimovici, 1997; Perez et al., 2009; Schroeder and Perez, 2010).

To contribute to the understanding of the distribution and population dynamics of the short fin squid *I. argentinus* in its northern range, data obtained in two surveys in 2001–2002 along South-eastern and Southern Brazil and commercial fishing landings in Rio Grande in 2007–2008 were analyzed to address three related issues: the seasonal pattern of distribution and abundance, the seasonal and latitudinal variation of growth and maturation and the interannual variation in the size at maturity and growth.

2. Materials and methods

2.1. Study area

The area under study was situated between 100 and 600 m isobaths. It was 90 km wide along Cabo Frio (23°S), enlarged to a maximum of 130 km in the Southern Brazilian Bight (26°S) and narrowed to only 60 km along Chui (34°40'S) which totals 152,354 km² (Fig. 1). Bottom sediments on the outer shelf are mostly mud, rich in silts and clay, although large patches with biodebitric sediments and sand were found near the shelf break and along Cabo Frio; on the slope, muddy sediments predominate (AFigueiredo and Madureira, 2004).

The most remarkable hydrographic characteristics on the shelf are the seasonal variation of the water temperature and the water column stratification, which is strong in summer and weak, or non-existent, in winter and the southward flow of the Brazil Current meandering along upper slope (Castro and Miranda, 1998). Increased productivity on the shelf and upper slope are associated with three main processes: (1) the lateral intrusions of the mixture of Subantarctic Surface Waters on the shelf and the La Plata river runoff flow northward in the cold season, reaching Southern and, occasionally, Southeastern Brazil (Matano et al., 2010); (2) the ascent and upwelling of the South Atlantic Central Waters (SACW) that enhances subsurface productivity, mostly in the warm season from Santa Marta Grande to Cabo Frio (Matsuura, 1986; Gaeta and Brandini, 2006); and (3) the cyclonic eddies of the Brazil Current that enhance productivity on the outer shelf along the Southern Brazilian Bight (SBB). Bottom water temperatures of SACW beneath the Brazil Current range from 10° to 16° C between 100 and 400 m and a mixture of SACW and Antarctic Intermediate Waters between 400 and 600 m range from 4° C to 10° C (Castro and Miranda, 1998).

2.2. Survey sampling

The surveys were performed almost simultaneously by two research trawlers: R/V Atlântico Sul, between 28°S and 34°35'S and the R/V Soloncy Moura, between 23°S and 28°S in the 100 to 600 m depth range. Both boats were geared with Engel Star Ballon trawl nets with 439 meshes of 160 mm stretched between opposite knots in the mouth and 27 mm in the codend. The ground rope had a 40.4 m “rockhopper” of large rubber discs of 300 mm

in its center; they narrow to 200, 130 and 75 mm in the wings. The otter doors were rectangular Engel Hydro of 550 kg, connected to the wings by 5-m-long lengthening bridles and to the winch cables with 50-m bridles (Haimovici et al., 2008). The main scope of the surveys was to study the distribution and abundance of the whole fish fauna vulnerable to bottom trawls (Haimovici et al., 2008, 2009). For this reason, a systematic sampling design was used to cover the whole study area (Saville, 1977; Gunderson, 1993). Fishing stations were distributed along 18 profiles perpendicular to the coastline, approximately 55 miles apart from each other, in depth ranges of 100–149, 150–199, 200–299, 300–399 and 400–600 m (Fig. 1). Combining latitudes and depth ranges, 20 strata in which 4 to 6 fishing hauls were positioned were defined. The surface of each stratum was graphically calculated with ArcView 3.2 Software, integrating the polygons determined by the latitudinal transects and isobaths obtained from the GEBCO (General Bathymetric Chart of the Oceans) database (<http://www.gebco.net>) and complemented with data from acoustic surveys of the REVIZEE Program (Ferreira et al., 2005).

Overall, 224 effective fishing hauls were performed: 113 hauls in winter and spring 2001 and spring of 2002 and 111 in autumn of 2002. For each haul, the total number, total weight and mantle length composition of *I. argentinus* were recorded and samples were preserved for maturity and aging studies (Haimovici et al., 2008),

2.3. Vulnerable density and biomass estimates

Densities were calculated as catch per unit of areas (CPUA) in kg km⁻². The swept areas were estimated by multiplying the distances between the beginning and the end of the hauls recorded by the satellite positioning system and the width of the swept area calculated as 18.18 m or 45% of the length of the groundrope (Alverson and Pereyra, 1969). Geometry and net gearing, towing speed and fish behavior can affect catchability (q); since none of these effects could be measured, a value of 1 was attributed to q , as suggested by Alverson and Pereyra (1969).

The mean densities (kg km⁻²) of *I. argentinus* (D_i) in each survey were calculated by weighting the mean densities in each stratum by the fraction of the total area of each stratum A_e (Eq. (1)). The variances of the mean density in each stratum $\bar{S}_{D_i}^2$ were calculated by weighing the variances in each stratum $S_{D_{ie}}$ divided by the number of samples and multiplied by the square of the fraction of the area of each stratum (Eq. (2)).

$$D_i = \sum_e D_{ie} \cdot \left(\frac{A_e}{A} \right) \quad (1)$$

$$\bar{S}_{D_i}^2 = \sum_e \frac{S_{D_{ie}}^2}{n_e} \cdot \left(\frac{A_e}{A} \right)^2 \quad (2)$$

The vulnerable biomass of *I. argentinus* (B_i) in each survey was calculated as the sum of the products of the densities for the areas of all strata (Eq. (3)) and the total variances were calculated by multiplying the variances in each stratum by the respective squared areas (Eq. (4)).

