

Individual growth of the squid *Illex argentinus* off Brazil as reconstructed from the gladius microstructure

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Individual growth histories of the shortfin squid Illex argentinus were reconstructed in 1512 individuals obtained during seven years of commercial exploitation in southern-south-eastern Brazil. Growth increments were directly measured on the gladius dorsal surface from the anterior part to posterior end in two-thirds of the entire length. Gladius growth increments were deposited at the same rate as statolith rings and the daily nature of the growth increments was supported. Because gladius length is strongly related to mantle length, growth increments closely approximated mantle length growth rates, allowing the reconstruction of both size- and age-dependent growth. Individual reconstruction was possible between 4 and 347 mm of gladius length, almost the entire life cycle of the species. The variability of the acceleration in gladius growth evidenced four life history transitions where the most noticeable occurred between paralarval/juvenile stages, delimiting male/female size differentiation. The changes in acceleration in growth throughout the size-range may be influenced by the thermal gradients experienced by individuals during life history events transitions in Brazilian waters.

Keywords: shortfin squid, gladius, growth increments, life-history transitions

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INTRODUCTION

The gladius is the internal modified shell in squids of the orders Myopsida and Oegopsida. It originates during embryonic development located in the dorsal midline of the mantle. Throughout life it grows continuously through the accretive deposition of β -chitin in association with proteins (Hunt & Nixon, 1981) and is composed of outer, intermediate and inner layers (Arkhipkin *et al.*, 2012). Regular growth increments have been observed in all of these layers and were considered of potential value for age and growth studies (LaRoe, 1971; Arkhipkin & Bizikov, 1991; Bizikov, 1991; Jackson *et al.*, 1993; Perez *et al.*, 1996, 2006; Zaleski, 2010).

In squids of the families Ommastrephidae and Loliginidae, the gladius structure is mainly formed by the intermediate layer that grows longitudinally and correlates highly with the mantle length growth (Bizikov, 1991; Jackson *et al.*, 1993). In some species (e.g. *Sthenoteuthis ovalaniensis*, *Illex argentinus*, *Illex illecebrosus*, *Doryteuthis plei* and *Lolliguncula brevis*) growth increments of the intermediate layer have been demonstrated to be daily deposited and their width regarded as proxies for somatic growth (Arkhipkin & Bizikov, 1991; Bizikov, 1991; Perez *et al.*, 1996, 2006; Zaleski, 2010). Because cephalopod growth rates are influenced by body size, feeding rates and temperature (Forsythe & van Heukelem, 1987), growth rate variability, as assessed by the reconstruction of gladius growth, integrates

the effects of size (absolute growth) and environmental conditions (e.g. temperature and food availability) experienced by individual squid during a certain period of its lifetime (Perez & O'Dor, 1998, 2000). In that sense the gladius analysis can and has been used to describe life history events and to address ecological and population processes (see review in Arkhipkin & Perez, 1998).

Particularly interesting has been the application of this technique to understand early life ecology of a highly migratory ommastrephid squid, *Illex illecebrosus* in the north-west Atlantic. Paralarvae occur in the tropical waters off the coast of Florida and are transported northwards by the Gulf Stream to recruit in the continental shelf off Nova Scotia and Newfoundland. During that process individuals undergo important life history transitions and experience sharp temperature and food gradients as determined by the Gulf Stream and shelf/slope fronts (O'Dor, 1983). Gladius growth was shown to respond to food and temperature variability in the laboratory (Perez *et al.*, 1996). More importantly, in wild population samples, the acceleration in gladius growth changed during early life transitions and growth conditions are favoured as juveniles attained more productive areas in the shelf/slope front (Perez & O'Dor, 2000).

In the south-west Atlantic another ommastrephid, *Illex argentinus* displays a similar life history pattern combining spawning migrations to the transport of the Malvinas/Falkland Current and the dynamics of the Subtropical Convergence (Hatanaka *et al.*, 1985). The species is distributed from Rio de Janeiro to Southern Argentina, and important concentrations occur on the continental shelf and slope waters south of 35°S in the Patagonian Shelf and around the Falkland/Malvinas Islands (Brunetti *et al.*, 1998). Within

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that distribution range, life-history attributes have been found to vary in space and time and several geographically- and seasonally-established population groups have been differentiated (see review in Haimovici *et al.*, 1998).

Off Brazil, a 'tropical/subtropical' subset of these population groups has long been described, and recently targeted by the fishing industry (Santos & Haimovici, 1997; Perez *et al.*, 2009). In contrast with *I. illecebrosus* and the 'temperate' Patagonian population groups of *I. argentinus*, these squids have generally been characterized by a shorter life span (~6 months) with paralarvae, juvenile and adults concentrating in the continental shelf, shelf break and slope respectively (Haimovici *et al.*, 1998; Schwarz & Perez, 2012). Seasonal growth variation during early life have been evidenced by the analysis of gladius growth patterns and were associated with a year-round spawning and the environmental fluctuations of the shelf break/slope waters off southern Brazil (Schroeder & Perez, 2010; Schwarz & Perez, 2012). In the present study these patterns are further explored to assess size- and age-dependent life history events in the shelf break-slope waters off southern Brazil. A preliminary analysis was presented by Bizikov (1991) and involved specimens collected in Argentine Shelf and slope waters. This study addresses the patterns of growth in a tropical-subtropical environment at the northern extreme of the species distribution range in the south-west Atlantic.

