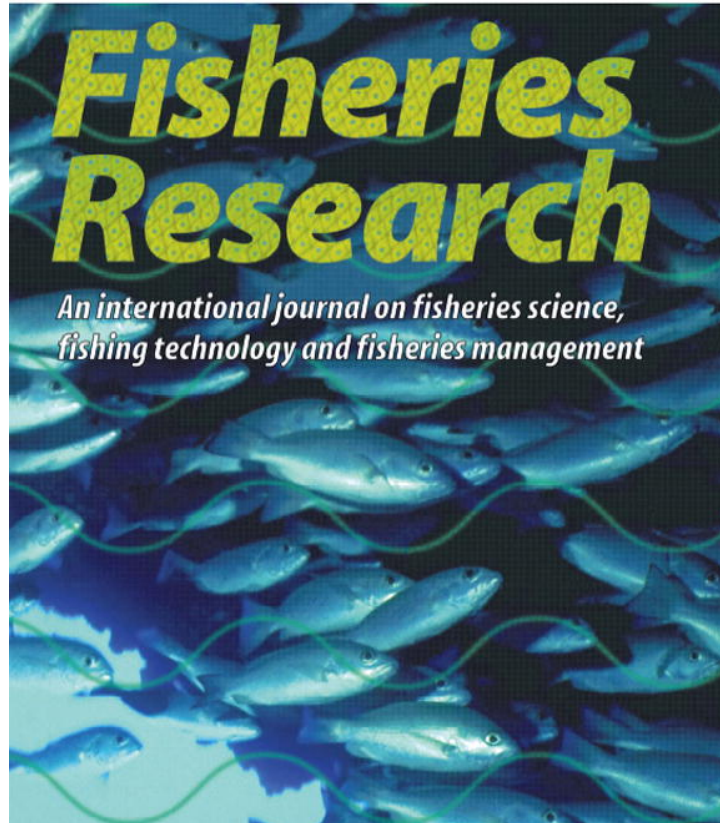


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## Differences in shell morphology and internal growth pattern of the Patagonian scallop *Zygochlamys patagonica* in the four main beds across their SW Atlantic distribution range

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### Abstract

Shell morphometry, internal shell growth patterns and growth rates of the Patagonian scallop *Zygochlamys patagonica* from four different beds across their SW Atlantic distribution range were compared. The northern beds (Uruguay, 36°17'S and Reclutas, 39°25') showed lower shell height, length and shell mass than the southern populations (Tango B bed: 42°30' and Beagle bed: 55°10'S). Mean height, length, and width increased following a N–S latitudinal gradient. Acetate peels revealed the presence of internal growth bands with alternating broad opaque and narrow translucent growth bands. In the Reclutas bed, the “cluster of translucent bands” representing external rings was formed mainly during winter at the same time of the higher gonadal condition index, and a regional decrease in food availability. The growth pattern observed for the first two or three growth bands was less pronounced than other growth bands, with sizes of these individuals corresponding to first maturity of the species. Thus, differences can be due to differential allocation of energy investment to shell production between juvenile and adult organisms. The internal growth patterns and maximum age differed between beds, with an increase in the maximum age from the N to the S (Uruguay bed: 13 years old, Reclutas bed: 14 years old, Tango B bed: 20 years old, Beagle bed: 21 years old). Our study provides evidence of variation of growth in *Z. patagonica* in the four main beds across their SW Atlantic distribution range, where a significant increase in  $H_{\infty}$  from N to S coincides with different internal growth pattern, maximum age and a trend toward higher von Bertalanffy  $k$  parameter in the northern beds.

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**Keywords:** *Zygochlamys patagonica*; Scallops; Internal shell growth bands; Acetate peels; Age

### 1. Introduction

The Patagonian scallop *Zygochlamys patagonica* is distributed around the southern tip of South America reaching 42°S in the Pacific (Valladares and Stotz, 1996) and 35°50'S in the Atlantic within a depth range of 40–200 m (Waloszek and Waloszek, 1986; Lasta and Zampatti, 1981; Defeo and Brazeiro, 1994; Gutiérrez and Defeo, 2003, 2005; occasionally down to 960 m, Waloszek, 1991). In the Pacific, grounds occur in rel-

atively shallow waters (less than 25 m; Andrade et al., 1991) while in the Atlantic the most important beds are located along the 100 m isobath (Defeo and Brazeiro, 1994; Lasta and Bremec, 1998) matching the location of three major oceanic frontal systems (Bogazzi et al., 2005). Variation of seasonal bottom temperature at this depth is less than 2–3 °C. In the northern range of their Atlantic distribution (i.e., Uruguay bed; 36°10'S) maximum values are during March to June (8.8, S.D. = 0.7 °C) and minimum during September to November (austral spring, 7.5, S.D. = 0.3 °C). In central beds (i.e., Reclutas; 39°20'S and Tango B beds; 42°30'S) the maximum are during early winter (May to July, 6.5, S.D. = 0.4 °C) and minimum during spring-summer (5.8, S.D. = 0.3 °C; Lomovasky et al., 2007). However, maximum annual sea-bottom temperature variation (4.5 °C) was observed on the Beagle bed (55°10'S, southern range of species

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distribution) with lowest values from September to December (5.7, S.D. = 0.7 °C) and maximum from January to May (8.5, S.D. = 0.4 °C; Baldoni and Guerrero, 2000; Lomovasky et al., 2007).

