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# Analysis of shape variability and life history strategies of *Illex argentinus* in the northern extreme of species distribution as a tool to differentiate spawning groups

Rafael Schroeder [a], Richard Schwarz [b], Augusto César Crespi-Abril [c,d] and José Angel Alvarez Perez [a]

aGrupo de Estudos Pesqueiros, Universidade do Vale do Itajaí, Itajaí, Brazil; bEvolutionary Ecology of Marine Fishes, GEOMAR, Kiel, Germany; cCentro Nacional Patagonico (CENPAT-CONICET), Puerto Madryn, Argentina; dUniversidad Nacional de la Patagonia San Juan Bosco, Puerto Madryn, Argentina

**ABSTRACT**

This study aimed to differentiate local and migratory spawning groups of the shortfin squid *Illex argentinus* caught in Brazilian waters using geometric and traditional morphometric methods and size-selective processes. The back-calculated length distributions reconstructed from daily growth increments deposited in the gladius allowed the identification of size-selective processes that may be related to different life history strategies. Landmark analysis on body shape (geometric morphometric) revealed that spawning groups presented significant ontogenetic variations in terms of body outline. In addition, traditional morphometric methods, based on multivariate analysis, associated juveniles of the expected migratory group (large size) and differentiated them from the local group individuals (small size). The changes in form, probably linked to the environmental gradients experienced by individuals throughout ontogeny, were interpreted as adaptations to improve swimming capacity. Migrant individuals have being differentiated from the smaller sizes group by body characteristics (broad fins, elongated and thicker mantle), which may increase the ability to perform long migrations.

## Introduction

The Argentine shortfin squid, *Illex argentinus* (Castellanos, 1960) (Teuthida: Ommastrephidae), is a neritic–oceanic species associated with the oceanographic system Falkland (Malvinas)/Brazil current (Haimovici et al. 1998) and is distributed on the continental shelf and slope of southwest Atlantic, where it sustains one of the largest world squid fisheries (Arkhipkin, Rodhouse et al. 2015). Like most ommastrephid squid, *I. argentinus* has a life cycle of about 1 year (Arkhipkin 1990, 1993), fast growth and semelparity, dying after one single spawning event. In this reproductive strategy, population renewal depends exclusively on the success of recruitment (Boyle 1983). However, the recruitment failure risks involved in this particular life cycle are believed to

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be attenuated by a long spawning period and transport of planktonic offspring by geostrophic currents resulting in the formation of geographic and seasonal population subunits, typically composed of individuals with different biological attributes, such as growth rate, size and age of maturity (Carvalho and Nigmatullin 1998).

On the Patagonian Shelf, Brunetti (1988) distinguished three spawning stocks based on the distribution of early life stages, juveniles and adults: one Summer Spawning Stock and two winter spawning stocks, the South Patagonian Stock and the Bonaerensis North Patagonian Stock, separated by feeding grounds and size of the adults (Rodhouse et al. 2012). The studies of the biological attributes of *I. argentinus* distributed between 27° and 34°S showed the presence of juveniles and spawning individuals throughout the year, but especially in winter months (Haimovici and Perez 1990; Santos and Haimovici 1997). This winter group was defined as the South Brazil Stock, and because of biological similarities, these spawners have been considered a reproductive extension of the Bonaerensis North Patagonian Stock, which migrated northwards during winter months to spawn in the south-southeastern waters of Brazil (Santos and Haimovici 1997; Haimovici et al. 1998). The offspring generated could supply local stocks of the species or be transported by the oceanographic system Falkland (Malvinas)/Brazil currents beyond latitudes south of 34°S (Haimovici et al. 1995). Fishing and population aspects of the Argentine squid distinguished another group referred to as the Central Brazil Stock composed of small squid distributed from 22° to 34°S with juveniles and spawning individuals present throughout the year (Perez et al. 2009).

The slope waters north of 38°S may represent the spawning ground for winter spawners between May and September, based on paralarvae concentration (Rodhouse et al. 2012) and environmental characteristics that confer optimal survival conditions to hatchlings (Crespi-Abril and Barón 2012). After hatching, winter spawning groups migrate to forage over the Patagonian shelf in December and January (Rodhouse et al. 2012) whereas those retained in Brazilian waters may experience more oligotrophic conditions (Santos and Haimovici 1997). Environmental gradients are known to cause inter- or intra-specific variations in morphometry of both soft and hard structures, especially in species with a wide range distribution (Darwin 1859; Thompson 2005). The exposure to low temperature during early life as well as feeding conditions experienced by juveniles and at the onset of maturity, may delay maturation to a larger size promoting a longer lifespan (Mangold 1987; Arkhipkin and Scherbich 1991). Evidence of intraspecific variability in longevity was observed in squid of the genus *Illex*, which can perform long migratory routes with stocks exhibiting distinct geographical ranges in the average life cycle from 6 months in tropical areas extending to more than 1 year in temperate and subpolar waters (Arkhipkin et al. 2000; Schwarz and Perez 2013).

Considering that the environmental factors directly affect the onset of maturity and growth (Arkhipkin, Argüelles et al. 2015) and that species are likely to adapt to the environment where they live, the local group of spawning individuals observed in Perez et al. (2009) may perform a life-history strategy in which organisms grow fast, mature earlier and produce offspring sooner (Wood and O'Dor 2000). *Illex argentinus* captured off southern Brazil exhibits highly flexible of life cycles, typical of cephalopods in general (Boyle and Boletzky 1996) displaying a continuum of lifespan strategies according to annual changes in environment. The lifespan of small-size squid populations is about 6 months whereas large spawners can reach 1 year lifespans, maximizing the use of

highly variable food resources of the tropical shelf and upper slope (Schwarz and Perez 2013; Schroeder and Perez 2013).

The interactions of environmental conditions affecting growth and form have been widely discussed for several organisms (Thompson 2005). For cephalopods, morphometric analysis has extensively been used to assess shape variability through ontogeny to distinguish different taxa or population units (Haefner 1964; Brunetti and Ivanovic 1991; Arkhipkin 1993; Arkhipkin and Laptikhovsky 1994; Vidal 1994; Zecchini et al. 1996; Carvalho and Nigmatullin 1998; Hernández-García and Castro 1998; Barón and Ré 2002; Martínez et al. 2002; Shea and Vecchione 2002; Vega et al. 2002). Classical methods based on analysis of measurement over body dimensions (Cadrin 2000) may not fully represent shape variation (Bookstein et al. 1985; Adams et al. 2004; Zelditch et al. 2004). Advances in geometric morphometrics methods (Rohlf, 1998; Richtsmeier et al. 2002; Adams et al. 2004) have been used to discriminate few squid species by the morphology of statoliths (Lombarte et al. 2006; Neige 2006) and to differentiate spawning groups of *I. argentinus* by morphometrics of beaks and body (Crespi-Abril et al. 2010). In this study three methodologies were tested with the objective to differentiate local and migratory spawning groups of the Argentine shortfin squid off southern Brazil, the northern extreme of species distribution. Methods used assessed (a) the use of geometric morphometrics to differentiate spawning groups present in south-southeastern Brazilian waters, (b) possible correspondences between juveniles from the migratory group and the expected spawning groups that migrated into Brazilian waters by using traditional morphometrics and (c) influence of size-selective processes that acted upon squid during migration. Large sized squid captured in slope waters during the winter months (July–September) have been considered members of the migratory group (MG) while small sized squid captured throughout the year over the shelf and shelf-break will be considered as the local group (LG).

