

## **Seasonality in Growth and Hatching of the Argentine Short-Finned Squid *Illex argentinus* (Cephalopoda: Ommastrephidae) Inferred from Aging on Statoliths in Southern Brazil**

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## SEASONALITY IN GROWTH AND HATCHING OF THE ARGENTINE SHORT-FINNED SQUID *ILLEX ARGENTINUS* (CEPHALOPODA: OMMASTREPHIDAE) INFERRED FROM AGING ON STATOLITHS IN SOUTHERN BRAZIL

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**ABSTRACT** Specimens of *Illex argentinus* from trawl catches along southern Brazil were sampled between March 2007 and January 2008 to study aspects of their life cycle and the connectivity with stocks from the southern range of the distribution of the species. Small mature specimens occurred year-round, whereas those with a mantle length (ML) of more than 250 mm were rare in the warm months, from December to May. More than 79% of the mature females were mated, providing evidence of year-round spawning in southern Brazil. Mature males were 131–330 mm and 147–275 days old, and females were 166–341 mm and 146–257 days old; mean ML at 50% maturity was 156.3 mm and 181.2 mm, respectively. The number of daily increments decreased from the capture date showed that hatching occurred year-round, mostly from August to January. Daily mean ML increment of juveniles to adults hatched during the warm season and caught during the cold season was larger than that of those hatched during the cold season and caught during the warm season, suggesting greater growth in winter and spring associated with increasing primary productivity in the region. A life cycle shorter than 1 y suggests genetic isolation neither between both seasons nor among larger and smaller adult squids. The number of daily increments in the postnuclear zone of the statoliths was substantially lower than that recorded for specimens maturing along Patagonian waters, suggesting that those squid do not reach southern Brazil.

**KEY WORDS:** statoliths, maturity, reproductive cycle, growth, population dynamics, short-finned squid, *Illex argentinus*, stock

### INTRODUCTION

Shelf and slope ommastrephids are typically fast-growing, migratory, voracious nektonic predators, with a semelparous short life cycle that, in productive regions, can sustain large fisheries (Hatanaka et al. 1985, Arkhipkin 2005, Boyle & Rodhouse 2005). Semelparity and microcohorts spawning throughout the year in different regions are important components of their life strategy (Carvalho & Nigmatullin 1998, O'Dor 1998). One of the most abundant species of cephalopods in the world, with catches along the Patagonian shelf that peaked at 1.14 million mt in 1999 (FAO 2005), is *Illex argentinus* (Castellanos, 1960), endemic in the southwestern Atlantic between 22° S and 54° S (Haimovici et al. 1998). Off southern Brazil, it appears to be far less abundant because commercial landings have been only sporadic, usually as a by-catch of the hake *Merluccius hubbsi* (Marini, 1933), attaining (at most) 2,613 t in 2002 (Haimovici et al. 2006, Perez et al. 2009). However, its catches in both bottom trawl and midwater trawl surveys (Rahn & Santos 1978, Haimovici & Perez 1991, Madureira et al. 2005, Haimovici et al. 2008) and trophic relation studies (Santos & Haimovici 1997a) have shown that *I. argentinus* is an important component of the pelagic and demersal food chains of the upper slope.

Ommastrephids have large growth plasticity. Large forms of squids are associated with migratory “roving” forms whereas the small ones are more prone to “stay at home” (O'Dor & Coelho 1993, O'Dor 1998). O'Dor and Coelho (1993) observed a latitudinal decline in the size at maturity of *Illex illecebrosus* (Lesueur, 1821) in the northwestern Atlantic, with larger spawners in the colder northern waters and smaller ones in the south. There are also larger and smaller seasonal forms of ommastrephids associated with colder and warmer spawning

seasons (Hatanaka et al. 1985). These patterns were observed for *I. argentinus*: Large spawners have been recorded from autumn to spring off Patagonia, northern Argentina, and Uruguay (Arkhipkin & Scherbich 1991, Brunetti et al. 1998, Crespi-Abril et al. 2008), and the southern Brazilian slope (Haimovici & Perez 1990, Santos & Haimovici 1997b, Perez et al. 2009). Small spawners were formerly recorded in the summer in the northern Patagonian shelf and gulfs (Arkhipkin & Scherbich 1991, Brunetti et al. 1998, Crespi-Abril et al. 2008). Haimovici et al. (2008) and Perez et al. (2009) show that small squid mature year-round along southern Brazil, between 22° S and 34° S.

To date, no clear evidence of the relationship between fishing grounds and the corresponding spawning and hatching grounds of *I. argentinus* in different regions and periods of the year has been found, but several hypotheses have been proposed. Brunetti et al. (1998) postulated that squid maturing in spring in northern Argentina and on the Uruguayan shelf spawn offshore at the mouth of the De La Plata River. Haimovici and Perez (1990), Santos and Haimovici (1997b), and Perez et al. (2009) provide evidence that cold-season (winter and spring) “large” squid spawning off southern Brazil may be northward migrants from southern feeding grounds. Arkhipkin and Scherbich (1991) and Arkhipkin (1993) suggest that maturing squid fished along the Patagonian shelf and slope spawn farther north up to southern Brazil, a hypothesis that has also been considered by Schroeder and Perez (2010).