MATERIALS AND METHODS

Biological samples and fishery data

Biological samples of *Illex argentinus* were obtained from the catches of 34 trawlers that operated off the Brazilian coast between 22–33°S and 45–722 m depth from 2001 to 2008. Part of the examined samples was collected from landings of national trawlers at the harbours of Santa Catarina State (south Brazil) (Perez *et al.*, 1998). Information on the fishing area, effort (mean trawl duration, number of trawls per day and trip duration) and total catch were obtained during interviews with skippers at the time of the landings. Additional samples were obtained during commercial fishing operations and trawl surveys conducted by the international trawl fleet and research vessels, respectively (Table 1). These had information on trawl position (latitude–longitude–depth), date, time and fishing effort (trawling hours) and were deep-frozen for later analysis in the laboratory.

In the laboratory, mantle length (ML) and body weight (BW) were recorded to the nearest millimetre and gram, respectively. After dissection of the mantle, gladius and statoliths were both extracted. Gladius length was measured in millimetres (GL) and stored in plastic bags with formalin (4%). Statoliths were stored in ethanol 70% (see Schroeder & Perez, 2010 and Schwarz & Perez, 2010 for details). Males and females were differentiated and maturity stages were assigned according to the macroscopic scale proposed by Brunetti (1990). This scale defined seven and eight maturity stages for males and females respectively including: immature (Stages I and II); in maturation (Stage III); early maturity (Stage IV); advanced maturity (Stage V); spawning (Stage VI for males and Stages VI and VII for females); and spent (Stage VII for males and Stage VIII for females).

Gladius growth interpretation

The preparation and interpretation of gladius growth increments followed the procedures previously defined by Perez *et al.* (1996) for *I. illecebrosus*. Gladii were washed in clean water and dried in paper tissues. Growth increments were observed directly on the gladius plate (intermediate layer) over the central rachis using a dissecting microscope (40×) connected to an image analysing system (Image-Pro Plus Media Cybernetics®). Increments were identified in the anterior, most recently deposited end (head) and counted backwards, towards the posterior end (fins) (Figure 1) until the increments become faint due to overgrowth (Perez *et al.*, 1996). Readability of both the entire structure and along the gladius length was assessed. The relation between gladius and somatic growth was tested by fitting linear and power models to ML_xGL and BW_xGL relationships, respectively, using the least squares method.

The accuracy of growth increments counts were obtained from a comparison among three independent counts in a subsample of 30 gladii conducted by three different readers. The consistency of the counts was estimated by calculating the coefficient of variability (CV; Chang, 1982), the average percent error (APE; Beamish & Fournier, 1981) and by a one-way analysis of covariance (ANCOVA) between counts. Each ANCOVA was preceded by a test of homogeneity of slopes (Zar, 1984).

The periodicity of gladius growth increment was investigated comparing the number of increments deposited in statolith and gladius of 84 individuals varying from 174 to 330 mm GL. This procedure assumed that statolith rings are daily deposited as demonstrated by Uozumi & Shiba (1993)

Table 1. Gladii of *Illex argentinus* captured in south-southern (22–33°S) Brazil used in the evaluation of age and growth studies. N_{IND} , individuals of indeterminate sex; $N \text{ ♂}$, males; $N \text{ ♀}$, females; GL, gladius length range.

Year	Latitude	Depth	N_{IND}	GL_{IND}	$N \text{ ♂}$	$GL \text{ ♂}$	$N \text{ ♀}$	$GL \text{ ♀}$
1987	–32°25'12"	65	20	14–47				
2001	–23°40'48"–28°49'55"	40–510			141	116–273	141	137–330
2002	–23°36'00"–28°51'39"	80–524	1	167	377	113–315	444	104–342
2003	–23°40'33"–24°04'59"	298–733			1	155–155	4	145–208
2004	–27°04'12"–28°51'14"	190–590	12	100–127	37	94–266	61	107–343
2005	–26°19'05"–27°13'01"	80–199	33	32–92	2	92–93	6	81–111
2006	–24°28'12"–24°35'06"	100–722	3	110–132	56	111–285	84	132–351
2007		150–500			21	224–282	43	230–344
2008		150–500			3	207–273	22	290–335
Total		40–722	69	14–167	638	92–315	805	81–351

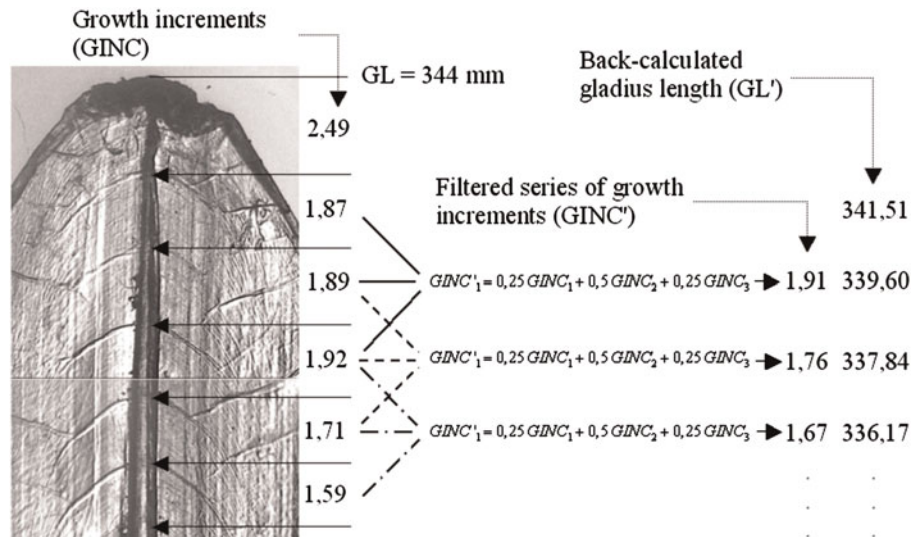


Fig. 1. Schematic representation of the series of growth increments (GINC) measured over the dorsal surface of the gladius and the back-calculation of gladius growth.