## Materials and methods

### Biological samples and fishery data

Biological samples of *I. argentinus* were obtained from the catches of trawlers that operated off the Brazilian coast between 22° and 33°S and 45 and 722 m depth between 2001 and 2013 (Figure 1(a)) and during trawl surveys conducted by a research vessel (Figure 1(d)). Those had information on trawl position (latitude–longitude–depth), date, time and fishing effort (trawling hours). Samples were deep-frozen and sent to the laboratory. In each specimen, mantle length (ML) and body weight (BW) were recorded in millimetres and grammes, respectively. Sex was differentiated and maturity stages were assigned according to the macroscopic scale proposed by Brunetti (1990). This scale defined eight maturity stages: 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). After dissection of the mantle, the gladius was extracted, measured in millimetres (GL), and stored in plastic bags with formalin (4%). Stomach contents were only assessed for presence and absence of food remnants.
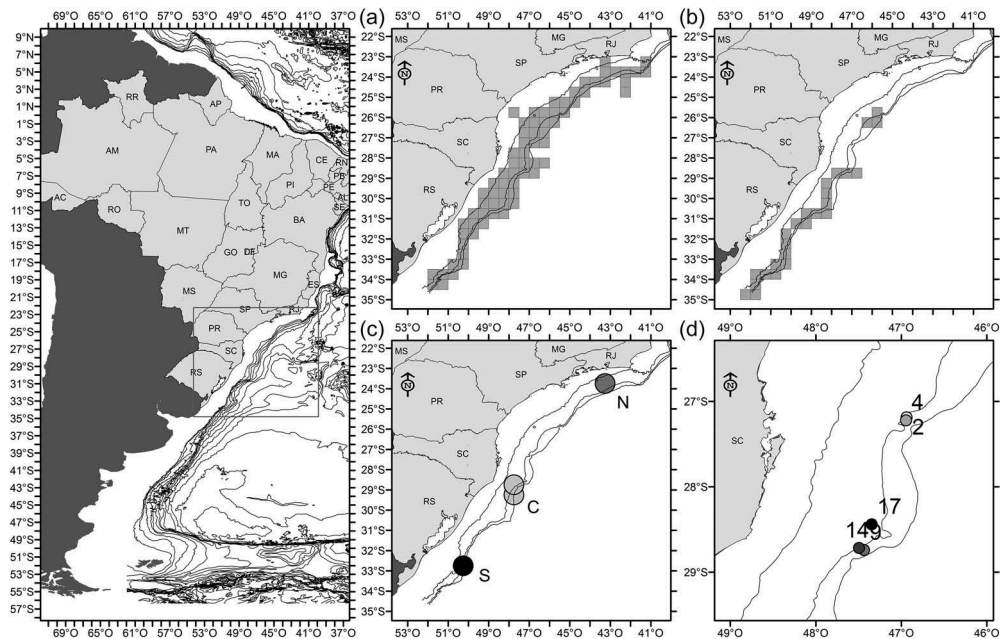
**Figure 1.** Spatial representation of the study area. (a–c) Positions of the samples of *Illex argentinus* collected from trawlers south-southeast of Brazil between 22° and 33°S and 45 and 722 m depth from 2001 to 2013. (b) Samples used in geometric morphometric analysis. (c) Samples used in traditional morphometric analysis. (d) Samples collected during a research cruise during August of 2004 in the same area to identify size-selective processes. Lines in maps represent 100, 300 and 700 m depth.

Analyses were conducted according to the objectives of this study: geometric morphometric analysis (Figure 1(b)), traditional morphometric analysis (Figure 1(c)) and to identify size-selective processes (Figure 1(d)). Population groups were represented by samples with different biological attributes (e.g. size, size-at-maturity, depth of catch) collected in shelf-break/slopes waters, based on the study of Perez et al. (2009) (Table 1).

## Geometric morphometrics

The photographs were taken over the dissecting table of each specimen for landmark analysis with a digital camera Sony DSC-S2000 (10.1 megapixels) mounted on a table top to ensure that the plane of the camera was parallel to the frontal plane of the squid. Animals were spread ventral side facing up to avoid the fins hanging from the lateral sides of the mantle, according to the methodology proposed by Crespi-Abril et al. (2010). Each photograph included a scale to standardize individual size. Body shape was characterized by nine landmarks arranged in two dimensions (Figure 2). Landmarks 1–7 are composed by the encounter of at least two structures (i.e. the posterior tip of the body) while landmarks 8–6 are supported by geometric criteria; i.e. projection of the connecting point of fin and mantle margins on the longitudinal axis of the body (Bookstein 1991; Dryden and Mardia 1998). Landmark coordinates were obtained using the software TPSDig version 2 (Bookstein 1998).

**Table 1.** Summary of data for *Illex argentinus* obtained off Brazil between 2001 and 2013 separated according to Figure 1.

| Year | A/T | Date | TD (min) | Lat (°S) | Depht (m) | ML (mm) | BW (g) | J | M | F | Figure 1 |
|------|-----|------|----------|----------|-----------|---------|--------|---|---|---|----------|
| 2001 | – | – | – | 23.675–28.832 | 35–510 | 78–395 | 8.15–655 | 22 | 1206 | 1039 | a |
| 2002 | – | – | – | 23.600–46.602 | 80–622 | 98–376 | 18.00–830 | 37 | 1352 | 1440 | |
| 2003 | – | – | – | 23.676–33.750 | 179–740 | 105–290 | 29.24–645 | 1 | 282 | 240 | |
| 2004 | – | – | – | 27.070–28.854 | 190–603 | 94–375 | 11.02–921 | 25 | 214 | 240 | |
| 2005 | – | – | – | 26.318–28.750 | 80–400 | 45–351 | 1.80–745 | 38 | 33 | 124 | |
| 2006 | – | – | – | 24.470–33.750 | 100–722 | 110–351 | 41.30–870 | 4 | 823 | 812 | |
| 2007 | – | – | – | 23.750–33.250 | 150–500 | 135–353 | 37.35–910 | 1 | 281 | 389 | |
| 2008 | – | – | – | 23.750–33.750 | 150–500 | 128–343 | 46.48–845 | 45 | 1776 | 3215 | |
| 2009 | – | – | – | 23.106–32.250 | 44–615 | 73–320 | 7.88–674 | 22 | 312 | 208 | |
| 2010 | – | – | – | 23.250–34.250 | 120–550 | 102–394 | 20.11–926 | 0 | 3787 | 4051 | |
| 2011 | – | – | – | 23.750–33.750 | 250–450 | 112–333 | 28.70–623 | 157 | 1170 | 901 | |
| 2012 | – | – | – | 32.000–34.300 | 300–420 | 127–325 | 39.23–626 | 0 | 148 | 320 | |
| 2013 | – | – | – | – | 280–400 | 195–350 | 147.63–866 | 0 | 40 | 84 | |
| 2009 | NM | – | – | 32.250 | 180 | 122–245 | 44.05–405 | 1 | 18 | 13 | b |
| 2009 | NM | – | – | 26.250 | 380 | 141–233 | 57.26–280.88 | 0 | 12 | 17 | |
| 2009 | NM | – | – | 33.250 | 240 | 189–300 | 179.50–590 | 0 | 15 | 15 | |
| 2009 | M | – | – | 28.750 | 557 | 210–320 | 157.00–674 | 0 | 22 | 8 | |
| 2010 | M | – | – | 30.750 | 400 | 231–361 | 315.00–881 | 0 | 1 | 19 | |
| 2013 | M | – | – | 34.750 | 250 | 195–345 | 147.63–695 | 0 | 10 | 20 | |
| 2005 | J* | – | – | – | – | 152–263 | 37.12–319 | 0 | 74 | 72 | c |
| 2006 | C | – | – | 29.250 | 335–335 | 178–344 | 93.29–615 | 0 | 12 | 29 | |
| 2006 | N | – | – | 23.750 | 335–365 | 110–210 | 25.15–189.92 | 4 | 45 | 29 | |
| 2006 | S | – | – | 32.750 | 165–165 | 140–338 | 41.30–870 | 0 | 16 | 19 | |
| 2004 | 2 | AUG/09 | 32 | 27.188 | 314 | 105–301 | 17.54–198 | 2 | 5 | 4 | d |
| 2004 | 4 | AUG/09 | 31 | 27.223 | 450 | 94–186 | 12.15–164 | 6 | 7 | 0 | |
| 2004 | 9 | AUG/11 | 30 | 28.742 | 575 | 213–340 | 109.50–885 | 8 | 7 | 0 | |
| 2004 | 14 | AUG/11 | 45 | 28.718 | 305 | 124–335 | 218.28–650 | 2 | 11 | 0 | |
| 2004 | 17 | AUG/12 | 31 | 28.440 | 297 | 112–211 | 31.64–59.94 | 6 | 7 | 0 | |