Aging is an important tool in population dynamics. The microstructure of the statoliths of ommastrephids has been used widely for estimating squid age since the late 1970s (Lipinski 1978, Arkhipkin 2005), in addition to the duration of the paralarval phase and mating events (Dawe & Beck 1997). The squid *I. argentinus* was initially “aged,” using statoliths, by Arkhipkin and Scherbich (1991) and Uozumi and Shiba (1993) to study their growth and population structure in its southern range. Two recent articles included aging as a tool to study the ecology of the Argentine short-finned squid in Brazil: Schwarz

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and Perez (2010) used statolith readings to study their growth and maturation, and Schroeder and Perez (2010) used recent daily increments (DIs) recorded on the gladius to compare growth among different seasonal spawners.

The regular landings of a bottom trawler for 1 y of fishing on the upper continental slope between 32° S and 34° S (Fig. 1) provided the opportunity to collect sequential samples of *I. argentinus* off southern Brazil for almost a year. These samples provided data on size composition, sexual maturation, and aging of squid caught during different seasons for a better understanding of their life cycle in the northern range of the species' distribution. The aim of this study was to analyze the seasonality of hatching and the growth of squid maturing in southern Brazil.

## MATERIALS AND METHODS

### Sampling

Samples of *I. argentinus* were obtained from commercial catches by a bottom trawler landed in the harbor in Rio Grande (Fig. 1). Eleven monthly trips, between March 2, 2007, and February 8, 2008, provided the samples. Fishing was carried out along the upper slope of southern Brazil between Mostardas (31°15' S) and Chui (33°45' S), at depths ranging from 260–490 m.

Specimens were measured for mantle length (ML) distribution, and some of them were measured for total weight (in grams) and nidamental gland length (in millimeters). The presence or absence of bundles of spermatophores attached to the gills or inner mantle surface for females, and the hectocotylus length (in millimeters) and quantity of spermatophores (absence, few, many) in the Needham sac were recorded for males. The maturity stages were attributed according to the 8 stages of Brunetti (1990). The statoliths of 10 specimens of each sex, from each monthly sample, were collected and stored in 96° GL alcohol.

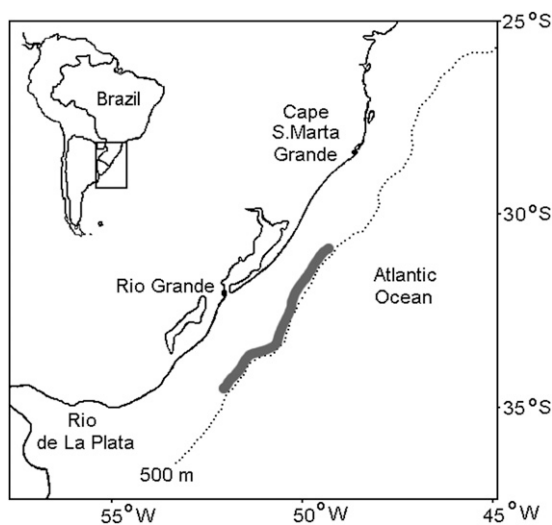


Figure 1. Fishing area of *Illex argentinus* catches were carried out during 11 fishing trips by the bottom trawler *Xodó do Milenium* off southern Brazil, between March 2007 and January 2008.

### Aging

The terminology used to describe the parts and microstructure of the statoliths follows Clarke (1978), as modified by Arkhipkin (2005). To determine ageing, both sides of the frontal plane and statoliths were ground until the focus was exposed. The procedure described by Schwarz and Perez (2010) was followed for statolith preparation and reading. Initially, the concave inner surface was ground with 30- $\mu$ m microabrasive sheets (3M) to provide an attachment surface to be glued with a drop of nail polish to a glass slide. After at least 24 h, the convex surface was ground with 30-, 12-, 9-, and 3- $\mu$ m lapping films (3M) until the nucleus was reached (Fig. 2).

DIs were counted with 1,000 $\times$  magnification for the post-nuclear zone (PNZ) and the dark zone (DZ) and the peripheral zone (PZ), separately. Counting was possible in 104 of the 213 statoliths examined. Statoliths of 109 specimens (51%) appeared partially or completely amorphous after grinding and polishing; therefore, they were inadequate for the reading of DIs. Statistical differences in the rate of legible and illegible statoliths were not observed between sex ( $P = 0.683$ ) or warm and cold seasons ( $P = 0.147$ ). The loss of the crystalline aragonite structure of almost half the statoliths may have been a consequence of the onboard storage of the squid on ice for up to 3 wk, and former freezing for several months before the extraction of the statoliths. Illegibility of statoliths of stranded *Architeuthis* resulting from bacterial attack and acidification has been reported previously by Roeleveld and Lipinski (1991).