and Sakai *et al.* (2004). The statoliths were prepared following procedures described in Schwarz & Perez (2010) and growth rings were examined under a microscope at 1000× magnification. In each squid, the number of statolith growth rings was compared to the number of gladius increments deposited anterior to 170 mm of the gladius length. A linear regression fitted to this data and the H_0 : slope = 1 was tested using a *t*-test with 5% of significance (Zar, 1984). If this hypothesis was statistically acceptable, it would imply that both structures deposited growth increments with the same periodicity.

Absolute growth reconstruction

Individual absolute growth was reconstructed measuring the distance between consecutive growth increments visualized (Figure 1) where the distance between one mark and the next correspond to one gladius growth increment (GINC). A series of growth increments, obtained from the most recently deposited at the anterior border backwards to the posterior sectors of the gladius plate, were submitted to a ‘low-pass’ filter in order to eliminate sharp discrepancies between following increments, normally produced by reading errors. In formula 1, each filtered growth increment (GINC’) resulted from a weighted average among three consecutive growth increments (GINC) measured on the gladius:

$$GINC'_i = 0.25 GINC_{i-1} + 0.5 GINC_i + 0.25 GINC_{i+1} \quad (1)$$

where, $GINC_i$, is the inner filtered increment and $GINC_{i-1}$ and $GINC_{i+1}$ is the immediately anterior and posterior increments respectively where each filtered increment (GINC’) represented the absolute growth during one day (Perez *et al.*, 1996). The length of each squid gladius at previous ages (GL’) was back calculated by subtracting its GL by all its visible increments. A mean absolute growth trajectory was reconstructed using the average GINC’ per 1 mm interval of GL’ reconstructed for all individuals and for males and females separately. The slopes of the absolute trajectories were compared between sexes by an ANCOVA that was preceded by a test of homogeneity of slopes.

Age-dependent growth

A growth curve was reconstructed from the cumulative number of growth increments counted in each centimetre of gladius length interval following Perez *et al.* (1996). This procedure required: (1) the assumption of a daily deposition of gladius growth increments; and (2) that age of squid of 10 mm GL (the size at which gladius growth increments began to be seen) might be either 30 or 40 or 60 days, according to different results of statolith readings in juveniles of a sibling species, *Illex illecebrosus* (Hurley & Beck, 1979; Morris & Aldrich, 1985; Balch *et al.*, 1988) and *Illex argentinus* (Arkhipkin & Scherbich, 1991).

RESULTS

Gladius growth interpretation

A total of 1512 gladii were examined including juveniles (N = 69), with a mode in 70 mm GL, maturing and mature males (N = 638), with a more pronounced mode in 160 and a less evident one in 220 mm GL and females (N = 805), that presented a strong mode in 210 and a secondary between 290 to 310 mm GL) (Table 1). The 100–240 mm GL size-range included males and females in all gonad stages and above 200–240 mm GL mature squid predominated in both sexes (Figure 2). These were distributed in two modal groups, i.e. small female spawners (140–240 mm GL) and large female spawners (240–360 mm GL).

Linear and power models adequately described the relationship established between $GL_x ML$ and $GL_x BW$, respectively (Figure 3). The analysis of the residuals generated by the fitted models revealed that the $ML_x GL$ (Figure 3B) relationship achieved homoscedasticity, therefore, the variance of GL remained constant while ML increased. However, in the relationship $GL_x BW$ residuals showed heteroscedasticity, where variance of BW increased with an increase on GL. This increase was pronounced in individuals larger than 250 mm GL (Figure 3D), and the fitted model poorly explained the variability of the large individuals.