* This sample does not have the precise place of capture, but it was in the Argentinean/Uruguay common fishing zone.
Year, year of capture; A/T, area of capture or number of trawl; Date, date of capture; TD, trawl duration (in minutes); Lat (°S), minimum and maximum latitude of capture; Depth (m), minimum and maximum depth of capture (in metres); ML (mm): smallest and largest mantle length (in milimetres); BW (g) total wet body weight (in grammes) and squid separated by sex (J = juveniles. M = males and F = females).
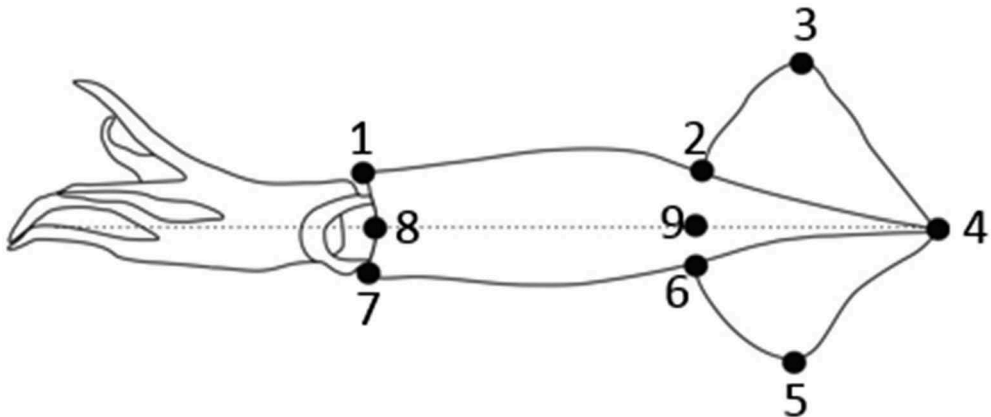


**Figure 2.** Landmark configuration on the body of *Illex argentinus*. Dashed line represents the longitudinal axis of the body.

Landmarks 1, 9 and 8 were forced to the main longitudinal axis. This correction was necessary to correct for possible bending of individuals (Rohlf 2001; Crespi-Abril et al. 2010). These transformations were performed under TpsUtil 1.37. Landmark configurations were translated, rotated and scaled for all individuals by Generalized Procrustes Analysis (Zelditch et al. 1998; Rohlf 2001; Adams et al. 2004). Translation and rotation were achieved by a superimposition method and adjusted for individual inclination and relative position by minimizing the square root of the sum of square differences between corresponding landmarks (Rohlf 1999). Corrections were applied to landmark configurations so that all individuals were scaled to the same centroid size. Shape differences were analysed by the difference between Procrustes coordinates derived from Generalized Procrustes Analysis (Adams et al. 2004; Zelditch et al. 2004). The estimation of the size of each individual was taken from the centroid size, which is the square root of the sum of the squared deviations of landmarks from a centroid point (Rohlf and Cannatella 1998; Richtsmeier et al. 2002). The presence of allometry (changes in shape related to changes in size) was examined by a multivariate regression analysis between shape scores as a dependent variable (Procrustes coordinates) and size as an independent variable. The main shape changes in body were visualized through a principal component analysis performed over the variance–covariance matrix of the Procrustes coordinates. All shape analyses were performed using MorphoJ v1.05d (Klingenberg 2011). Additionally, to analyse ontogenetic shape variation of the mantle, a scatter plot of the first principal component and the logarithm of centroid size (CS) was built, as suggested by Crespi-Abril et al. (2010).

Shape analysis was first conducted by plotting the principal component 1 ($PC_1$) and axis 2 ($PC_2$) separated by sex and groups (LG and MG). Then, the ontogenetic variation of shape was conducted by plotting the axis 1 versus the centroid size and body weight. Considering that fully mature gonads may occupy a large portion of the mantle and this may affect its shape, the influence of female reproductive organs, ovary weight (OvW) and nidamental gland weight (NgW) divided by body weight was explored. Shape variability ($PC_1$) was confronted to centroid size and the indexes were created (OvWBW and NgWBW) by a one-way analysis of covariance (ANCOVA). In this analysis, centroid size, OvWBW and NgWBW were the covariates and group (LG and MG) was used as the grouping factor.

## Traditional morphometrics

Considering the differences previously found in the length versus weight relationship (Schroeder and Perez 2013), variables that could have different relationships between groups through maturation, such as, BW, mantle weight, the perimeter of mantle aperture and the length of the fourth right arm, were used in a principal component analysis. This analysis used samples of adult squid collected in different parts in the northern extreme of species distribution during the fourth semester of 2006 (Figure 1(c), Table 1) and a sample composed mostly of juveniles from the Uruguayan/Argentine common fishing zone, here defined as juveniles from the migratory group (J). This analysis aimed to verify a possible correspondence of J and the expected MG, represented by two samples collected in the south (S) and central (C) portions of the studied area and whether J was morphometrically different from individuals of the similar size of

the LG, captured in the north (N) portion of study area (Figure 1(c)). All variables were standardized per ML to remove the effect of size.

### Individual growth reconstruction

The preparation and interpretation of gladius growth increments followed adaptations of the procedures previously defined by Bizikov (1991), Perez et al. (1996) and Schroeder and Perez (2010, 2013). 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) until the increments become faint due to overgrowth (Perez et al. 1996) (Figure 3). Individual absolute growth was reconstructed measuring the distance between consecutive growth increments visualized (Figure 3) where the distance between one mark and the next corresponds 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 subject to a 'low-pass' filter to eliminate sharp discrepancies between consecutive increments,
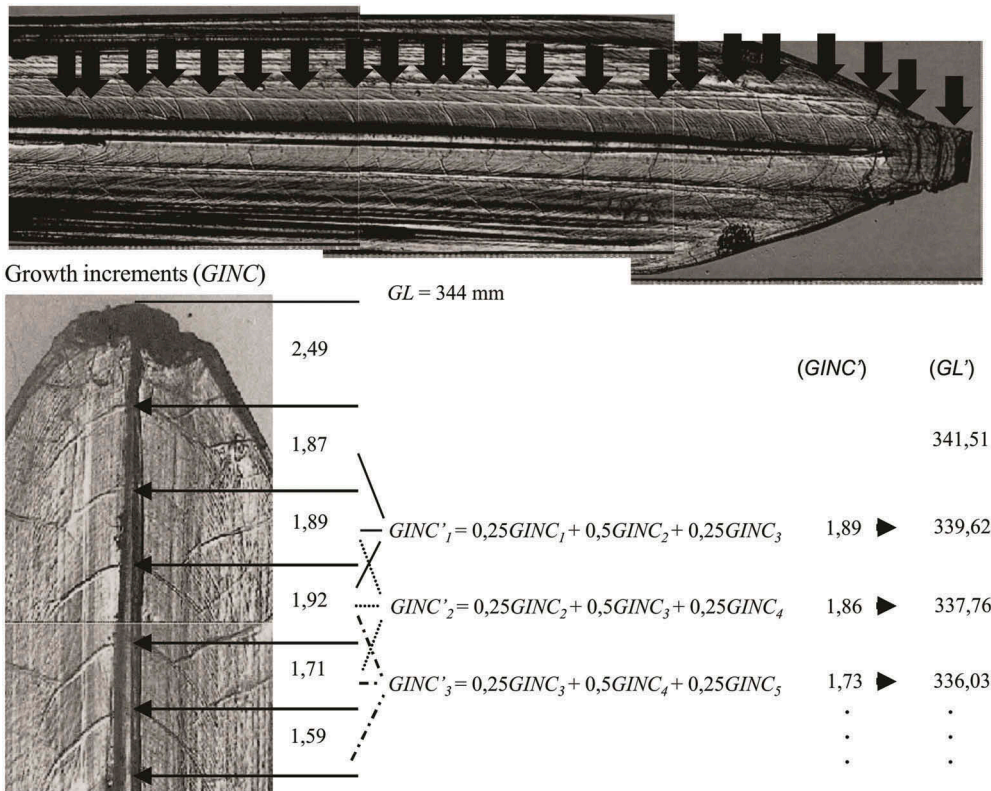