On the mounted statoliths, 3 measures were taken with 400 $\times$  magnification: (1) the maximum radius of the statolith (MRS), (2) the distance from hatching check to the beginning of the dark zone corresponding to the PNZ and (3) the distance between the beginning of the DZ and the end of the PZ at the edge of the statolith (DZ + PZ; Fig. 2).

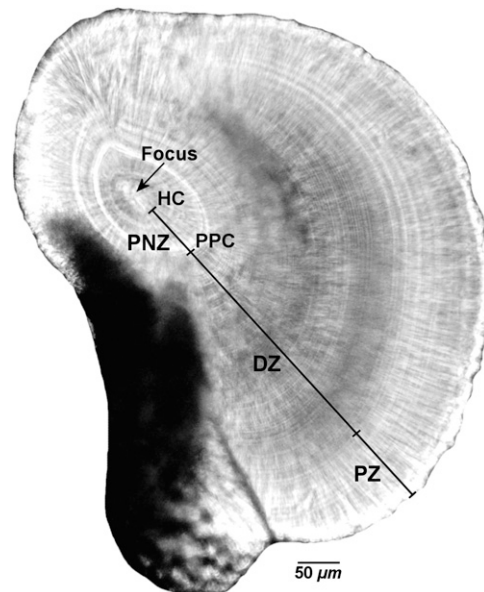


Figure 2. Ground and polished statolith of *Illex argentinus* (mantle length, 195 mm; male) at 400 $\times$  magnification. DZ, dark zone; HC, hatching check; MRS, maximum statolith radius; PNZ, postnuclear zone; PPC, postparalarval check; PZ, peripheral zone. MRS = PNZ + DZ + PZ.

The coefficient of variation (CV) was used to evaluate the accuracy of DI counting (Campana 2001):

$$CV_i = \frac{1}{R} \sum_{i=1}^R \frac{|X_{ij} - X_j|}{X_j} \times 100\% \quad (1)$$

where  $X_{ij}$  is the age determination of the squid  $j$  by the reader  $i$ ,  $X_j$  is the mean age of the  $j$ th squid, and  $R$  is the number of readers.

The CV between two different readers in a set of 25 statoliths was 5.9%, and among 3 readings of 104 statoliths for a single reader (M. B.) was 6%. These values are some of the most frequently reported in the literature for fish of moderate longevity and reading complexity (Campana 2001). In addition, they are similar to the CV reported by Schwarz and Perez (2010) for *I. argentinus*.

Arkhipkin and Perez (1998) described sliced statoliths of Illicinae ommastrephids in which there is a “nuclear zone,”