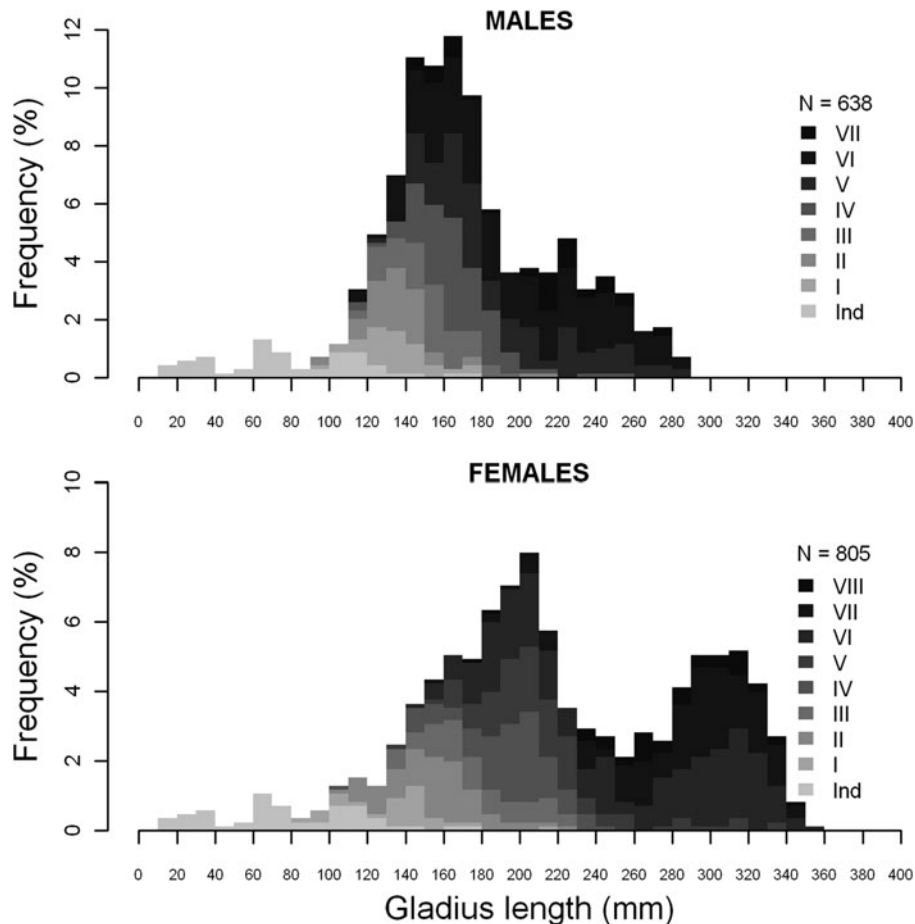


Fig. 2. Size-frequency and maturity stage distribution of males and females used in this work.

Growth increments were readable in 99% of the extracted gladii, and could be counted on the anterior half ($57 \pm 8\%$) of its length. Increments deposited in the early posterior region of the gladius plate were faint and could not be enumerated. Values of APE and CV found among three distinct readers were, respectively, 8.04 and 10.84%.

The ANCOVA applied did not find significant differences among readers (Table 2) reinforcing the accuracy of the counts. Because gladius counts for each squid included all increments deposited anterior to 170 mm GL, this assumption predicts that the fitted line should intercept the y axis at an age estimate for squids of 170 mm GL in statoliths counts. The slope obtained ($b = 0.99$) was not significantly different from the hypothesized slope = 1, and the intercept of the fitted line was 160.14 statolith rings. The number of statolith increments estimated for *I. argentinus* of 170 mm GL analysed in other studies in Brazilian waters (Schwarz & Perez, 2010) was 164 increments (Schwarz, personal communication) which approximate the regression's intercept. Moreover, the accretion of 20 growth rings in statoliths is followed by 20 gladius growth increments, which suggests that both structures deposit growth increments with the same periodicity, probably daily (Figure 4).

Absolute growth

The examined material allowed the reconstruction of mean gladius growth rate variability along almost the entire

size-range of the species (4–347 mm GL) (Figure 5A). Four growth phases were delimited by three growth discontinuities at 79 mm, 213 mm and 294 mm GL. The first three phases occupied together 85% of the GL range. These phases, however, could be differentiated by noticeable decreases in the acceleration of growth rates (principally from I to II) as confirmed by a test of homogeneity of slopes (ANCOVA) conducted for grouped sexes (Table 3). In the last phase at GL over 294 mm, absolute growth rate variability increased and stabilized at $1.43\text{--}1.99\text{ mm day}^{-1}$ (Figure 5A).

Males and females presented different gladius growth patterns during the reconstructed period, as confirmed by the test of homogeneity of slopes (ANCOVA) (Figure 5A; Table 4). Males and females absolute growth patterns started to differ at around 60 mm GL. Until 213 mm GL, males exhibited absolute growth rates significantly higher than females (Figure 5B and C). Between 214 and 282 mm GL this pattern was inverted, with females continuing to grow fast while males passed to grow less accelerated from this size (Figure 5D).

Age-dependent growth

Growth increments deposited in the initial 10 mm of gladius growth were only visible in four juveniles of 14, 15, 19 and 20 mm GL. Although the number of growth increments deposited at juvenile stage was not visible in the gladius of adult squid, in these four individuals 32, 33, 48 and 79