$$B_i = \sum_1^e A_e \cdot D_{i,e} \quad (3)$$

$$varB_i = \sum_1^e A_e^2 \cdot \bar{S}_{D_{ie}}^2 \quad (4)$$

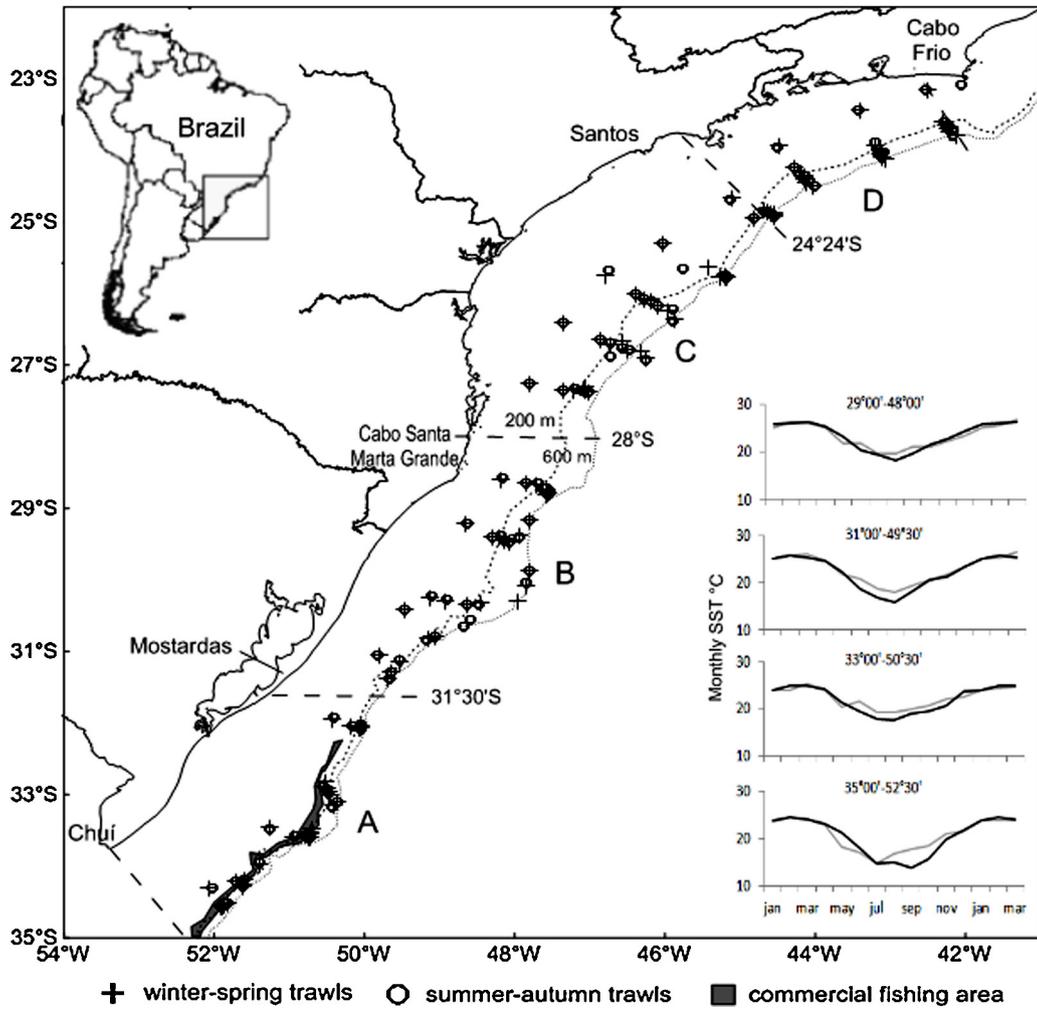


Fig. 1. Positions of the fishing stations in the bottom trawl surveys (2001/2002) and commercial fishing areas (2007/2008). Histograms represent the annual cycle of the monthly average sea surface temperature (SST) on the shelf break between January 2001 and March 2002 (gray line) and between January 2007 and March 2008 (black line).

The 90% confidence intervals of the vulnerable biomass estimates were calculated based on Student's "t" distribution for $\alpha = 0.1$ and ν degrees of freedom (Zar, 1984) according to Eqs. (5) and (6).

$$IC_{\alpha\%} = B_i \pm t_{\alpha, \nu} \cdot \sqrt{S_{D_{ie}}^2} \quad (5)$$

$$\nu = \sum_e (n_e - 1) \quad (6)$$

2.4. Sexual maturation

In the laboratory, specimens from different hauls were sexed and measured for mantle length (ML) and total weight (WT). Females had their nidamental gland length (mm) measured and ovaries and oviducts examined and males the hectocotylized arm and its modified portion were measured and spermatophoric sac examined. The macroscopic maturity stage of each specimen was recorded following the scale proposed by Brunetti (1990). Males and females were classified as immature (stages 1–2), maturing (stages 3–4) and functionally mature at stages 5 and higher (functionally mature *sensu* Arkhipkin (1992)). As an additional criteria, following Santos and Haimovici (1997), females with nidamental glands over 40% of the mantle length and males with hectocotylus over 45–50% of the length of the hectocotylized arm were considered functionally mature.

For the estimation of the mean mantle length at maturity (ML_{50}), the total number of individuals (n_i) and the total number of sexually mature individuals (y_i) were calculated in length classes of 10 mm interval for each sex, season and time period. If θ_i denotes the probability of an individual of the i -th length class being mature, y_i follows a binomial distribution $Bin(n_i, \theta_i)$. Data were fitted to a logistic model, defined by a *logit* link function that transforms θ_i , restrict to the range [0,1] in the binomial distribution, in m defined between $(-\infty, +\infty)$ (Kinas and Andrade, 2010). The logistic model was defined as follows:

$$m_i = g(\theta_i) = \log \left(\frac{\theta_i}{1 - \theta_i} \right)$$

$$m_i = \beta_0 + \beta_1 \cdot x_i$$

From this model the ML_{50} were defined as: $ML_{50} = -\beta_0/\beta_1$.

To compare the estimates of ML_{50} throughout years and seasons, the posterior distribution $p(\beta_0, \beta_1 | D)$ where $D = \{(y_i, n_i, x_i); i = 1, \dots, k\}$, was obtained via the stochastic process Monte Carlo Markov Chain (MCMC). Normal distribution with mean 0 and large variance (1000) were used as priori distribution. It was simulated 59,000 values of which the first 50,000 were discarded as burn-in. Every third value of the remaining 9000 was retained, resulting in a final sample of 3000 in the posterior distribution $p(\beta_0, \beta_1 | D)$. The posterior distribution of each estimated ML_{50} provides an easy and

clear way to compare the results among data sets. The MCMC was performed with OpenBUGS using the libraries R2WinBUGS (Sturtz et al., 2005) and BRugs (Thomas et al., 2006).

2.5. Aging and growth

Statoliths were extracted and stored in vials in 96° ethanol. Statoliths preparation for aging was described by Baily and Haimovici (2012) who followed the procedures described by Schwarz and Perez (2010). Statoliths from Southern Brazil (28°–34°S) extracted from squids that were frozen shortly after catch on board in the research surveys were suitable for aging after 10 years of storage. Statoliths from squids frozen on board in the surveys along Southeastern Brazil, that suffered accidental temperature raises in the following year, before extraction and storage in ethanol, were not suitable for reading.

On the mounted statoliths, the number of daily increments was counted in the postnuclear zone (PNZ) between the hatching check and the beginning of the dark zone and from this point to the edge of the statoliths. Each pair of dark and clear bands in the microstructure of the statoliths of *I. argentinus* were considered daily increment (DI), following the same criteria used in previous studies (Arkhipkin, 1993, 2003; Schwarz and Perez, 2010, 2012; Baily and Haimovici, 2012). The coefficient of variation (CV) between two successive readings was under 6%, similar to the CV reported in previous studies and considered moderate (Campana, 2001).

The daily periodicity of marks formation in the dark and peripheral zones of the statoliths of *I. argentinus* validated by Uozumi and Shiba (1993) by aging squids of the same stock sequentially along several months. Sakai et al. (2004) experimentally identified the hatching mark and validated the daily formation of a dark and a clear band on the statoliths of young paralarvae. Others, including Jackson et al. (2003) for adult *Nototodarus gouldi*, validated aging with chemical markers in tank experiments.