**Figure 3.** Schematic representation of the series of growth increments (GINC) read over the dorsal surface of the gladius, the filtering process and the back-calculation of the gladius growth.

normally produced by reading errors. In the formula, each filtered growth increment (GINC′) resulted from a weighted average among three consecutive growth increments (GINC) measured on the gladius:

$$GINC'_1 = 0.25GINC_{i-1} + 0.5GINC_i + 0.25GINC_{i+1}$$

where, $GINC_i$ is the inner filtered increment and $GINC_{i-1}$ and $GINC_{i+1}$ are the immediately anterior and posterior increments, respectively. Each filtered increment (GINC′) represented the absolute growth during 1 day (Perez et al. 1996). The length of each squid gladius at previous ages (GL′) was back-calculated by subtracting its GL from all its increments. A mean absolute growth trajectory was reconstructed using the filtered GINC′.

## *Size-selective processes*

The identification of size-selective processes was based on squid samples collected from a research cruise in slope waters during August 2004 (Figure 1, Table 1). Recent growth of individuals captured in five trawls was analysed. Trawls were performed from 9 October to 12 October 2004 during the day for 30 min (Table 1). A one-way analysis of variance was first applied to detect differences between mean gladius length in different trawls. The 15 most recent growth increments deposited on the gladius (RGi) were used to describe the recent growth conditions and to eliminate the possible effects of spatio-temporal variability in growth. Recent growth patterns in these trawls considered as different geographical situations were compared by an ANCOVA. To remove the effect of size on growth increments width the initial gladius length (GLi) back-calculated for 15 days before the capture was the covariate and GINC was the dependent variable. Because the measured increments on the gladius cannot be considered fully independent observations, the procedure called 'repeated measures' was used, being more appropriate in these cases (Zar 1984). In this procedure, ANCOVA was applied in two steps:

- Between subjects, where the full interval of growth over the last 15 days was compared between the grouping factors (TRAWLS);
- Within subjects, where individual growth trajectories during the last 15 days were compared and DAYS was also considered as a grouping factor.

All ANCOVA were preceded by the homogeneity-of-slopes test. After that, four trawls performed at the same place and almost the same dates were used. A series of 60 growth increments from the first mark were used to reconstruct gladius length in past intervals, which was used to reconstruct size frequency distributions of groups caught in the same trawl, assuming that they belong to the same school, squid that have been swimming together during the 60 days that preceded the capture. The study of the variation of the form of these distributions over time, described by the asymmetry coefficient ($g_1$) (Zar 1984), was used to infer population processes that involve selection by size and compare with the length distributions observed (Arkhipkin and Perez 1998).

## Results

### *Geometric morphometrics*

The multivariate regression of shape on centroid size was significant (permutation test with 10,000 random permutations, $p < 0.017$). Consequently, subsequent analyses performed with the residuals of the regression are free of allometric effects (Klingenberg 2016). Principal component analysis performed on body shape of *I. argentinus* showed that the first and second PC explained 83% of the total shape variation (Figure 4). Despite the great variability explained by the first two axes, the shape was similar between sex (Figure 4(c)) and groups (Figure 4(e)). Shape variation for positive values in $PC_1$ was characterized by larger fins and wider mantle than for negative values (Figure 4).

The ontogenetic variation in shape showed the same pattern (Figure 4(d)). The great difference occurred when groups were compared. Individuals of the MG presented a mean centroid size of 0.43, and few small individuals of this group were present in the samples. Individuals of the LG presented mean centroid size of 0.33, a difference consistent with the difference in length distribution observed in these groups (Figure 4(a,b)). When $PC_1$ was expressed against body weight, shape variability of small members of MG was approximately the same as that of the LG for the same interval, stabilizing after 350 g. Only a few individuals of the LG attained the same pattern as the MG, showing that large individuals of the MG have a shape that is distinct from the LG (Figure 5(a,b)).

Despite the high variability observed in $PC_1$ for both groups, the MG presented more positive values along centroid size (Figure 4) and body weight (Figure 5(a,b)) and also for the same values of OvWBW and NgWBW (Figure 5(c,d)). Statistical analysis showed that
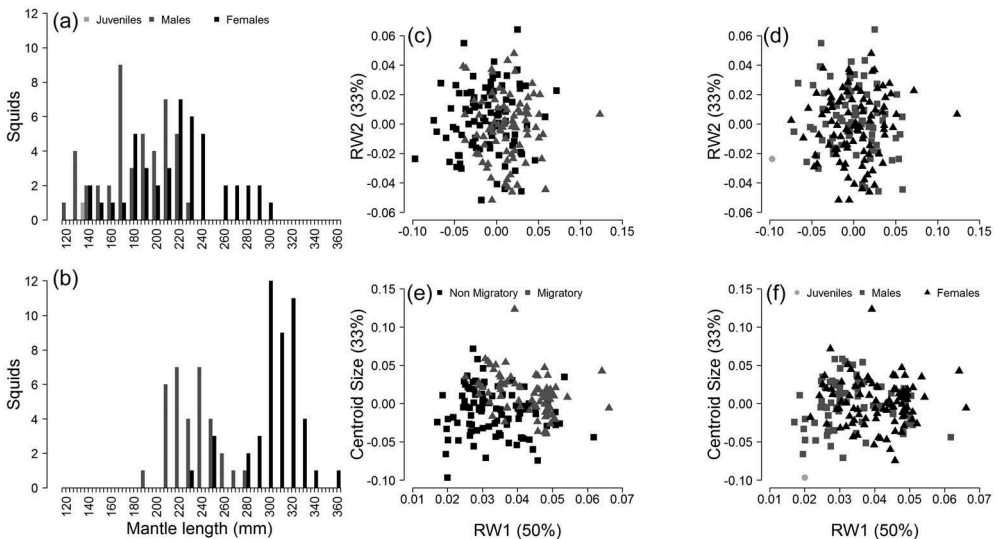