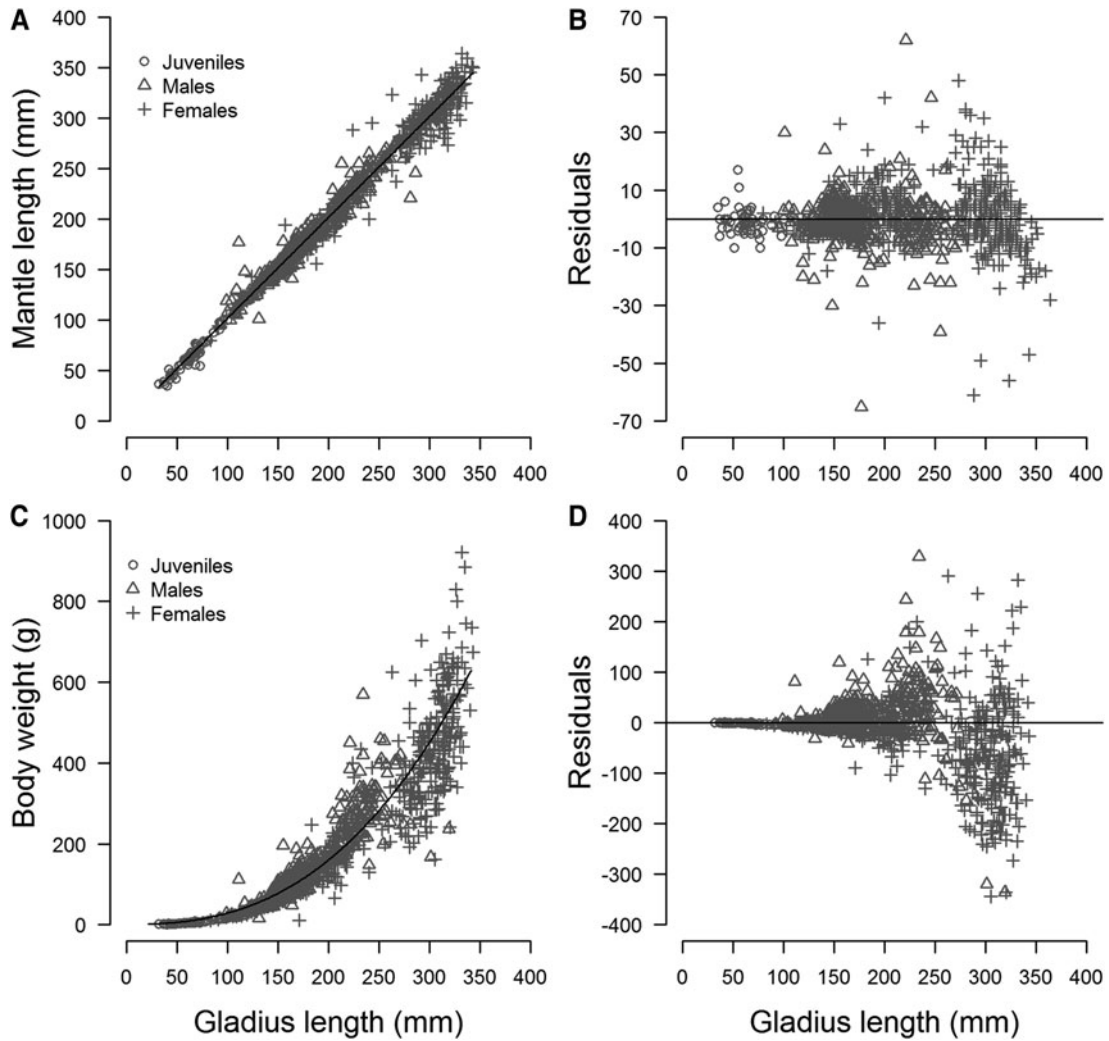


Fig. 3. Relationship between mantle length (ML), gladius length (GL) and body weight (BW): (A) the linear relationship found ($ML = 1.70 + 0.99 (GL)$ ($r^2 = 0.98$)); (B) residuals; (C) the power relationship found ($BW = 6E-05 (GL)^{2.7876}$ ($r^2 = 0.95$)); (D) residuals.

growth increments counted in these gladius sectors are in accordance with the initial values assumed. Ages estimated were 368, 369, 384 and 415 days respectively, for the initial ages of 32, 33, 48 and 79 days (Figure 6).

DISCUSSION

The patterns of use of the gladius as a tool for age and growth studies corroborated previous investigations conducted on *Illex argentinus* (Bizikov, 1991), *Sthenoteuthis ovalaniensis* (Arkhipkin & Bizikov, 1991; Bizikov, 1995), *Sepioteuthis*

Table 2. Homogeneity of slopes and analysis of covariance (ANCOVA) tests for regressions between readers (factors). Reader 1 was used as covariate. Significant values of *P* are printed in bold. Degrees of freedom (DoF), mean squares (MS), and F ratios are also indicated.

Homogeneity of slopes	DoF	MS	F	<i>P</i>
Factor × covariate	2	233.604	0.753	0.474
ANCOVA	DoF	MS	F	<i>P</i>
Factor	2	923.922	2.996	0.055
Covariate	1	129793.763	420.872	<0.001

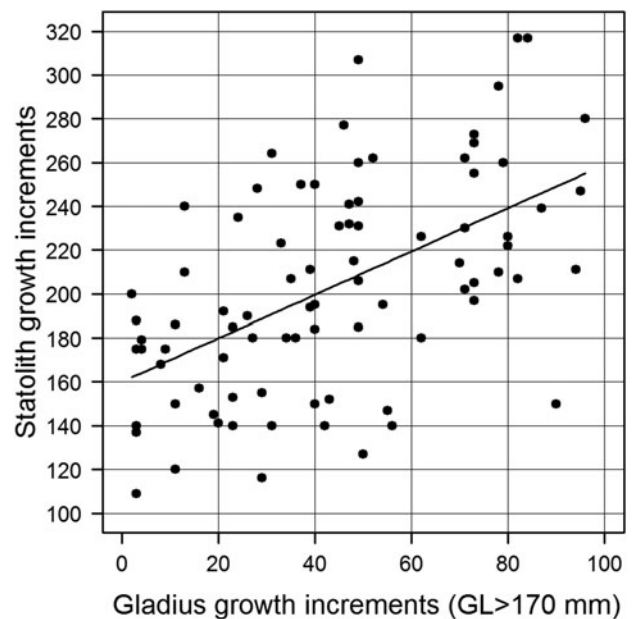


Fig. 4. Linear relationship between growth rings counted in statolith and growth increments enumerated anterior to 170 mm gladius length (GL) in gladius of 84 individuals. The solid line represents the linear model fitted to the data set.

Table 3. Homogeneity of slopes and analysis of covariance tests for regressions between growth phases for grouped sexes (factors). Gladius length was used as covariate. Significant values of *P* are printed in bold. Degrees of freedom (DoF), mean squares (MS), and F ratios are also indicated.