The hatching date of each individual was back calculated by decreasing the number of daily increments counted on the statoliths, from the date of capture in the research surveys, or the mean between the beginning and the end of the commercial fishing trips.

Specimens were grouped according to their date of capture because most sampled specimens were maturing and mature non-spawned squids at sizes at which absolute growth in length is more intensely influenced by the feeding conditions in the previous months (Jackson et al., 2003).

There are evidences that, when the whole lifespan is sampled, asymptotic functions, such as the logistic or Gompertz models, better describe the growth of *Illex argentinus* (Arkhipkin and Roa-Ureta, 2005; Schwarz and Perez, 2010). However, when early juveniles and large spawners are excluded, a linear model does not provide worse fits (Arkhipkin, 2004). Assuming a linear growth, for comparisons among sexes, seasons and periods, individual mean daily mantle length increments (MDML), from juveniles to adults, were calculated for each aged specimen as the quotient of the ML decreased 9 mm and the number of daily increments minus the increments in the postnuclear zone, as

$$MDML = \frac{ML - 9}{DI - PNZ}$$

The value of 9 mm as the ML at the end of the paralarval phase was chosen because Vidal (1994) showed that the mean ML at which *I. argentinus* from Southern Brazil becomes juvenile, i.e., with complete formation of the tentacles, was between 8 and 10 mm.

For the comparative analysis among seasons and regions, the winter-spring 2001 and late autumn 2002 research survey and commercial fishing from late autumn to early spring (June to November 2007) were considered the “cold season”. Those from

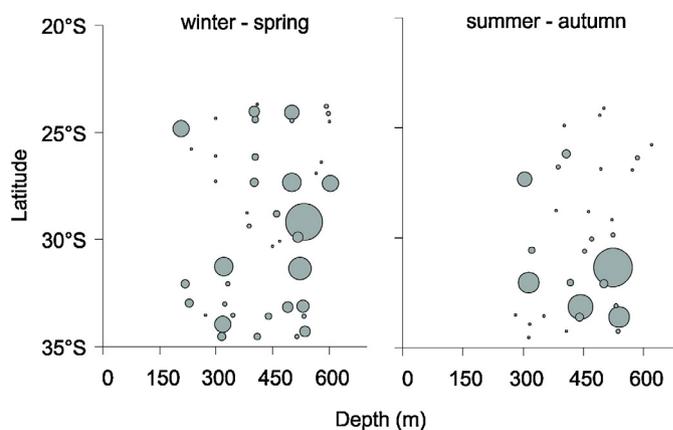


Fig. 2. Densities of *I. argentinus* in kg/km² per latitude and depth in the bottom trawl surveys in the cold season of 2001/2002 and the warm season of 2002 along southern and southeastern Brazil.

the late summer survey in 2002 and commercial samples from late spring to mid-autumn (December 2007 to May 2008) were considered the “warm season” samples. ANOVA tests were used for comparisons among regressions (Zar, 1984).

2.6. Sea surface temperatures

Monthly average sea surface temperatures (SST, °C) along Southern Brazil were obtained from the Physical Oceanography Distributed Active Archive Center (PODAAC, 2012). These means were calculated by the “optimum interpolation method” of satellite data and *in situ* measurements (ship and buoy) to generate high resolution sea surface climatology (Reynolds and Smith, 1995). The sea surface temperatures (SST) on the shelf break and upper slope off Southern Brazil from January 2001 to March 2002 and from January 2007 and March 2008, in four latitudes along the slope, are plotted in Fig. 1.

3. Results

3.1. Distribution and abundance

I. argentinus occurred in 179 (79.9%) of the hauls in all latitudes, depth ranges and in both seasons (Fig. 2). Total vulnerable biomass and numerical abundance was estimated in 11.283 t and 113.3 millions (±52%) in the cold season survey in 2001. In the autumn survey, it was the most abundant species in the catches with 41.658 t and 476.9 millions (±92%) (Haimovici et al., 2008). The wide confidence intervals were due to large catches in only a few hauls, most of which were at bottom temperatures ranging from 6 to 10 °C (Fig. 3).

The vulnerable biomass and number at different sizes in both seasonal surveys in different latitudinal sectors and depth ranges are shown in Figs. 4 and 5. In the cold season survey, the highest biomasses were in the B sector, south of Santa Marta Grande, between 300 and 550 m depth, composed of specimens ranging from 180 to 335 mm ML in a bimodal distribution with peaks at 260 and 320 mm. Immature squids under 120 mm ML were observed in all sectors mostly on the outer shelf but also near the shelf break (200–300 m) and upper slope (300–600). In the warm season cruise, a large number of immature specimens smaller than 120 mm were observed on the outer shelf, mostly between Chui and Santos (A to C). Mid-sized squids were more abundant in the B sector and the ones larger than 180 mm were very abundant between Chui and Santa Marta but also occurred in Sector C near Cabo Frio on the

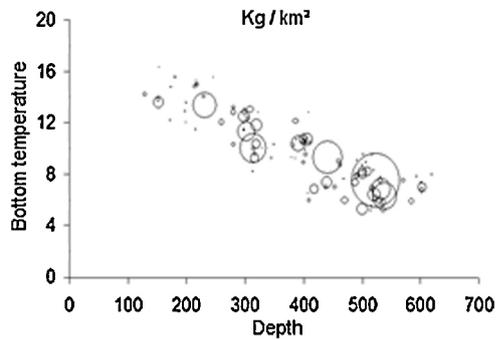


Fig. 3. Density (Kg/km^2) of *I. argentinus* by depth and bottom temperature in the bottom trawls in 2001 and in 2002 along southern and southeastern Brazil.

upper slope. No large specimens, over 300 mm, were captured in the autumn survey.

3.2. Maturation

Overall, 2035 specimens ranging from 30 to 350 mm ML and 1.4 to 910 g TW were sampled for size, sex and maturity from the surveys in 2001–2002 and 420 specimens from 110 to 350 mm ML from commercial fishing in 2007–2008 (Fig. 6).

The ML_{50} and the credibility intervals, at which male and female *I. argentinus* attained functional maturity were calculated by sex, region, season and annual period, are shown in Table 1 and the corresponding logistic curves were plotted in Fig. 7. When compared between seasons, ML_{50} from Southern Brazil in both annual periods was larger in the cold season for both females and males. In Southeastern Brazil in 2001–2002, no significant differences in ML_{50} were observed for females between seasons but males were larger in the warm season. In the Southern region, when compared between annual periods, in 2001–2002 ML_{50} was larger for females in both seasons and for males in the warm season, but did not differ significantly in the cold season. When compared between regions in the 2001–2002 surveys, ML_{50} of females was larger in both seasons in Southern region while males were larger in the warm season in the Southern region and in the cold season in the Southeastern region.

Mantle length of functionally mature specimens ranged from 120 to 350 mm (Fig. 6). The mean mantle length and total weight mature male and females were calculated for regions, periods and seasons (Table 2). Factorial ANOVA showed high significant differences ($p < 0.001$) among all factors. In Southern Brazil, mean ML of mature males and females in both periods were significantly higher ($p < 0.0001$) in the cold season and differences in weight ranged from 67 to 70% for males and from 55 to 78% for females.