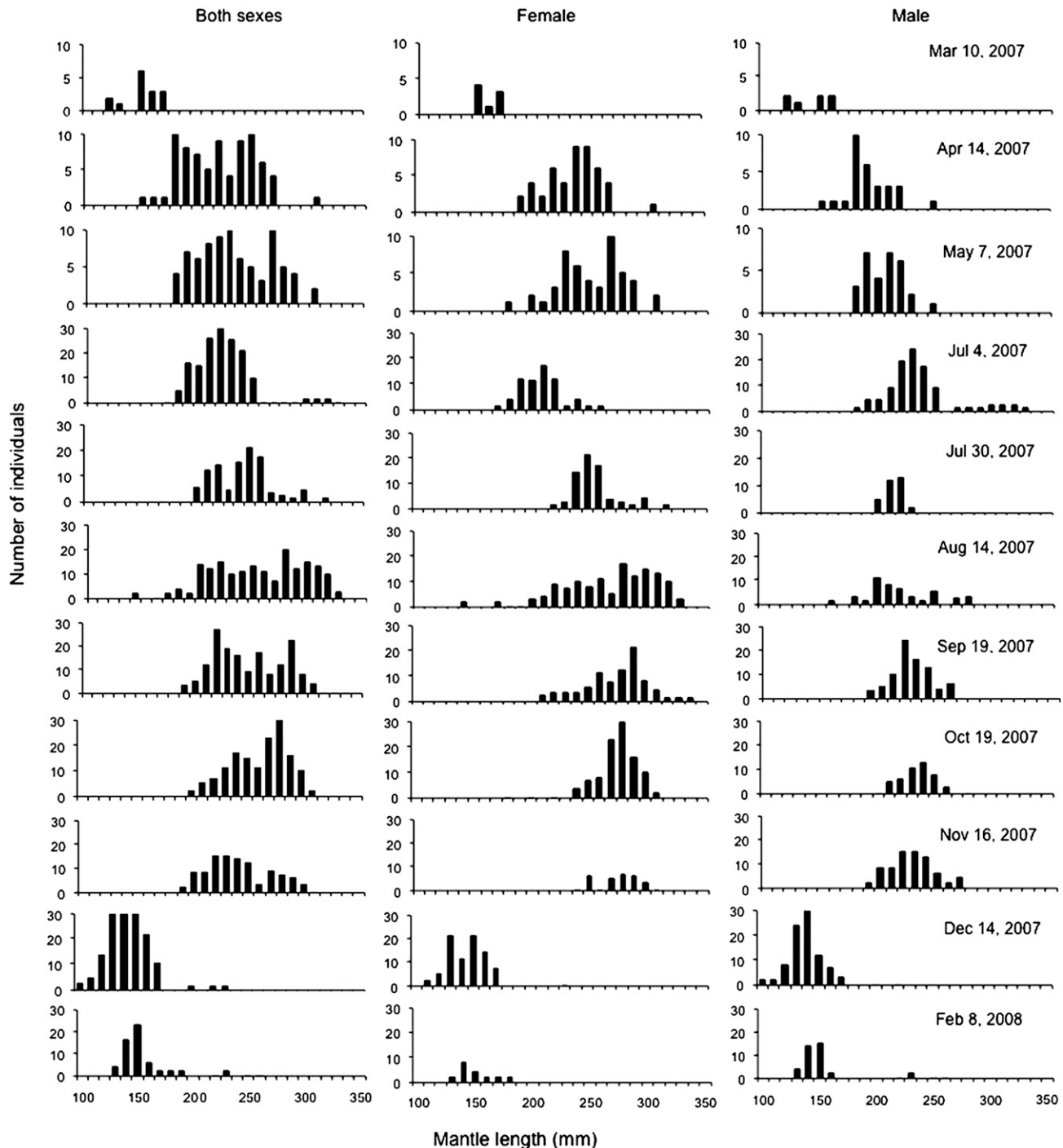


Figure 3. Mantle length distribution of 1,270 *Illex argentinus* caught off southern Brazil by the commercial trawler *Xodó do Milenium* from March 2007 to January 2008.

from the focus to hatching mark followed by the PNZ, with clear and near-uniformly spaced increments that are assumed to represent the paralarval growth and end in a postparalarval check. Juvenile and adult growth is recorded in the DZ, following the PNZ. It is brownish when observed with transmitted light and contains broader increments. The DZ is followed, without a clear transition, by the PZ, which is formed by translucent, narrow, and rather regularly spaced increments.

The criterion that considers a pair of dark and clear bands as a DI in the microstructure of the statoliths of *I. argentinus* has been assumed by different authors (Arkhipkin 1993, Uozumi & Shiba 1993, Schwarz & Perez 2010). For the paralarvae of *I. argentinus*, Sakai et al. (2004) identified the hatching mark experimentally and validated the daily formation of a dark band and a clear band on the statoliths—hereafter referred to as the daily increment (or DI). The DI formation in the DZ and PZ of *I. argentinus* was not directly validated, but Dawe et al. (1985) validated it for *I. illecebrosus* by using chemical marking. Furthermore, Uozumi and Shiba (1993) indirectly validated the one growth increment—1-day hypothesis for subadult and adult sampling sequentially for several months.

#### Sexual Maturation and Hatching

To estimate ML at 50% maturity ( $ML_{0.5}$ ), females were classified as functionally mature (*sensu* Arkhipkin 1992) when maturity stages were V or greater (Brunetti 1990). These stages were correlated strongly to the nidamental glands more than 40% of the mantle length in females. The hectocotylus was more than 50% of the length of the hectocotyli in males (Santos & Haimovici 1997b).

The proportions of immature and mature specimens were fitted to the logistic model

$$P_i = \frac{1}{1 + e^{(S_1 - S_2 ML)}} \quad (2)$$

where  $P_i$  is the proportion of mature specimens in the  $i$  10-mm ML class. Eq (2) was linearized as  $S_1 - S_2 ML = \ln(1 - P_i)/P_i$  to calculate the values of the intersection ( $S_1$ ) and the slope ( $S_2$ ) by regression. The ML at the inflection point of the curve (Eq 2) corresponding to  $P_i = 0.5$  was calculated as the quotient  $ML_{0.5} = S_1/S_2$ .

$ML_{0.5}$  can be used as a criterion to classify squid as “small” and “large” spawners in different regions and periods of the year (Brunetti et al. 1998, Crespi-Abril et al. 2008, Perez et al. 2009).

The hatching date of each individual was back-calculated by decreasing the number of DIs counted on the statoliths from the date of capture. This last was estimated as the mean between the beginning and the end of the fishing trip during which it was caught.

#### Growth Comparisons

For comparative analysis of growth between seasons, samples were grouped as the “cold season” from June to November (late autumn to early spring) and the “warm season” from December to May (late spring to mid autumn).