**Figure 4.** Length distributions of the (a) Local Group (LG) and the (b) Migratory Group (MG) captured south-southeast of Brazil between 2009 and 2013. Scatterplots of the first ($PC_1$) and second ($PC_2$) components of the principal component analysis using body landmarks separated by group (c) and by sex (d). Scatterplot of relationship of $PC_1$ on centroid size separated by group (e) and by sex (f).
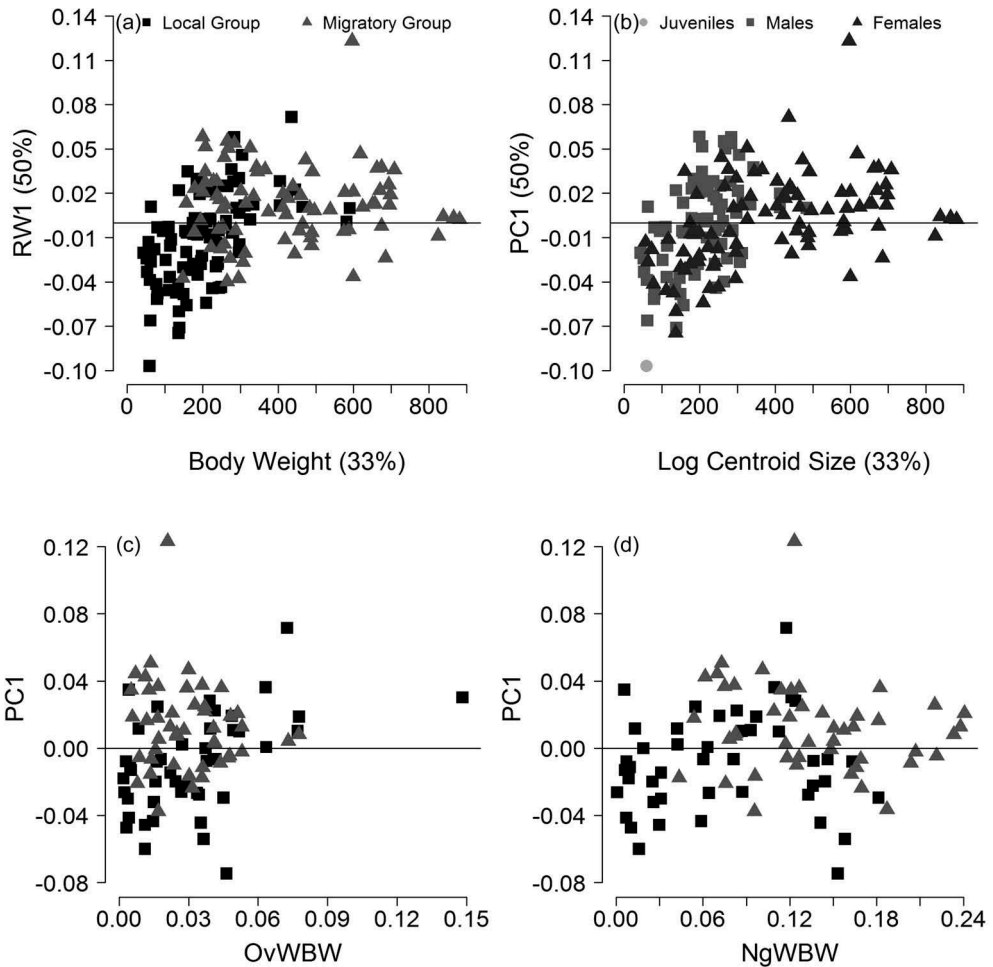
**Figure 5.** Scatterplot of the relationship of $PC_1$ on body weight separated by group (a), on body weight separated by sex (b), OvWBW (c) and NgWBW (d) for females separated by group.

significant differences in shape ($PC_1$) occurred between groups (Table 2), with more positive values of $PC_1$ in the MG indicating a different shape, at least for the largest individuals of this group.

## *Traditional morphometrics*

The principal component analysis showed that traditional morphometric variables of the samples analysed displayed a continuous variation from juveniles (J) to the expected migratory group and were different from individuals of the LG of similar size (Figure 6). This difference was mainly explained by body weight (BW), mantle weight (MW) and mantle perimeter (MP) for both sexes (Table 3). Because length was removed from the analysis, the results demonstrate that these groups present a different length versus weight relationship and a different aperture of the mantle. The variability of the second axis was mainly explained by the length of the fourth right arm (FRAL) (Figure 6).

**Table 2.** Comparison of shape changes ($PC_1$) throughout centroid size and reproductive indexes (OvWBW and NgWBW).

| Test | Fonts | df | Sq | MS | F | p |
|---|---|---|---|---|---|---|
| Centroid Size × $PC_1$ | HS | CS | 1 | 0.0000227 | 0.0000227 | 0.1685 | 0.682 |
| | | Group | 1 | 0.0035107 | 0.0035107 | 260.775 | **0.001** |
| | | CS:Group | 1 | 0.0000266 | 0.0000266 | 0.1979 | 0.657 |
| | ANCOVA | CS | 1 | 0.0000227 | 0.0000227 | 0.170 | 0.681 |
| | | Group | 1 | 0.0035107 | 0.0035107 | 26.315 | **0.001** |
| OvWBW × $PC_1$ | HS | OvWBW | 1 | 0.0005764 | 0.00057635 | 42.195 | **0.042** |
| | | Group | 1 | 0.0020538 | 0.00205378 | 150.359 | **<0.001** |
| | | OvWBW:Group | 1 | 0.0006146 | 0.00061462 | 44.997 | **0.036** |
| | ANCOVA | OvWBW | 1 | 0.0005764 | 0.00057635 | 40.581 | **0.047** |
| | | Group | 1 | 0.0020538 | 0.00205378 | 144.608 | **<0.001** |
| NgWBW × $PC_1$ | HS | NgWBW | 1 | 0.0007911 | 0.00079105 | 53.238 | **0.023** |
| | | Group | 1 | 0.0013070 | 0.00130696 | 87.959 | **0.003** |
| | | NgWBW:Group | 1 | 0.0002332 | 0.00023322 | 15.696 | 0.213 |
| | ANCOVA | NgWBW | 1 | 0.0007911 | 0.00079105 | 5.29 | **0.023** |
| | | Group | 1 | 0.0013070 | 0.00130696 | 8.74 | **0.003** |

Analysis of covariance (ANCOVA) tested the variability of the dependent variable ($PC_1$) on centroid size (CS), OvWBW and NgWBW. Group was the grouping factor. df, degrees of freedom; MS, mean of squares; F, values of F. Significant values of p ($p < 0.05$) are shown in bold type. A test of the homogeneity of slopes (HS) was performed before each ANCOVA.
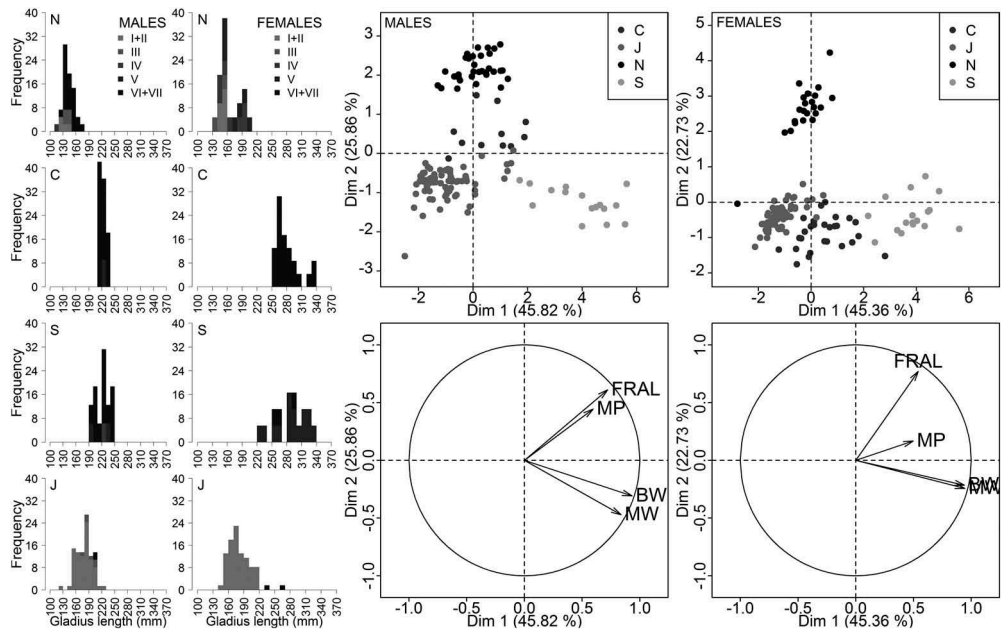


**Figure 6.** Barplots represents the length distributions of males and females of *Illex argentinus* captured during the fourth trimester of 2006 south-southeast of Brazil and a sample from the Uruguayan/Argentine common fishing zone collected in 2005, here defined as pre-migratory group (J). The analysis aimed to verify a possible correspondence between J and the expected MG, represented by two samples collected in the south (S) and central (C) portions of the studied area and if J is morphometrically different from the LG, captured in the north (N) portion of study area (Figure 1(c)). Plots represent the principal component analysis of the samples N, C, S and J. FRAL, length of the fourth right arm; BW, body weight; MW, mantle weight; MP, mantle perimeter.