When periods were compared, both males and females were consistently larger in 2001–2002 than in 2007–2008 in the warm season ($p_{\text{♀}} = 0.0139$; $p_{\text{♂}} = 0.0001$) but only males, in the cold season ($p_{\text{♂}} = 0.0030$). No significant ML difference was observed for females in the cold season among periods ($p_{\text{♀}} = 0.6928$). In Southern Brazil, differences between periods were smaller than between seasons (Table 2). In Southeastern Brazil mature females were larger in the cold season ($p < 0.0001$) and males were larger in the warm season ($p = 0.033$) (Table 2).

3.3. Ages and growth

Daily increments were counted in statoliths of 337 specimens (Fig. 8). The number of total daily increments ranged from 51 to 275 days in the 2001–2002 surveys, except two all aged specimens were under 210 days old and, in the commercial catches in 2007–2008, all except one were less than 250 days old. The number of daily increments in the postnuclear zone ranged from 20 to 43; the mean was 29.2 (Fig. 8). No significant difference was observed between sexes ($p = 0.386$), seasons ($p = 0.469$) or periods ($p = 0.089$).

Mean ages of mature specimens differ neither between sexes ($F = 2.35$, $p = 0.1270$) nor seasons ($F = 0.709$; $p = 0.400$) but between periods ($F = 44.49$; $p < 0.0001$). It was 159.7 days, or approximately 5½ months, in 2001–2002 and 191.3, or 6½ months, in 2007–2008.

The mean daily mantle length increment (MDML) per sex, region and season and its respective 95% confidence interval are shown in Fig. 9. MDML were significantly higher for both seasons and sexes in the 2001–2002 periods characterizing faster growth by comparison with 2007–2008. Higher MDLD were observed in both periods for both sexes in the cold season, however differences were larger and significant only in 2007–2008 (Table 3).

3.4. Hatching seasonality

In Southern Brazil, back-calculated hatching dates were observed year round from the monthly commercial samplings in 2007–2008. Back-calculated hatching dates in 2001/2002 show a gap of around three month from June to August 2001 corresponding to the difference between the 10-month lag between the end of the winter cruise in 2001 and the beginning of the late summer cruise in 2002, and the larger estimated ages (Fig. 10). No back-calculated hatching data are available for the Southeastern region, however the presence of mature specimens was observed in September, October 2001 and February, April and June 2002 along the cruises (Haimovici et al., 2008) leads to conclude that *I. argentinus* also hatch year round in all the northern range of its distribution.

The integration of the results on distribution aging and maturation led to the following conclusions: (1) *I. argentinus* is a common component of the nekton on the outer shelf and slope of Brazil

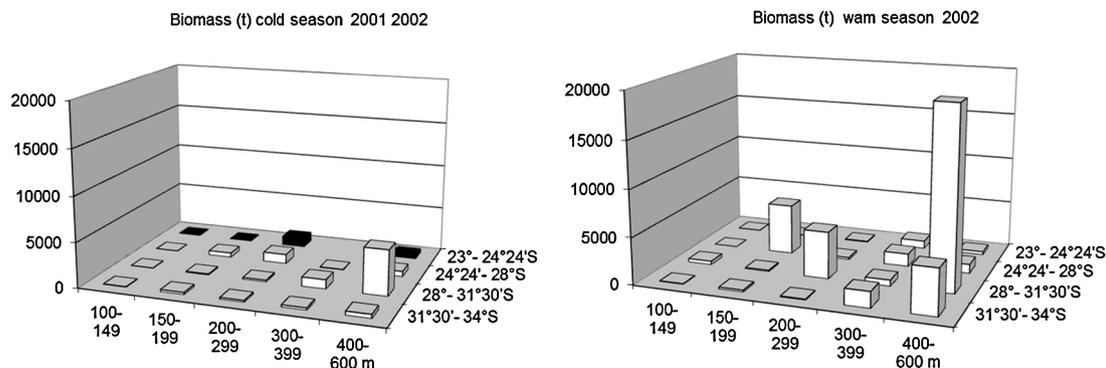


Fig. 4. Estimated vulnerable biomass (t) of *I. argentinus* per season in latitudinal and depth strata (columns: in black June 2002) in the bottom trawl surveys in 2001/2002 along Southern and Southeastern Brazil.