No *a priori* growth model was assumed. Instead, comparisons were based on the mean of the daily ML increments between hatching and capture ( $\Delta ML$ , measured in millimeters per day). Biases originated by eventual age composition differences

between squid groups were reduced in part by using age as a covariate. Regressions were compared with the covariance analysis performed with Statistica Release 7 (Statsoft), and means were compared with the Student *t*-test (Zar 1984). The decrease in the  $\Delta ML$  with age is in agreement with the asymptotic growth models such as the logistic Gompertz and Schnute models used to describe squid growth (Uozumi & Shiba 1993, González et al. 1996, Arkhipkin & Roa-Ureta 2005).

## RESULTS

#### Size Frequency

A total of 1,270 *I. argentinus* were measured from 11 monthly samples landed from March 2007 to February 2008: 684 females, 114–341-mm ML (mean ML, 244.5 mm); and 586 males, 106–330-mm ML (mean ML, 207.1 mm). Females were, on average, 18.1% larger than the males. Almost all specimens with an ML more than 280 mm were captured during the cold season—mainly from July to September. The mean ML in the warm months (from March to May and from December to February) was 193.6 mm; in the cold season, it was 250.4 mm. Most of the monthly ML frequency distributions showed a single modal group and, most often, a few large specimens at the right end of the distributions (Fig. 3). No modal progressions covered all the sampling periods, but modal progressions were observed for males between March and July and, for females, from March to May and from July 4, 2007, to August 2007. The sample collected on July 4, 2008, showed two distinct groups of males: one of them with ML less than 250 mm and the other with ML more than 270 mm. However, the latter group had a few specimens only between August and October. Females with an ML larger than 300 mm were observed during August and September (Fig. 3). These ML distributions showed that small specimens occurred year-round, whereas males and females larger than 250 mm were rare from December to May (Figs. 3 and 4).

#### Daily Increments and Hatching Dates

DIs ranged from 96–275 in the 104 read statoliths. Hatching dates, which were calculated by decreasing the number of DIs

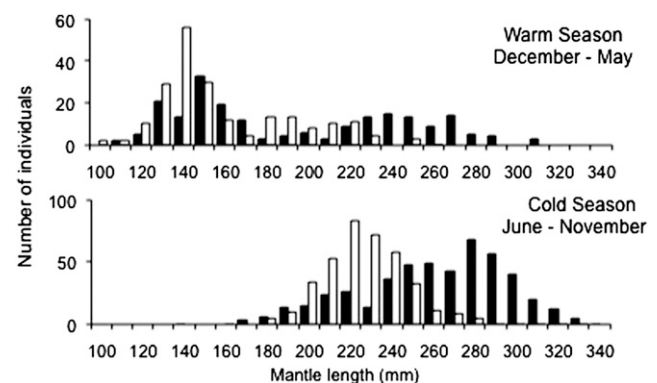


Figure 4. Mantle length distribution of *Illex argentinus* caught by commercial fisheries off southern Brazil during the warm season (from March to May 2006 and from December 2006 to February 2007) and during the cold season (from June to November 2006). Males ( $n = 586$ ), white columns; females ( $n = 684$ ), dark columns.

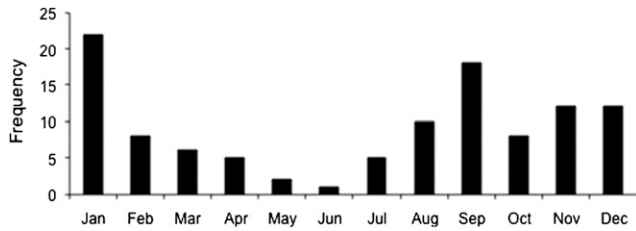


Figure 5. Frequency distribution of back-calculated hatching date of 104 *Illex argentinus* caught by commercial fisheries off southern Brazil between March 2007 and January 2008.

from the capture date, showed that hatching occurred year-round: 75% between August and January (Fig. 5).

The number of DIs in the PNZ ranged from 17–38 days, and the number of DIs in the DZ and PZ together was between 70 and 245. The mean duration of the paralarval stage, calculated when the number of growth increments in the PNZ of the statoliths, was  $28.38 \pm 3.78$  days ( $n = 104$ ). No differences were observed when it was compared among sexes, hatching, and capture seasons (Table 1).

To investigate whether the larger spawners, which hypothetically have longer migrations along growth, differ in the number of PNZ increments from the smaller ones, only mature specimens were compared. The mean number of PNZ increments of males with an ML smaller than 220 mm (27.2, SD = 3.3,  $n = 8$ ) differs significantly neither from those larger than 240 mm (28.6, SD = 5.4,  $n = 6$ ;  $P = 0.2790$ ) nor from mature females smaller than 220 mm (29.3, SD = 4.0,  $n = 11$ ) nor from those larger than 280 mm (29.8, SD = 4.0,  $n = 17$ ;  $P = 0.3746$ ).