**Table 3.** Principal component analysis employed to evaluate a possible correspondence between juveniles (J) and the expected migratory group (MG), represented by two samples collected in the south (S) and central (C) portion of the studied area and if J is morphometrically different from the LG, captured in the north (N) portion of study area (Figure 1(c)).

| Sex | Variables | PC$_1$ | PC$_2$ | PC$_3$ | PC$_4$ | PC$_5$ | PC$_6$ | PC$_7$ |
|---|---|---|---|---|---|---|---|---|
| Males | BW | 27.145 | 5.243 | 1.069 | 0.007 | 5.780 | 0.186 | 60.570 |
| | MP | 11.048 | 10.923 | 5.295 | 66.055 | 6.668 | 0.006 | 0.005 |
| | MW | 21.869 | 12.262 | 0.873 | 0.300 | 19.014 | 14.449 | 31.233 |
| | FRAL | 16.227 | 20.635 | 1.071 | 4.892 | 8.793 | 44.102 | 4.280 |
| | Eigenvalue | 3.207 | 1.810 | 1.053 | 0.569 | 0.245 | 0.102 | 0.015 |
| | Variance explained (%) | 45.817 | 71.674 | 86.714 | 94.843 | 98.338 | 99.790 | 100.000 |
| Females | BW | 27.877 | 2.901 | 2.244 | 2.429 | 0.042 | 9.093 | 55.414 |
| | MP | 7.795 | 1.764 | 27.569 | 52.493 | 9.810 | 0.046 | 0.524 |
| | MW | 28.121 | 3.720 | 0.030 | 0.366 | 1.186 | 25.749 | 40.828 |
| | FRAL | 9.235 | 37.360 | 0.129 | 1.021 | 48.766 | 3.386 | 0.102 |
| | Eigenvalue | 3.176 | 1.591 | 1.134 | 0.746 | 0.203 | 0.126 | 0.024 |
| | Variance explained (%) | 45.365 | 68.092 | 84.297 | 94.954 | 97.855 | 99.652 | 100.000 |

Plots represent the correspondence analysis of the samples N, C, S and J. FRAL, length of the fourth right arm; BW, body weight; MW, mantle weight; MP, mantle perimeter. The linear values of the variables in the seven factors rotated are indicated. The eigenvalues and the variance explained by each factor, including the first two used for the analysis are indicated in the last two rows.

## *Spatio-temporal variability of individual recent growth conditions*

Individuals captured in the research cruise showed significant differences in mean GL in all trawls ($p < 0.0001$, Figure 7(a)). In trawls 9 and 14, individuals were significantly larger than in the other trawls (Figure 7(a)).Trawls 9–14 may represent individuals of the MG while trawls 2–4 individuals belonged to the LG.

The slopes (interactions between factors and covariate) showed homogeneity among trawls, both between and within subjects (Table 4). The ANCOVA test did not show significant differences in recent growth between subjects (total growth increments
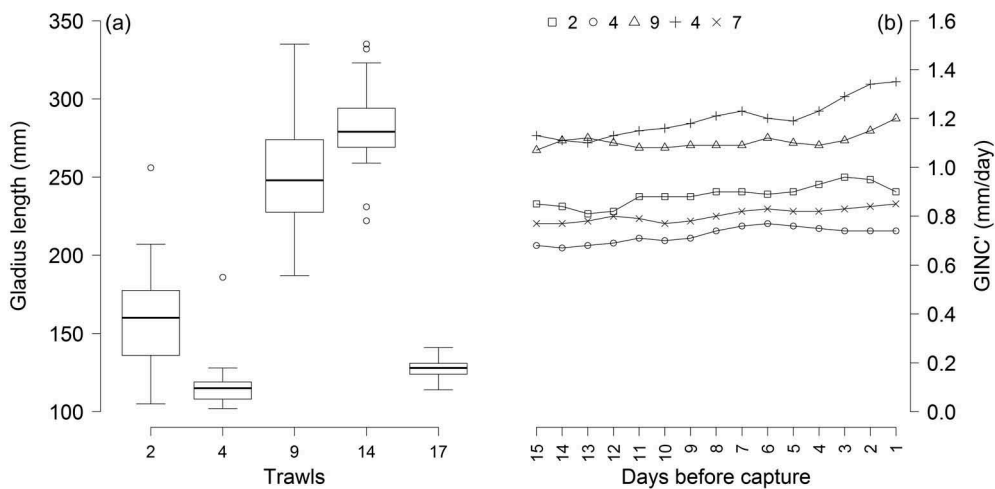


**Figure 7.** (a) Mean gladius length (GL) in research cruise, and (b) mean individuals recent growth trajectories of squid captured in research cruise reconstructed from gladius.

Table 4. Recent growth comparison of *Illex argentinus* between trawls of a research cruise over the continental shelf and slope of Santa Catarina State.

| Fonts | df | MS | F | p |
|---|---|---|---|---|
| Homogeneity of slopes | | | | |
| Between objects | | | | |
| TRAWL × Gli | 4 | 0.058 | 0.575 | 0.682 |
| Within subjects | | | | |
| DAYS × TRAWLS × GLi | 56 | 0.012 | 1.035 | 0.409 |
| ANCOVA | | | | |
| Between objects | | | | |
| TRAWLS | 4 | 0.186 | 1.899 | 0.123 |
| Gli | 1 | 4.27 | 43.517 | **<0.001** |
| Within subjects | | | | |
| DAYS | 14 | 0.026 | 2.283 | **0.005** |
| TRAWL | 56 | 0.014 | 1.188 | 0.168 |
| Gli | 14 | 0.016 | 1.384 | 0.154 |

Analysis of covariance (ANCOVA) tested the variability of total increments deposited on gladius during 15 days that preceded the capture (Between subjects) and in mean growth trajectories during the same period (Within subjetcs i.e. GINC was considered as repeated measures in the gladius of each squid). TRAWL was the grouping factor; DAYS was the period in which GINC was considered a repeated measure and $GL_i$ was the covariate that represented GL in the beginning of the growing period. df, degrees of freedom; MS, mean of squares; F, values of F. Significant values of *p* ($p < 0.05$) were printed in bold.

during 15 days, $p = 0,123$) nor within subjects (growth trajectories during 15 days, $p = 0,168$) (Figure 7(b), Table 3).