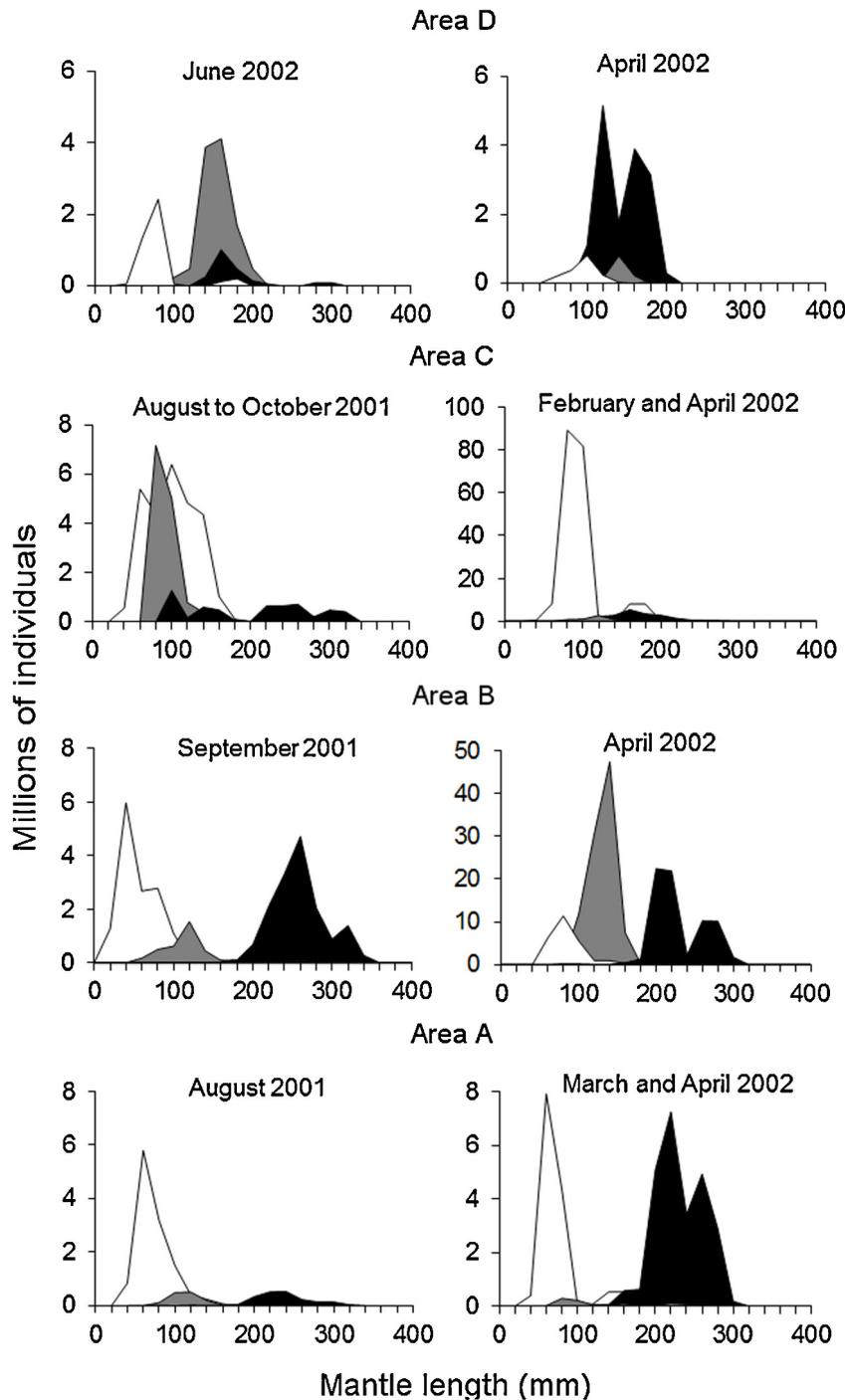


Fig. 5. ML composition of the of *I. argentinus* in the bottom trawl surveys along southern and southeastern Brazil in the cold (left) and warm (right) seasons in four latitudinal sectors (as in Fig. 1). In millions of specimens and three depth ranges: 100–199 m: white, 200–299 m: gray, >300 m: black).

south of 23°S, it appears to be more abundant in the region north and south of Santa Marta Grande Cape in autumn and south of Santa Marta Cape in winter. (2) Spawning and hatching occurs year round all along Southern and Southeastern Brazil. (3) In Southern Brazil: growth was faster and maturity was attained at larger sizes in the cold season for both sexes, but no differences between seasons were observed in the mean age of functionally mature specimens. (4) There is a large inter-annual variation in growth and lifespan. In Southern Brazil in 2001/2002, growth was faster, maturity was attained at larger sizes and lower ages and maximum age was lower: 159 and 210 days, respectively, by comparison with 2007/2008, when growth was slower, maturity was delayed and

maximum age was higher: 191 and 250 days. (5) In Southeastern Brazil, maturity was attained at smaller sizes.

4. Discussion

4.1. Distribution and abundance

I. argentinus is a common component of the nekton of the outer shelf and slope of Brazil south of 23°S. Several evidences point to the conclusion that it is more abundant north and south of Santa Marta Grande Cape. The first report of concentrations of *I. argentinus* (identified as *Loligo* sp) were from exploratory fishing in 1973

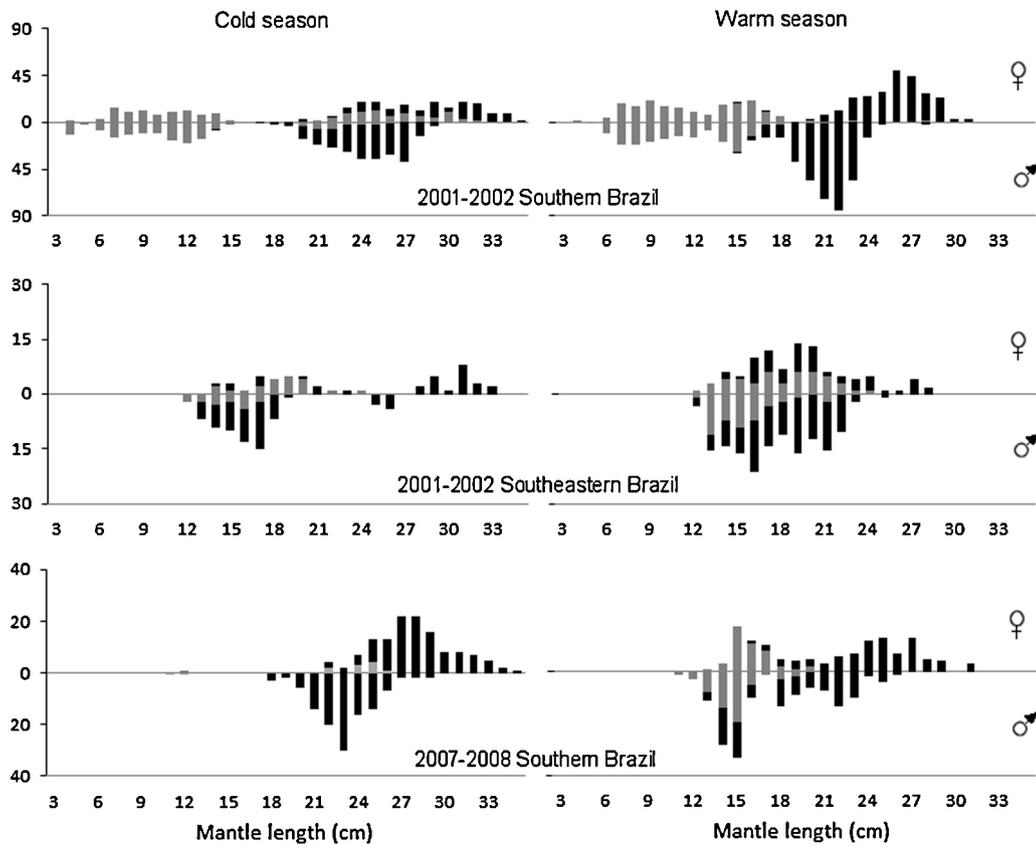


Fig. 6. Numbers of functionally mature (black) and immature and maturing (gray) females and males of *I. argentinus* sampled in the bottom trawl surveys (2001/2002) and commercial fishing areas (2007/2008) in the cold the warm season of 2002 along southern and southeastern Brazil.

Table 1

Mean mantle length at maturity (ML_{50}) of *I. argentinus* by sex, period, regions in the warm season from December to May and the cold season from June to November. (β_1 : angular coefficient, CrI: credibility interval).

| Period | Season | Parameters | Females | | | DIC | Males | | | DIC |
|-------------------------------|--------|------------|---------|---------|----------|------|-------|---------|----------|------|
| | | | Mean | CrI2.5% | CrI97.5% | | Mean | CrI2.5% | CrI97.5% | |
| Southeastern Brazil 2001/2002 | Cold | β_1 | 0.03 | 0.02 | 0.05 | 39.2 | 0.05 | 0.02 | 0.08 | 23.3 |
| | | ML_{50} | 204.1 | 179.4 | 230.7 | | 122.2 | 79.4 | 141.2 | |
| | Warm | β_1 | 0.02 | 0.01 | 0.04 | 48.0 | 0.05 | 0.03 | 0.07 | 37.4 |
| | | ML_{50} | 181.7 | 152.7 | 206.6 | | 144.4 | 133.2 | 153.8 | |
| Southern Brazil 2001/2002 | Cold | β_1 | 0.03 | 0.02 | 0.04 | 68.9 | 0.05 | 0.04 | 0.06 | 50.1 |
| | | ML_{50} | 261.8 | 249.9 | 273.4 | | 185.2 | 175.7 | 193.8 | |
| | Warm | β_1 | 0.08 | 0.06 | 0.10 | 43.6 | 0.16 | 0.13 | 0.20 | 30.2 |
| | | ML_{50} | 198.6 | 190.9 | 205.9 | | 166.2 | 162.6 | 169.8 | |
| Southern Brazil 2007/2008 | Cold | β_1 | 0.05 | 0.03 | 0.08 | 36.8 | 0.06 | 0.04 | 0.10 | 25.1 |
| | | ML_{50} | 225.3 | 201.4 | 242.0 | | 178.6 | 157.4 | 193.4 | |
| | Warm | β_1 | 0.07 | 0.05 | 0.09 | 33.7 | 0.05 | 0.04 | 0.07 | 35.5 |
| | | ML_{50} | 186.5 | 177.3 | 195.8 | | 151.3 | 143.1 | 159.0 | |