#### Sex Ratios and Sexual Maturity

Sex ratio did not differ from 1:1 ( $P = 0.767$ ,  $n = 559$ ). However, males predominated at MLs smaller than 250 mm, and females were more numerous at larger MLs (Fig. 4). Mature males and females were observed during all seasons. Sixty-six of 283 males were immature, measuring from 106–199 mm from

96–146 days old, and 217 were mature or spent (131–330 mm, 147–275 days old). Fifty-three of 276 females were immature (114–260 mm, 124–192 days old) and 223 were mature or spawned (166–341 mm, 146–257 days old). Mated females were in the ML range of 180–350 mm and included both immature (10.8%) and mature (79.8%) females.

Logistic models were fitted to the proportions of mature males ( $n = 272$ ;  $S_1 = 7.24$ , SE = 0.658;  $S_2 = 0.0463$ , SE = 0.00363) and females ( $n = 264$ ;  $S_1 = 7.34$ , SE = 2.609;  $S_2 = 0.0405$ , SE = 0.01200; Fig. 6). MLs in which 50% of the males and females were mature were 156.3 mm and 181.2 mm, respectively.

#### Growth

A positive correlation was observed between the ML and the number of DIs ( $R = 0.551$ ), thus larger specimens were consistently older than smaller ones (Fig. 7A). Mean daily ML increment (measured in millimeters per day) correlated negatively to age at capture ( $R = -0.3334$ ,  $P < 0.0004$ ; Fig. 7B). The mean DI of the MRS (measured in micrometers per day) also decreased with increasing age at capture ( $R = -0.8070$ ,  $P < 0.0001$ ; Fig. 8A). These results indicate that, in the case of specimens larger than 110 mm, growth slows with age.

On the other hand, no significant correlation was observed between the mean daily width of the PNZ (measured in micrometers per day) and age ( $R = 0.0223$ ,  $P < 0.819$ ; Fig. 8B). This lack of correlation favors the conclusion that growth of the PNZ is not related to age at capture.

The adjusted mean of the ML DIs regressed against age was used to compare the growth between specimens grouped according to the hatching season and capture season (Table 2). Both males and females hatched during the warm season had larger mean MLs and mean MRS DIs than those hatched during the cold season. These results indicate that squid hatched during the warm season (and that became subadults and adults during the cold season) grew faster and larger than those hatched during the cold season (and that became subadults and adults in the warm season).

TABLE 1.

Mean mantle length (ML), and number of daily increments (DIs) in the statoliths and in the postnuclear zone (PNZ) of 104 *Illex argentinus* caught by commercial fisheries off southern Brazil between March 2007 and January 2008.

	Males				Females			
	Cold	Warm	Test	P	Cold	Warm	Test	P
	(A) Grouped by hatching season							
<i>n</i>	29	27			25	28		
Mean ML (mm)	191.8	236.2	$t = -5.072$	0.000*	228.1	295.2	$t = -5.170$	0.000*
Mean total no. of DI	193.1	185.4	$t = 0.711$	0.479	191.5	197.1	$t = -0.583$	0.562
Mean no. of DI in the PNZ	28.2	28.2	$t = -0.029$	0.977	27.5	29.4	$t = -1.772$	0.082
	(B) Grouped by capture season							
<i>n</i>	28	28			32	21		
Mean ML (mm)	238.9	187.5	$t = -6.405$	0.000*	297.6	211.7	$t = -7.767$	0.000*
Mean total no. of DI	190.0	188.8	$t = -0.110$	0.913	202.1	182.9	$t = -1.984$	0.053
Mean no. of DI in the PNZ	28.4	28.1	$t = -0.353$	0.725	29.1	27.6	$t = -1.398$	0.168

\* Significant at 0.05.

Comparisons between cold and warm seasons were grouped by hatching season (A) and capture season and sex (B). *t*, Student test.

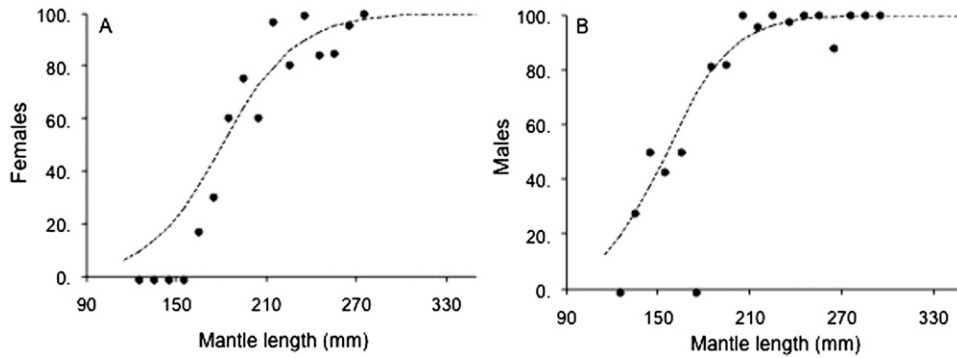


Figure 6. (A, B) Proportions of mature females (A) and males (B) by 10-mm mantle length intervals fitted to a logistic curve of *Illex argentinus* caught by commercial fisheries off southern Brazil between March 2007 and January 2008.