Growth phase I × II				
Homogeneity of slopes	DoF	MS	F	<i>P</i>
Factor × covariate	1	0.449	1967	<0.001
Growth phase II × III				
Homogeneity of slopes	DoF	MS	F	<i>P</i>
Factor × covariate	1	0.010	58	<0.001
Growth phase III × IV				
Homogeneity of slopes	DoF	MS	F	<i>P</i>
Factor × covariate	1	0.155	25	<0.001

lessoniana (Jackson *et al.*, 1993), *Illex illecebrosus* (Perez *et al.*, 1996), *Doryteuthis plei* (Perez *et al.*, 2006) and *Lolliguncula brevis* (Zaleski, 2010). Gladius plate was unsuitable for age determination because the number of growth increments deposited throughout life were not visible during the juvenile growth phase. Yet the daily nature of gladius growth increments of the

intermediate shell layer was supported and a high correlation with body growth was established. Combined, these elements allowed the interpretation of gladius growth rate series as proxies for individual growth ‘histories’.

The most remarkable feature of *I. argentinus* absolute growth off the Brazilian coast was the continuous increase of growth increments, consistent throughout most of the species size-range (Brunetti *et al.*, 1998). This trend, however, is not homogeneous, but exhibits discontinuities, the most noticeable of them at approximately 80 mm GL. This transition may be related to the lifestyle shift to demersal habits in the outer shelf and also by environmental components (i.e. bottom temperature) as demonstrated in the present study. It is also interesting to note that gladius growth rates of *I. illecebrosus* also shift their accelerating pattern at a similar size (Perez & O’Dor, 2000). Yet in this species (and geographical area) absolute growth rates (mm day⁻¹) completely stabilize in larger squid, a pattern that has been principally attributed to important environmental transitions experienced by juvenile squid (Perez & O’Dor, 2000). During early life, paralarvae of *I. illecebrosus* are concentrated offshore, mostly under the influence of Gulf Stream warm and oligotrophic waters (temperature >16°C). As juveniles move shoreward into shelf/slope front they experience a sharp temperature decrease as they become

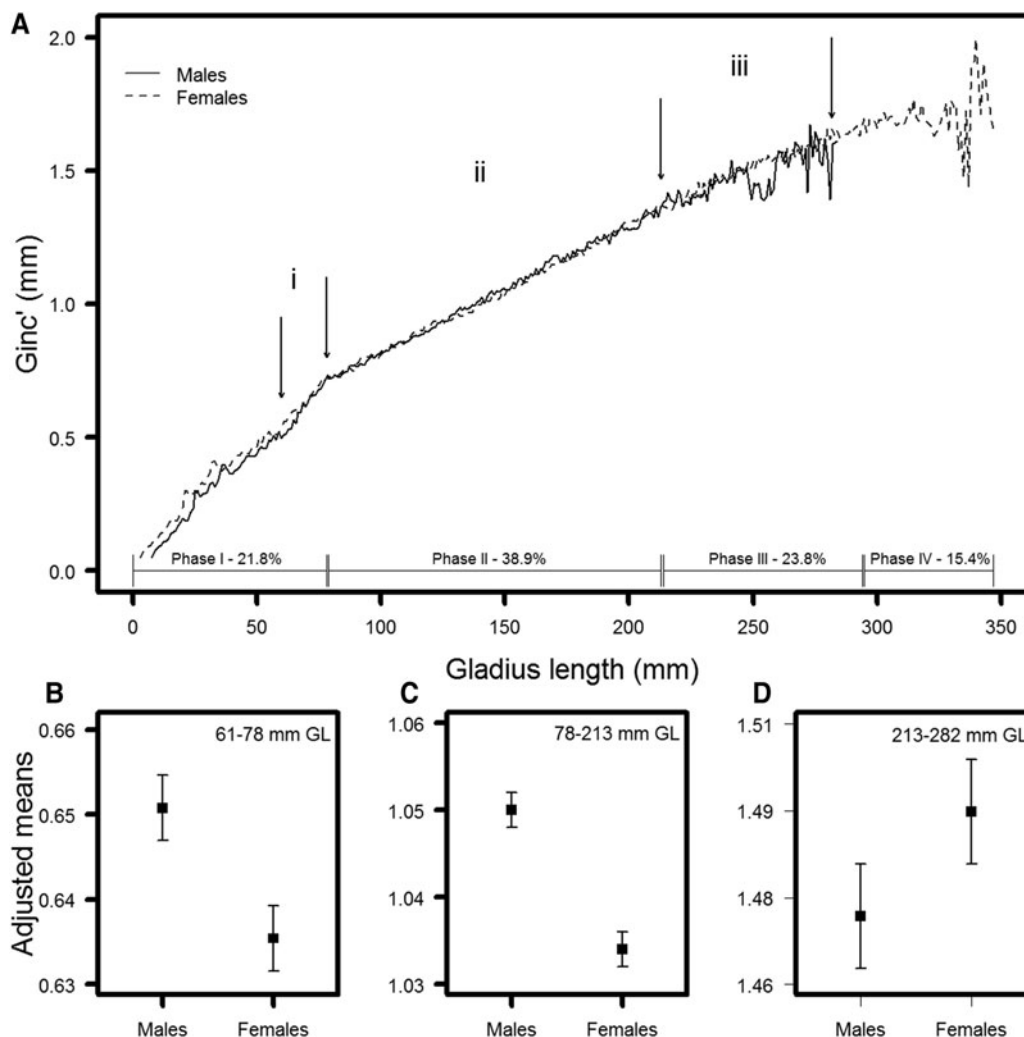


Fig. 5. (A) Mean absolute growth curves reconstructed for males and females and the growth phases identified. i, ii, iii are the growth intervals compared between males and females; (B–D) are the adjusted means for males and females in i, ii and iii, respectively.