Table 2

Mean mantle length (ML), total weight (TW) of mature *I. argentinus* caught in the two regions and sampling periods (2001/2002 and 2007/2008) in the warm season from December to May and the cold season from June to November.

| Sex and season | Southern Brazil | | | Southeastern Brazil | | | Southern Brazil | | |
|----------------|-----------------|-----------------|-----|---------------------|------------------------------|-----|-----------------|-----------------|-----|
| | ML | 2001/2002 TW | n | ML | 2001/2002 TW ^a | n | ML | 2007/2008 TW | n |
| Males | | | | | | | | | |
| Warm | 214.7 | 215.1 | 358 | 185.1 | 138.1 | 107 | 199.5 | 195.9 | 124 |
| Cold | 246.0 | 335.2 | 236 | 174.4 | 110.4 | 56 | 236.5 | 327.5 | 87 |
| Females | | | | | | | | | |
| Warm | 262.2 | 307.2 | 251 | 204.8 | 160.7 | 53 | 252.2 | 288.9 | 122 |
| Cold | 292.3 | 478.6 | 114 | 267.4 | 344.8 | 31 | 290.4 | 504.5 | 89 |

^a Very small sample.

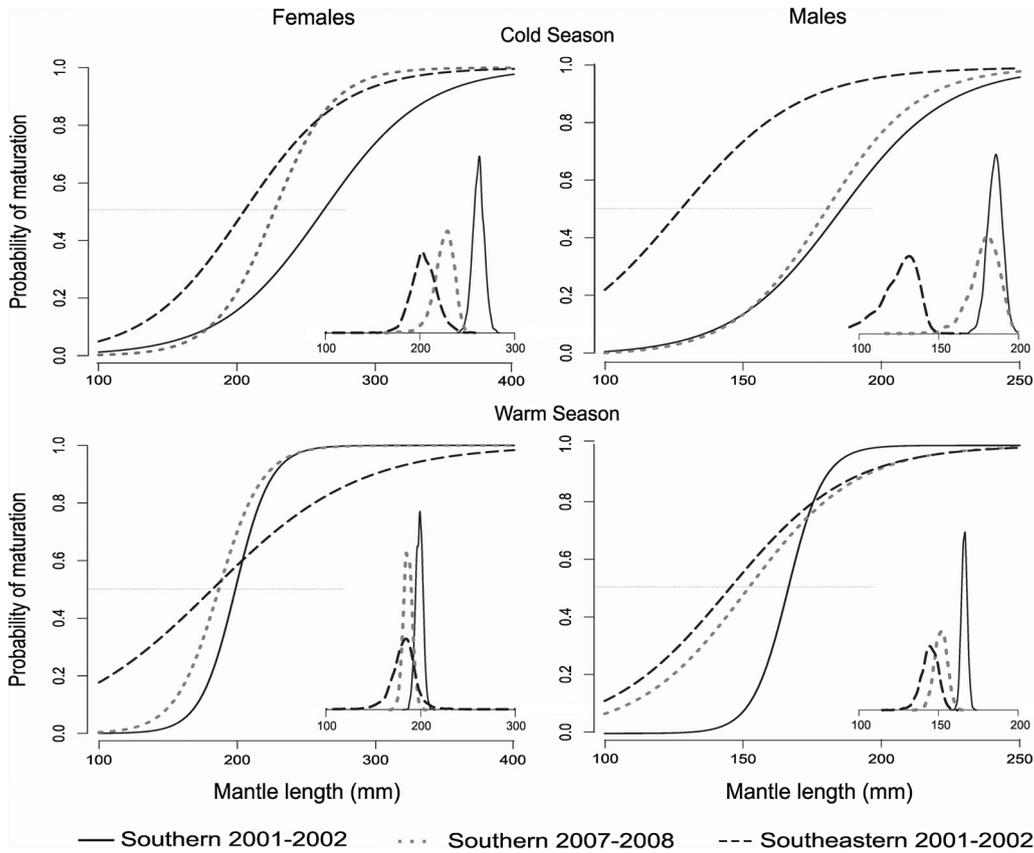


Fig. 7. Mantle length maturity ogives and the posterior distribution of the ML_{50} of females and males of *I. argentinus* by season for the Southern region in the 2001–2002 period (black continuous line), for the Southern region in the 2007/2008 period (gray dotted line) and for the Southeastern in the 2001/2002 period (black dashed line). Light-gray horizontal lines indicate the 50% probability of maturation on the ogives.

followed by experimental fishing from May to July 1976 at 250 to 350 m depth and between 28°S and 29°30' (Yesaki and Rahn, 1974 and Rahn and Santos, 1978, in Haimovici, 2007). In the 1980', paralarvae of *Illex* were found to be abundant in bongo net samples

(Haimovici et al., 1995) and juveniles were caught on the outer shelf and upper slope and large specimens up to 500 m deep in bottom trawl surveys between 30° and 34°S (Haimovici and Perez, 1991; Haimovici et al., 1994). Following this first observations, since

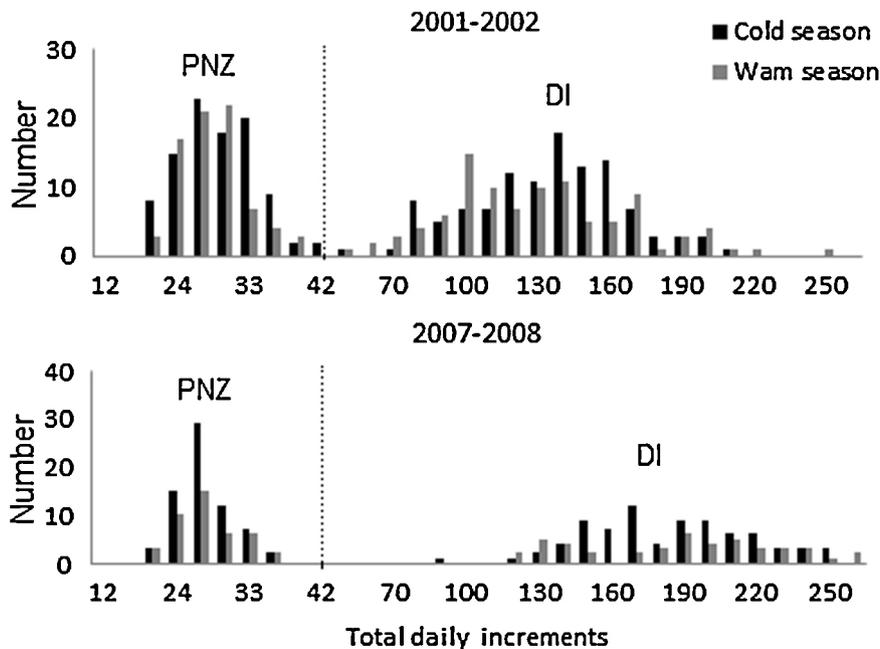


Fig. 8. Number daily increments in the postnuclear zone (PNZ, left) of total number at capture (DI, right) and in statoliths. of *I. argentinus* sampled in Southern Brazil in 2001/2002 and 2007/2008 ($n = 375$).