### DISCUSSION

Earlier studies on *Illex argentinus* on the outer shelf and slope off Patagonia showed a life expectancy of around 1 y (Arkhipkin & Scherbich 1991, Uozumi & Shiba 1993, Arkhipkin & Laptikhovskiy 1994). In the northern range of the species, Schwarz (2009), Schwarz and Perez (2010) and we (in the current study) have shown that off southern Brazil, mean age at capture was between 6 mo and 7 mo (Table 1), and that most females were mature—thus indicating a life expectancy substantially less than 1 y. Therefore, smaller squid at lower latitudes may be associated not only with slower growth, but also with a shorter life expectancy. Furthermore, the high percentage of mated and spent females recorded in the current study and by Perez et al. (2009) indicates the proximity of the fishing areas to the spawning grounds during both cold and warm seasons. The fact that, off southern Brazil, spawning takes place in different seasons and at ages substantially less than 1 y suggests that, along a genealogical line, some generations of local spawners may have been hatched during the cold season whereas others may have hatched during the warm season. This asynchrony may reduce reproductive isolation and may increase genotypic plasticity of the stock. In other words, small winter spawners in 1 y may become large winter spawners the following year. Interbreeding of different seasonal spawners has also been mentioned in the case of *I. illecebrosus* (O'Dor & Coelho 1993).

The mean daily ML growth of *I. argentinus* was greater for specimens hatched during the warm season that grew from juveniles to adults during the cold season. This result is consistent with Schroeder and Perez (2010) that, by reconstruct-

ing the growth on the gladius of spawners in different seasons, steeper growth trajectories for mature squid captured during the winter are observed. Greater growth may be associated with the higher productivity on the shelf and slope off southern Brazil (Ciotti et al. 1995). During the cold season, southwesterly winds predominate, and Buenos Aires shelf waters mixed with the De La Plata River outflow, and the Malvinas/Falkland Current waters, which are richer in nutrients, flow northward and penetrate the southern Brazilian shelf and upper slope. In contrast, during the warm season, northeasterly winds, coastal waters, and the warm oligotrophic waters of the Brazil Current flowing southward are dominant (Piola et al. 2000, Castro et al. 2006).

Our comparison of growth between seasons was based on the comparisons of the mean daily ML increments with age as a covariant, and did not assume any predetermined growth model. Several growth models have been proposed for squid, including nonasymptotic models (linear, exponential, and power). Uozumi and Shiba (1993) compared linear and logistic models and favored preliminarily the former; two more recent papers favored Gompertz and Schnute's asymptotic models over power and exponential nonasymptotic models (Arkhipkin & Roa-Ureta 2005, Schwarz & Perez 2010). The negative correlation between the daily ML increment and age observed in Figure 7 indicates that growth slows with increasing age, and consequently may be better represented by asymptotic models.

Following the interpretation of Arkhipkin and Perez (1998) of the direct relationship between the end of the PNZ and end of

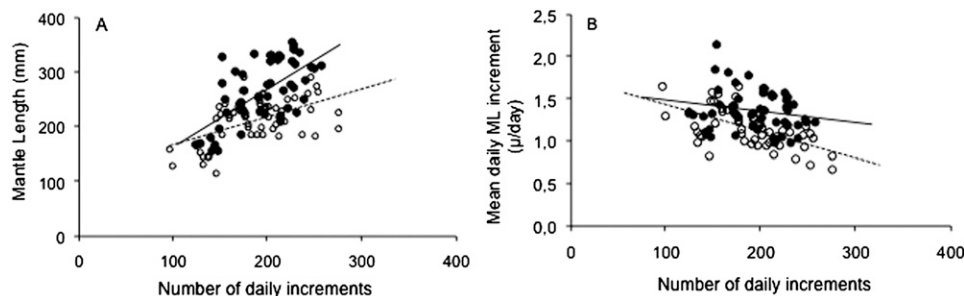


Figure 7. (A, B) Relationships between mantle length (A) and the mean daily mantle length increment (B), with the number of daily increments in the statoliths of *Illex argentinus* caught by commercial fisheries off southern Brazil between March 2007 and January 2008. Males, open circles and dotted lines; females: filled circles and solid lines.