Table 4. Homogeneity of slopes and analysis of covariance (ANCOVA) tests for regressions between sexes (factor). Gladius length was used as covariate. Significant values of *P* are printed in bold. Degrees of freedom (DoF), mean squares (MS), and F ratios are also indicated.

GL 61–78 mm									
Homogeneity of slopes	DoF	MS	F	<i>P</i>	ANCOVA	DoF	MS	F	<i>P</i>
Factor × covariate	1	<0.001	1.518	0.226	Factor	1	0.003	34.469	<0.001
					Covariate	1	0.101	949.937	<0.001
GL 79–213 mm									
Homogeneity of slopes	DoF	MS	F	<i>P</i>	ANCOVA	DoF	MS	F	<i>P</i>
Factor × covariate	1	<0.001	0.530	0.466	Factor	1	0.016	133.12	<0.001
					Covariate	1	9.277	75743.97	<0.001
GL 214–282 mm									
Homogeneity of slopes	DoF	MS	F	<i>P</i>	ANCOVA	DoF	MS	F	<i>P</i>
Factor × covariate	1	0.012	7.455	0.007	Factor	1	0.012	7.420	0.007
					Covariate	1	0.596	340.849	<0.001

exposed to a larger food supply (O'Dor, 1983). At approximately 90 mm GL squid reach the Scotian shelf experiencing temperatures as low as 5–6°C during the spring time (Perez & O'Dor, 2000). Such inshore movement seems energetically favourable, since their growth performance, measured as the wasted daily growth potential (the quantity of food required to achieve maximum growth), greatly improves (Perez & O'Dor, 1998). Yet squid in cold and productive shelf environments grow at a constant rate.

Contrastingly, paralarvae of *I. argentinus* off the Brazilian coast seem to concentrate on the shelf in association with coastal upwelling areas (Vidal *et al.*, 2010). As they develop into juveniles and sub-adults they move offshore to the shelf break and slope areas where spawning individuals are found (Haimovici *et al.*, 1998). No temperature measures were available at the capture sites of the examined samples. However, when mean bottom temperature profiles, measured throughout the year along the sampled area (Haimovici *et al.*, 2008) are compared with the depth of capture of individuals used for individual growth reconstruction (Figure 7) it is observed that: (a) small individuals (GL <89 mm GL) concentrated

below 150 m where temperatures oscillate around 15–16°C; and (b) as individuals increase in size they move into deeper sectors of the shelf break and slope experiencing progressively colder waters (14–7°C). In contrast to *Illex illecebrosus*, which linear absolute growth rates do not change with size in this colder environment (Perez & O'Dor, 2000), those in *I. argentinus* increase with GL though with lower rate than among juveniles in warmer shelf waters.

Another relevant factor associated with the growth rate trends observed in *I. argentinus* off Brazil refers to the potential interference of different spawning groups in the examined samples. According to reproductive patterns and statolith-derived age and hatching date data, most squid concentrations off Brazil were composed of 'local' spawning groups that live approximately half-year and spawn at small sizes (150–250 mm ML). Yet during winter–spring months concentrations of large (ML > 250 mm), nearly 1-year-old, mature males and females occur in the lower slope, possibly originated from migratory components of northern Patagonian Shelf spawning groups (Perez *et al.*, 2009; Schwarz & Perez, 2012). Both spawning groups have been mixed to compose the absolute growth rate analysis (Figure 5) but were differentiated by the maturation data (Figure 2) and also by disruptions of the GL_xBW relationships (Figure 3). As a consequence, gladius absolute growth phases would characterize growth patterns of 'local' spawning groups (phases I and II), large winter spawners (phase IV), and the mixture of both groups (phase III). The implications were of such effect were that:

- the discontinuity growth between phase II and III is unrealistic, i.e. not determined by real life-history transitions;
- large winter spawners may have a longer stable growth rate pattern (phase IV) such as the one observed in *I. illecebrosus*;
- 'local' spawners accelerate growth continuously to reach spawning sizes earlier within a 0.5 year life span, according to Schwarz & Perez (2012).

The growth curve as reconstructed by the cumulative growth increments in gladius differ from the one estimated for statolith (Schwarz & Perez 2010) which typically follow the Sachs cycle of growth with increase of growth in the first part and decrease in growth rates in the second part of ontogenesis, represented by an s-shaped curve (Arkhipkin & Roa-Ureta, 2005). One possible explanation is that as mantle shrinks the gladius tend to bow, the result being that it is longer than the projected mantle length (Perez, 1995).

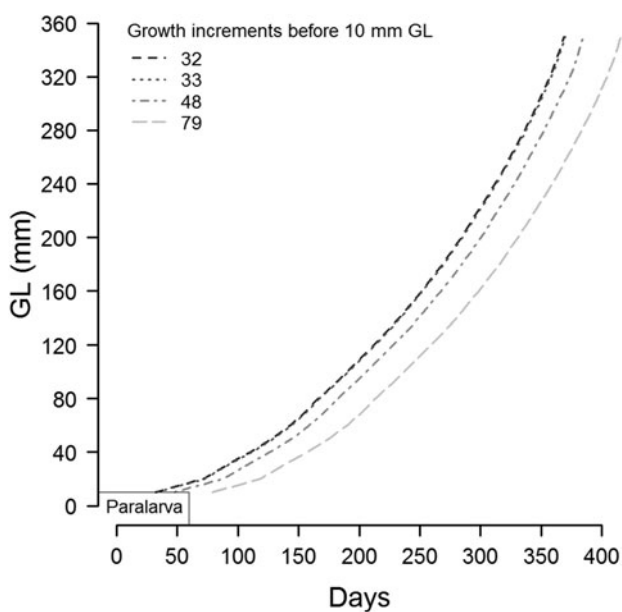


Fig. 6. Growth curve reconstructed from the cumulative number of growth increments reconstructed for the initial ages of 32, 33, 48 and 79 days.