Table 3

Mean mantle length daily increment (MLDI) of maturing juveniles and adult *I. argentinus* caught in the two sampling periods (2001/2002 and 2007/2008) in the warm season from December to May and the cold season from June to November (SD: standard deviation, IC: confidence interval, N: number of specimens).

| Period | Season | Sex | Mean MLDI | SD | 95% IC | N | |
|-----------|-------------|---------|-----------|-------|--------|------|----|
| 2001–2002 | Cold season | Males | 1.71 | 0.059 | 1.59 | 1.83 | 51 |
| | | Females | 1.93 | 0.074 | 1.78 | 2.08 | 48 |
| | Warm season | Males | 1.60 | 0.056 | 1.49 | 1.71 | 43 |
| | | Females | 1.83 | 0.065 | 1.69 | 1.96 | 39 |
| 2007–2008 | Cold season | Males | 1.48 | 0.039 | 1.40 | 1.56 | 39 |
| | | Females | 1.69 | 0.046 | 1.60 | 1.78 | 40 |
| | Warm season | Males | 1.12 | 0.048 | 1.02 | 1.22 | 23 |
| | | Females | 1.34 | 0.038 | 1.26 | 1.42 | 22 |

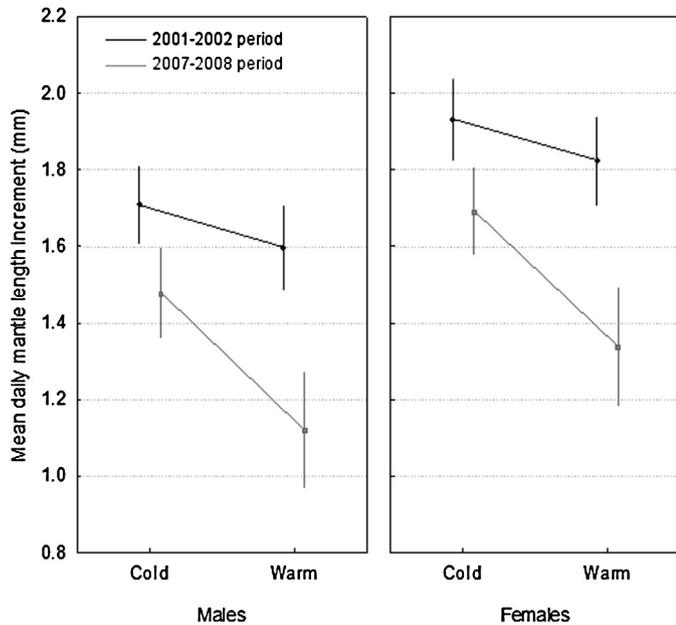


Fig. 9. Mean mantle length daily increment (MLDI) of mature juvenile and adult *I. argentinus* caught in the two sampling periods (2001/2002 and 2007/2008) in the warm season from December to May and the cold season from June to November (vertical bar 95%).

the late 1990', fishing and research expanded to deeper waters of the Brazilian ZEE (Perez et al., 2003; Revizee, 2006) and three approaches were used to study *I. argentinus* distribution and abundance: acoustic pelagic surveys in 1996–1997 (Madureira et al., 2005a) followed by the analysis of commercial fishing (Perez et al., 2009; Bainsy and Haimovici, 2012) and bottom trawl surveys in 2001–2002 (Haimovici et al., 2008, this paper).

Acoustic records were identified and eco-integrated by Madureira et al. (2005b). In late winter in 1996, the estimated biomass of *I. argentinus* between 23°S and 35°S was 19,537 t, distributed mostly on the outer shelf and shelf break between Santa Marta Grande and Cabo Frio. The highest abundance was estimated in autumn 1997 when it attained 31,742 t mostly off the shelf break along all region. The lowest abundance was in the late spring in 1997, with only 1612 t and a sparse distribution. Small juveniles were present along all the shelf break in all three surveys and paralarvae from bongo net samples were exceptionally abundant in the autumn survey between 26° and 31°S, less abundant in the late winter and absent in late spring (Santos and Haimovici, 2007).

The Revizee pelagic and demersal surveys showed that juveniles occur mostly on the outer shelf and shelf break whereas larger sub adults and adults occur on the upper slope extending to all Southeastern and Southern Brazil. This pattern has been previously observed between 31°S and 34°S by Haimovici and Perez (1991). Despite having been obtained in different time periods, both Revizee pelagic and demersal surveys were consistent in the order of magnitude of the biomass estimates, the highest values in autumn surveys by comparison with the winter surveys and in the

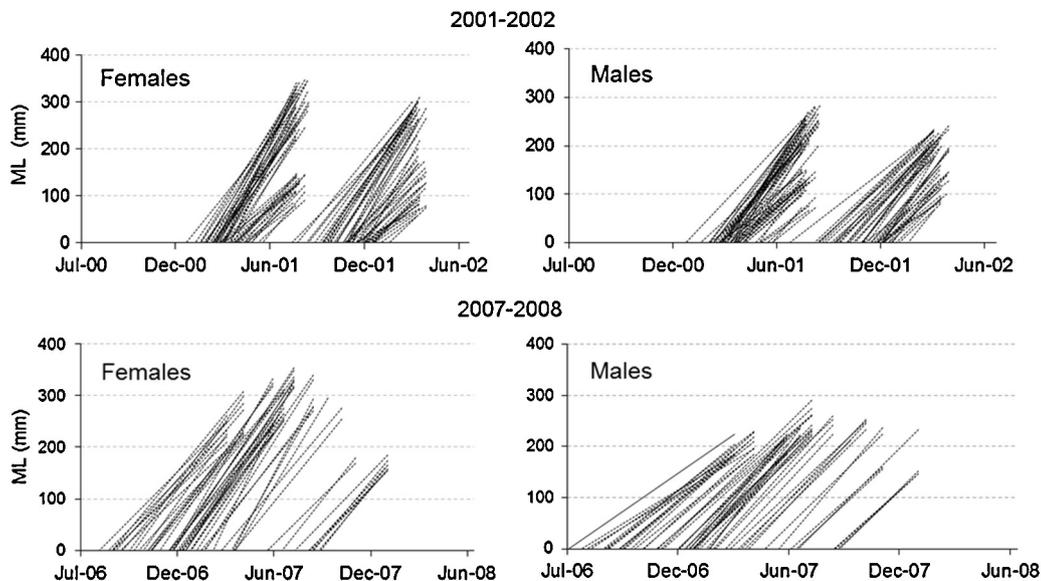


Fig. 10. Lines connecting the capture dates with the hatchling dates (on the horizontal axis) of females and males of *I. argentinus* captured in bottom trawl surveys (2001/2002) and commercial fishing (2007/2008) along Southern Brazil. Hatching dates were back-calculated from ages determined on statoliths.

location of the higher biomasses: north and south of Santa Marta Grande Cape.