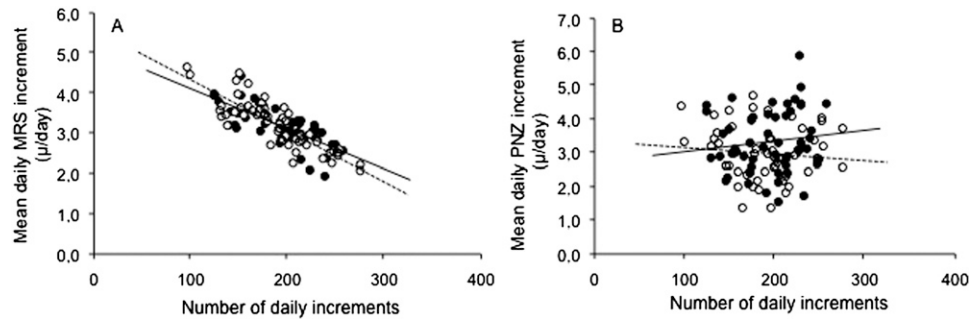


Figure 8. (A, B) Relationships between daily increments of the maximum statolith radius (A) and postnuclear zone (B) with the age of males (white) and females (black) of *Illex argentinus* caught by commercial fisheries off southern Brazil between March 2007 and January 2008. Males, open circles and dotted lines; females, filled circles and solid lines. MRS, maximum radius of the statolith; PNZ, postnuclear zone.

the paralarval stage, some inferences are possible. The ML size range at which the paralarval phase of ommastrephids ends—that is, when the proboscis splits completely and forms 2 tentacles—seems to be relatively narrow: 8–10 mm in *I. illecebrosus* (O’Dor 1983), 7–9 mm in *Todarodes pacificus* (Steenstrup, 1880) (Wormuth et al. 1992), and 8–10 mm in *I. argentinus* (Vidal 1994). If the end of the paralarval stage of *I. argentinus* occurs at similar sizes along its latitudinal distribution, it may be concluded that paralarvae grow faster in the northern portion of its distribution and that no differences in paralarval growth occur between seasons. Growth depends on food availability and temperature (Forsythe 2004, Vidal et al. 2006). In the current study, food availability is unknown for paralarvae in different regions and periods of the year; but, at all latitudes, adequate size, type, and quantity of zooplankton are necessary to promote survival and growth, if we assume that all specimens caught as mature adults were successful as paralarvae. The lack of significant seasonal differences in the paralarval daily ML increment suggests that enrichment processes associated with paralarval growth occur during different periods of the year. Subsurface intrusions of the South Atlantic Central Water are more common during the summer and during processes of shelf break upwelling, whereas, cyclonic

vortices are more common during winter (Gaeta & Brandini 2006). The rapid response given by *I. argentinus* paralarvae to upwelling events, as shown by Vidal et al. (2010), is well fit to environmental anomalies that are frequent in the region (Lentini et al. 2001).

In the current study, the 95% confidence interval of the number of DIs of the paralarval phase for *I. argentinus* ranged from 27.6–29.0, and no seasonal differences were observed between small and large mature specimens. These values are very similar to the maximum and minimum monthly means (25 and 33) in Schwarz (2009), from samples that were also captured along southern Brazil. The number of DIs in the PNZ observed in squid caught between 45° S and 47° S was substantially higher: 38.1–44.0 days for females and 37.0–40.5 days for males, with small differences throughout the year Arkhipkin (1990). This difference, around 25%, strongly suggests that egg masses spawned along Patagonia do not reach southern Brazil. This conclusion is not in conflict with the hypothesis of a southward displacing of hatchlings spawned in southern Brazil, and former return as large forms to lower latitudes for spawning in winter and spring as proposed by Santos and Haimovici (1997b) and Perez et al. (2009). The migrations of large spawners in southern Brazil seem to reach

TABLE 2.

Adjusted mean daily increments in ML, maximum radius of the statolith (MRS), and postnuclear zone (PNZ) of 104 *Illex argentinus* caught by commercial fisheries off southern Brazil between March 2007 and January 2008.

	Males				Females			
	Cold	Warm	Test	P	Cold	Warm	Test	P
	(A) Grouped by hatching season							
n	29	27			25	28		
Mean daily ML (mm/day)	1.02	1.29	F = 45.69	0.000*	1.20	1.51	F = 44.36	0.000*
Mean daily MRS (μ/day)	2.99	3.42	F = 21.66	0.000*	3.01	3.31	F = 23.63	0.000*
Mean daily PNZ (μ/day)	3.01	2.95	F = 0.12	0.729	3.55	3.14	F = 2.97	0.091
	(B) Grouped by capture season							
n	28	28			32	21		
Mean daily ML (mm/day)	1.28	1.03	F = 55.44	0.000*	1.49	1.17	F = 62.56	0.000*
Mean daily MRS (μ/day)	3.37	3.03	F = 25.36	0.000*	3.25	3.05	F = 30.27	0.000*
Mean daily PNZ (μ/day)	3.00	2.97	F = 0.03	0.872	3.25	3.47	F = 1.29	0.261

\* Significant at 0.05.

Comparisons between cold and warm seasons were grouped by hatching season (A) and capture season (B). F, Fisher’s test for covariance analysis.



feeding grounds off Uruguay and the Buenos Aires province in Argentina.

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