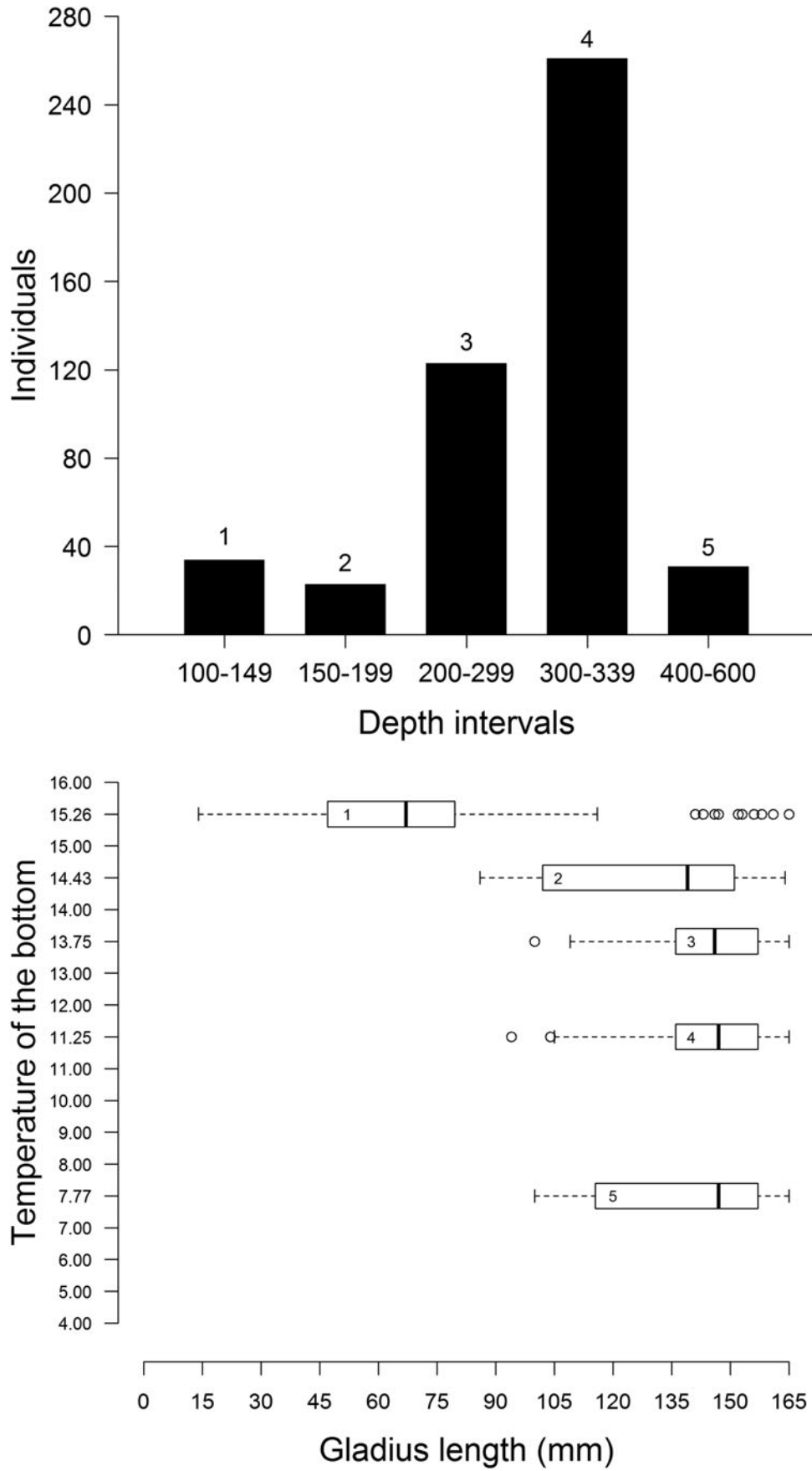


Fig. 7. (A) Distribution of gladius length (GL) samples under 165 mm according to depth strata obtained from Haimovici *et al.* (2008); (B) GL distribution of the same samples was plotted against the mean temperature obtained in each stratum.

Nevertheless, the initial age estimates of 30–40 days corroborate the studies of Arkhipkin & Scherbich (1991) and Schwarz & Perez (2012) for *I. argentinus*, and the ages achieved for older individuals were one year.

Considering that the environmental factors such as temperature and nutrition directly affect the onset of maturity and indirectly affect growth (Boyle & Rodhouse, 2005) and that species are likely to adapt to the temperature and environment at which they live, the accelerated absolute growth and earlier development of the gonads of the 'local' individuals observed in Perez *et al.* (2009) may represent a life-history strategy in which organisms grow fast, mature earlier and produced offspring sooner (Wood & O'Dor, 2000). Our data show that in Southern Brazil *Illex argentinus* fully exploit high flexibility of life cycles particular for cephalopods (Boyle & Boletzky, 1996) and display both possible ways of use of annual changes in environment. One population lives generally for six months and another for a whole year that ensures the maximum sustainable use of highly variable food resources of the tropical shelf and upper slope.

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