The region of Santa Marta Grande also appears to have adequate conditions for the hatching of *I. argentinus*. Near the coast, in spring 1989, a large number of paralarvae was captured associated to an SACW coastal upwelling episode (Vidal et al., 2010) and on the outer shelf break, the highest densities of *Illex* paralarvae were obtained in autumn 1997 (Santos and Haimovici, 2007).

I. argentinus appears to have been exceptionally abundant, in 2002, particularly north and south of Santa Marta Grande, where the largest catches of maturing and mature squids were obtained in the 450–550 m depth range in the autumn bottom trawl survey (Figs. 3 and 4). In the same region, Madureira et al. (2005c) report large densities of acoustic records in a series of surveys from March to May 2002 and mention that, in the winter of the same year, the commercial trawler “In Sung 207” caught 850 t in one month, amounting 30% of the landings in Brazil in that year. Perez et al. (2009) also mention large catches of *I. argentinus* by foreign and Brazilian trawlers in 2002.

4.2. Life cycle patterns in Brazil

The life cycle of *I. argentinus* in Brazil appears to be highly variable both seasonally and throughout years, but some patterns were consistently observed.

Size at maturity increases with latitude. We did not aged squids from Southeastern Brazil but Schwarz and Perez (2012) pooled the aging of squids from Southeastern and Southern Brazil and proposed a general pattern of a half year life cycle. If no differences in longevity between both regions is assumed, then growth in Southeastern Brazil is slower than in Southern Brazil, fitting into the general pattern of increasing size in colder waters or higher latitudes (Arkhipkin, 2004). However, larger mature females over 300 mm ML were observed at the lowest latitudes in June 2002 (Fig. 5), suggesting localized occurrence in space and time of conditions for higher growth along all its distribution range in Brazil.

In Southern Brazil, in both annual periods under study, maturity was attained at larger sizes in the cold season. As ages at maturity were the same in both seasons, it can be concluded that the summer and autumn spawners, that become large juveniles and subadults in winter and spring, grew faster than those spawned in winter and spring that mature in summer and autumn. The difference was associated to the higher winter and spring productivity in the region (Ciotti et al., 1995, 2010) that translates into higher biomass of zooplankton and juvenile fishes available to feed *I. argentinus*. In Southeastern Brazil, results were not conclusive as mature females were larger in the cold season and males, in the warm season. It may be possible that enhanced productivity in the Southeastern Bight in summer with the stronger subsurface upwelling of SACW (Matsuura, 1986) is associated to this inverted pattern.

Interannual variability in growth and lifespan was observed between 2001–2002 and 2007–2008 and larger growth was associated to anticipated maturation in the first period. Interannual variation in the growth of *I. argentinus* in its southern range was observed by Arkhipkin and Laptikhovskiy (1994) but no biological interpretation was provided by the authors.

Studies of the interannual variability in growth of ommastrephid squids are not frequent in the literature (Arkhipkin, 2004). Villanueva (1992) observed interannual differences in the growth of *Todarodes angolensis* from the Benguela upwelling system in which increased growth was associated to colder waters. Jackson et al. (2003) compared the growth of *N. gouldi* between seasons in two annual periods and also associated higher growth to colder SST. Oceanographic data and catch records of *I. argentinus* are far less available for the northern range of its distribution and differences in growth and maturity were observed in only two annual periods

for which the mean monthly sea surface temperature along the shelf break at different latitudes were compared (Fig. 1). The SST in autumn and winter 2007 were 0.2 to 1.6 °C lower than in the corresponding period in 2001. No interpretation can be inferred from that difference but higher daily growth rates in autumn 2002 were associated to exceptionally large catches; it suggests a positive relationship between growth and abundance.

Years of high abundance of the squids from the Patagonian stock were found to be associated with the low proportion of frontal waters and high proportion of favorable SST waters (16–18 °C) within the inferred hatching area, near the confluence of the Brazil and Malvinas currents, in the year preceding the fishery (Waluda et al., 2001). Chen et al. (2007) found that cold events on the northern portion of the Patagonian Shelf in the previous year could have been a key factor for the high squid abundance in the current year. Large catches of *I. argentinus* in autumn and winter 2002 may be related to warmer SST in the previous spring but more fishing and environmental data should be necessary to explore this relationship.

4.3. Connectivity

The hypothesis of large spawners migrating northward from higher latitudes and spawning along the Brazilian slope is still controversial, partly because a small number of paralarvae was observed south of the Brazil Malvinas (Falklands) confluence, by comparison with the large number observed along Brazil (Brunetti, 1988; Haimovici et al., 1998; Santos and Haimovici, 2007).

It is unlikely that large South Patagonian migratory winter spawners that mature at 10 to 12 month (Arkhipkin and Laptikhovskiy, 1994; Uozumi and Shiba, 1993), reach Brazil where mature specimens were younger and smaller (Schwarz and Perez, 2012; Baily and Haimovici, 2012). On the other hand, the possibility of migrants from the North Patagonian-Bonaerensis Spring Spawners stock (*sensu* Brunetti, 1988) reach Brazil is as difficult to discard as to prove. Until now, only few specimens caught in Brazilian waters were aged over 250 days (Fig. 8) or near one year (Schwarz and Perez, 2012) and large winter and spring spawners off Brazil could be short living fast growing specimens in years with favorable recruitment and growth conditions. The winter northward migrants hypothesis finds support in the presence of mature specimens caught along the slope in winter and spring that, in mean, matured at larger sizes than the ones observed in this study (Haimovici and Perez, 1991; Santos and Haimovici, 1997; Perez et al., 2009). On the other hand, several abundant pelagic and demersal fishes are known to migrate from Northern Argentina to Southern Brazil in the cold season (Haimovici et al., 1997) and there are no evident reasons to explain why *I. argentinus* should not, being an semelparous species similar to other ommastrephid squids, spread the risks of recruitment failures by occupying large areas and reproducing in all seasons (Carvalho and Nigmatulin, 1998). For this reason, the existence of both large non migrants and large migrants forms is perhaps the most likely hypothesis. Future research should focus on the importance of northward migrants to spawning and of the drifted egg masses and paralarvae to the recruitment south of the Brazil Malvinas (Falkland) Confluence.

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