## Size differentiation

Length distribution reconstructed from 2001 to 2013 showed two distinct patterns: curves depicted by positive asymmetry throughout the year and by negative asymmetry during the winter months (July to September) (Figure 8). In the winter months, a higher percentage of females (57%) was observed in relation to males (40%) than in the rest of the year (females 44%; males 52%). These patterns were compared with length distributions obtained by reconstructing individual growth histories from gladius growth
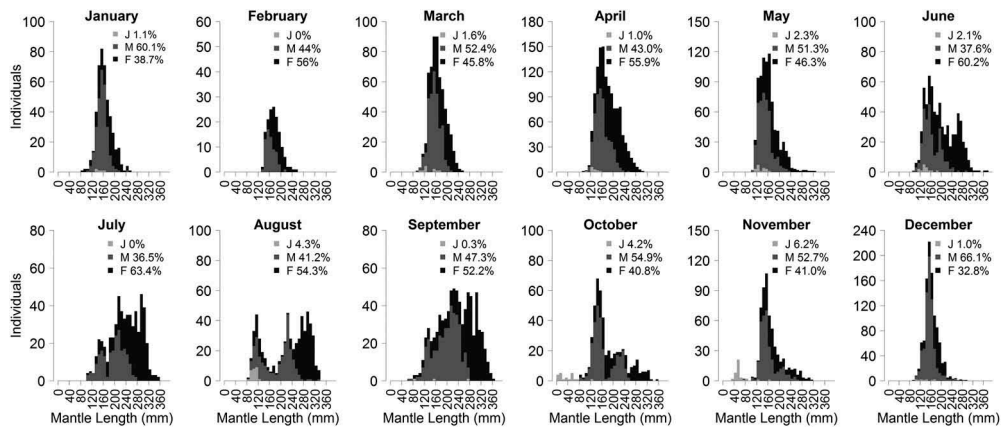


Figure 8. Length distributions of *Illex argentinus* captured in south-southeastern Brazil between 22° and 33°S and 45 and 722 m depth from 2001 to 2013.

increments of *Illex argentinus* schools captured during a research expedition (Figure 1(d), Table 1).

In this analysis, trawls 2–4 and 9–14 (Figure 7(a)) have been considered as two schools sampled (Figure 1(d)). These groups were based on the close proximity of the trawls and being on the same date. The length frequency distribution of GL constructed for both groups on the day of the capture was back-reconstructed for the 60 days that preceded it based on gladius growth increments (GINC') are shown in Figure 9. Non-empty stomachs represented 27% of the squid in trawls 2–4 and 26% in trawls 9–14.

The coefficients of asymmetry ($g_1$) calculated for the frequency distributions reconstructed from GL for the 60 days showed different trends for the two schools considered (Figure 10). The group comprising trawls 9–14 had slightly negative skewness and was relatively stable throughout the period whereas the group comprising trawls 2–4 presented a highly positive asymmetry that was accentuated over the 60 days analysed. These results suggest different growth conditions experienced by individuals captured in different geographical situations during research cruises.

## Discussion

Geometric morphometric analysis showed that individuals of the Argentine shortfin squid belonging to different groups can be differentiated by body shape. The variability observed in shape throughout ontogeny could be associated with an adaption of the environment occupied by the squid. Shape variations in large individuals of the MG group could be associated with allometric changes in mantle width, as observed in several squid species (Haefner 1964; O'Dor and Hoar 2000; Barón and Ré 2002; Zeidberg 2004; Crespi-Abril et al. 2010) associated with a more efficient swimming capacity of adults (O'Dor and Hoar 2000; Thompson and Kier 2002; Bartol et al. 2008; Crespi-Abril et al. 2010). Mature females of different groups, with different sizes, presented the same values of OvWBW and NgWBW. Shape variability observed for the same values of these indices in squid of different groups, suggested that shape adaptations are more relevant to improve the swimming capacity than the alteration of body shape to accommodate sexual organs during growth and maturation, as previously observed in other *I. argentinus* stocks (Crespi-Abril et al. 2010).

Ontogenetic changes in shape were clearer in individuals of the LG that complete all life stages in this area (Perez et al. 2009; Schwarz and Perez 2013; Schroeder and Perez 2013) whereas juveniles of the MG were not present in the catches. Variability in size at maturity, individual growth rates and lifespan suggest that juveniles of MG have fed in more productive areas, investing more energy in somatic growth than in maturation (Perez et al. 2009; Schroeder and Perez 2010; Schwarz and Perez 2013), and have attained a large size suitable to perform migrations to further spawning grounds (O'Dor and Coelho 1993). This hypothesis, however, implies that individuals require stronger mantle musculature to move by jet propulsion (O'Dor and Hoar 2000), in other words, they need a heavier mantle.

The results of traditional morphometrics showed the different weight relationship between individuals of the LG and MG. This difference is probably due to the early life investment in somatic growth leading to a thicker and wider mantle, which would allow the squid to migrate to spawn further north. Although it was not possible to apply the
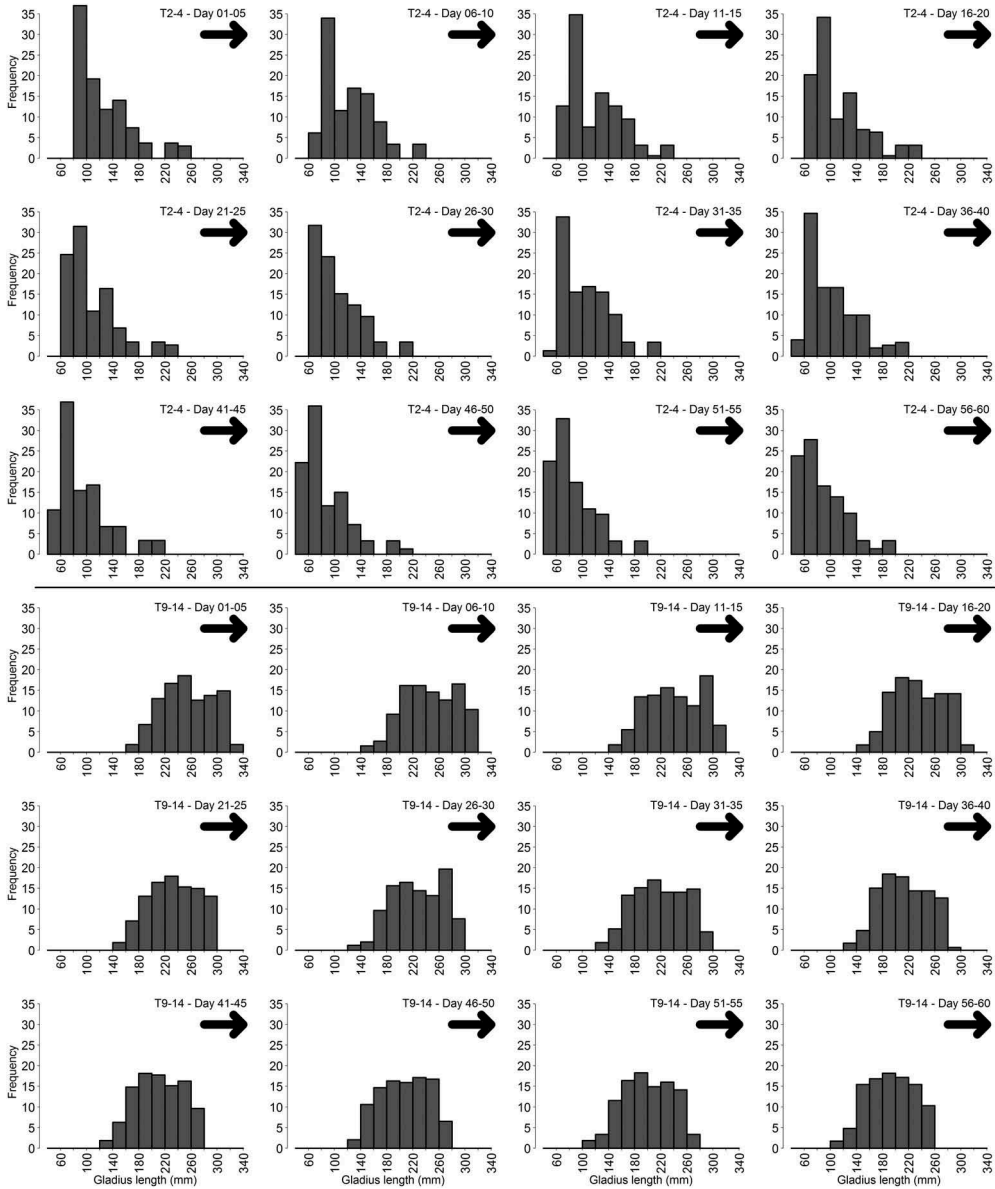
**Figure 9.** Gladius length frequency distributions of *Illex argentinus* reconstructed for the last 15 days before the capture from the measured increments on the gladius for the trawls 2–4 (T2-4) and trawls 9–14 (T9-14) of the research cruise.

same methodology to all the squid sampled, because the photographs for geometric morphometrics only began to be taken in 2009, and this methodology replaced the traditional morphometrics measurements, both analyses showed convergent results. It would be expected that squid that invest more in somatic growth during early life and attain larger sizes, will present a thicker wall of the mantle. The combination between mantle broadening, thicker mantle wall and larger fins maximizes the swimming
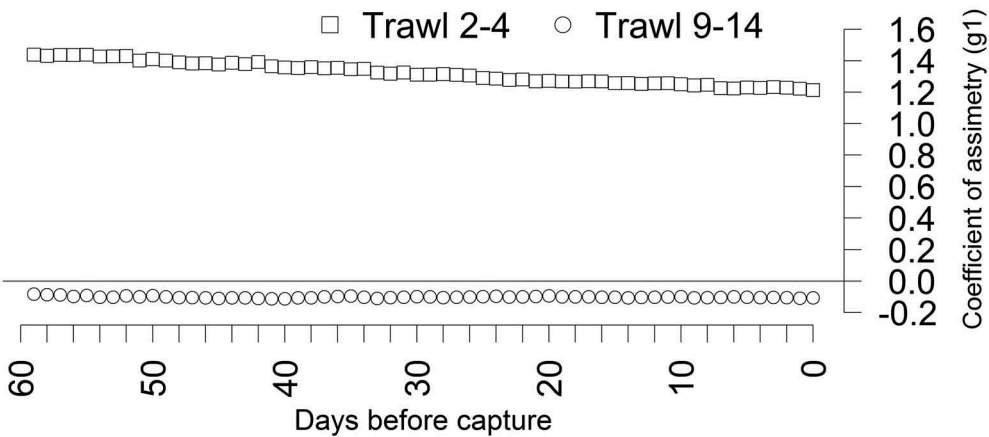
**Figure 10.** Size differentiation of squid groups during the period of growth reconstructed expressed by the variation of the coefficient of asymmetry (g1) of the length frequency distributions by growth interval (days).

capacity of these organisms (Staaf et al. 2014). Assuming that the largest individuals captured in the research cruise were part of the migratory group and that they swim as fast as 23–29 km.day$^{-1}$ (Arkhipkin 1993), then in the last 60 days they could have swum 1560 km on average, experiencing a variety of water conditions. The growth reconstruction of *I. argentinus* aimed to analyse the recent growth conditions to which individuals captured in different geographical situations were exposed 15 days before the capture. The results were considered independent of the size and reflected the growth performance over a recent period before capture (Perez 1995). Because no significant differences were found in growth performances, the growth conditions in which individuals lived recently, favourable or not, were similar. Despite no significant differences have being observed in the present study, high growth conditions were observed for the large sized group captured in deeper waters in the same area during the winter of 2002 (Schroeder and Perez Submitted).

One interesting feature of the long journey into the oligotrophic warmer waters necessary for egg development is that migratory *Illex* squid could benefit from cannibalism of small members of the population (Mouat et al. 2001). The combination of environmental stressors and intraspecific interactions acting upon each group could change the variability in size with time/age (Pfister and Stevens 2002). Assessments of environmental conditions and feeding regimens that schools have experienced during an interval that preceded capture can be obtained from analysis of the growth trajectories shown in the squid gladius for the same period and by back-calculation of the length frequency from gladius growth increments (Perez 1995; O'Dor 1998). This analysis would allow the identification of size-selective mechanisms by verifying the asymmetry of size distributions, and would separate two processes (Arkhipkin and Perez 1998; O'Dor 1998): (a) Growth Compensation, when the variability in mantle length-at-age decreases with time or age, and (b) Growth Depensation, when the variability in length-at-age increases with age (Hakoyama and Iguchi 2001; Fujiwara et al. 2004; Lorenzen 2016).

Although growth trajectories of individuals captured in research cruises did not show significant differences, the distinct skewness of the back-calculated length distribution may represent the combined effect of food availability and intraspecific interactions (Pfister and Stevens 2002). Because the percentage of stomachs containing food was the same in both groups, squid were probably facing the same food availability at the time of capture. The positive-skewed length distribution is the most common pattern observed in several organisms (Kozłowski and Gawelczyk 2002). For the LG group of *I. argentinus* off southeastern Brazil it may represent the strategy of a group that is 'accustomed' to the local environmental conditions and that completes its whole life cycle in a more oligotrophic area, in which higher temperature or lower food quality would decrease the final size and anticipate maturity at a smaller size (Dixon 1985). As individuals grow (and increase in age) length distribution variability increases, where the largest and fastest growing individuals of the population tend to become increasingly larger, compared with smaller individuals (Łomnicki 1980; Uchmański 1985). This process of growth depensation is enhanced by intraspecific competition when the amount of available food is scarce and unevenly distributed (Uchmański 1985).

Changes in skewness of length distribution throughout life history are observed in natural populations of diverse organisms (Kozłowski and Gawelczyk 2002) and could be associated with shifts in the availability and quality of food (Dixon 1985). Squid of the MG group may have experienced lower temperature or higher food quality, which would increase the final size and delay maturity until a larger size with nearly annual spawning. The migration into oligotrophic waters could cause the smaller and slower-growing individuals of the population to be eliminated by starvation, natural mortality and predation/cannibalism (Pfister and Stevens 2002), resulting in a negative skewed length distribution (Kozłowski and Gawelczyk 2002). In a situation of food scarcity, the largest and most aggressive squid tend to cannibalize smaller ones (i.e. mainly males) (O'Dor et al. 1980; Hirtle et al. 1981; Ibáñez and Keyl 2010), which could be a reasonable explanation for the larger number of large females in the winter months. Future studies have to investigate the importance of cannibalism during migration.

Commercial species that have rapid growth and short life cycles, such as squid, cannot be evaluated by the same methods applied to most fish fisheries (Boyle and Rodhouse 2005). The applications of morphometric analysis and individual growth reconstruction from the gladius explored in this study show the potential to improve our knowledge of the population structure of *I. argentinus*, and also the possibility of analysing the variation of the spatial conditions of growth that should define size-dependent population processes and allow relevant estimations for fisheries management. Morphological analysis showed that large sized winter squid with elongated and wider mantles as well as broader fins, are not large duplicates of small individuals, and in fact present a different form, that could be associated with early development in more productive areas before migration to the spawning grounds off southeastern Brazil, as suggested in previous studies (Santos and Haimovici 1997; Haimovici et al. 1998; Perez et al. 2009). The origin of the large sized winter spawners remains unknown. Methodologies used in this study should be tested in association with more accurate methods, such as the elemental composition of statoliths (Green et al. 2015; Liu et al. 2015) and stable isotopes along gladius length (Lorrain et al. 2011; Kato et al. 2016), to

determine the natal origin and distinguish ecological processes of the spawning units by reconstructing the individual chemical history.

## Disclosure statement

No potential conflict of interest was reported by the authors.

## ORCID

Rafael Schroeder ⓘ http://orcid.org/0000-0001-7340-0214
Richard Schwarz ⓘ http://orcid.org/0000-0002-7815-5809
Augusto César Crespi-Abril ⓘ http://orcid.org/0000-0002-6278-2787
José Angel Alvarez Perez ⓘ http://orcid.org/0000-0001-6431-5237

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