This scallop species is an important economic resource in the South Atlantic (e.g., Lasta and Bremec, 1998, 1999). The fishery started in Argentinean waters in 1996 (main grounds are between 38°S and 42°30'S) following surveys conducted during 1995 (Lasta and Bremec, 1998). Since then, the fishery has involved four 50 m long factory trawlers that process the catch on board, capturing up to 43,000 tonnes of commercial scallops in a year (e.g., year 2003, generating around 6,000 tonnes of adductor muscle; Lasta and Campodónico, 2004) for export market. Each bed is considered a management unit within two administrative sectors (south and north 39°30'S). Annually, a total allowable catch is established for each bed based on a model-based biomass estimates (Journal and Huijbregts, 1993). Between other management measures a series of closures within each main bed are imposed on the fishing activity to protect high density patches. However, a key parameter involved in this estimation is age, the possible variations across of which are unknown across the beds.

Indeed the determination of their individual age and thus growth rate, one of the key parameters for their stock assessment, has generated conflicting results probably due to geographic variations, but it has imposed a robust stock assessment. Most studies were based on observations of external shell surface growth lines (Waloszek and Waloszek, 1986; Lasta et al., 2001; Defeo and Gutiérrez, 2003; Gutiérrez and Defeo, 2005) and were performed on individuals from different locations across their latitudinal gradient (39°47'S–4°30'S; Fig. 1; Waloszek and Waloszek, 1986), in the Reclutas bed (39°20'S–35°S; Lasta et al., 2001) and in Uruguayan waters (35°50'S–36°40'; Defeo and Gutiérrez, 2003; Gutiérrez and Defeo, 2005). There were also analyses of internal shell structures in the chondrophores and ligaments (Waloszek and Waloszek, 1986; Bizikov and Middleton, 2002) from samples obtained along a latitudinal gradient extending from 39°47' to 54°30'S (Waloszek and Waloszek, 1986; Waloszek, 1991) and including the Malvinas (=Falkland) Islands (50°35'–47'; Bizikov and Middleton, 2002). The results from the Malvinas Islands beds obtained using external rings and chondrophores are different with substantial discrepancies regarding the estimates of maximum age (16 and 21 years old, respectively; Bizikov and Middleton, 2002), which may in part be due to the poor readability of external rings as individuals get older (see Bizikov and Middleton, 2002 and our observations). However, stable oxygen and carbon isotope ratio analysis from shells of this species from four large beds (Uruguay, 36°17'S; Reclutas, 39°20'S; Tango B, 42°30'; and Beagle, 55°10'S) together with the analysis of oceanographic parameters and condition indexes show that shell growth marks are formed annually during periods of higher water temperature where the energy input to gamete proliferation is the cause of decreased in shell growth indirectly mediated by food availability (Lomovasky et al., 2007).

The distribution of *Z. patagonica* in discrete beds along a large latitudinal gradient (approximately 20°) of the Atlantic coast is expected to generate different patterns of growth, aging, and/or morphometric characteristics. Indeed, Uruguayan pop-

ulations (35°50'–36°50'S) show differences in growth rates decreasing toward the northern limit of the species distribution (Gutiérrez and Defeo, 2005). Therefore, it is important to identify possible differences between beds in order to perform bed-specific stock assessment. Thus, the purpose of this work is to evaluate if there are differences in morphometry and growth rates in the four main beds along their extended latitudinal distribution in the Southwestern Atlantic.

## 2. Material and methods

### 2.1. Sampling sites

Samplings of *Z. patagonica* ( $n=2047$ ) were performed in four beds, which from North to South (Fig. 1) are: Uruguay ( $n=106$ , 36°17'S–53°49'W, depth = 108–109 m; samples obtained in April 2000 and June 2001), Reclutas ( $n=1346$ , 39°20'S–56°W and 39°30'S–55°52', depth = 101–110 m; monthly samples from January 2000 to December 2000), Tango B ( $n=200$ , 42°30'S–59°05'W, depth = 96–118 m; samples obtained in March 2000 and July 2001) and Beagle bed ( $n=395$ , 55°10'S–66°05'W, depth = 112 m; samples obtained in December 2003 and October 2004). The surveys were conducted using a 2.5 m wide dredge in all beds with the exception of the Beagle bed, which was sampled with a bottom otter trawl (foot rope of 22 m, net and cod-end of 10 cm mesh size). Previous information suggests that there are no differences in scallop size-selectivity between both fishing gears (Lasta and Bremec, 1997; Ciocco et al., 2006). A total of 24 trawls were made in the different beds. The initial and final positions of each trawl were registered (using GPS; precision:  $\pm 60$  m). Depth records were obtained using a depth sounder (precision:  $\pm 1$  m). Individuals were collected and frozen at  $-20$  °C for laboratory measurements. In the laboratory, epibionts were removed by brushing the shell surface.

### 2.2. Morphometric relationship

For all collected individuals from the different beds we measured shell height (SH, umbo to the ventral margin), length (SL, anterior–posterior axis) and width (SW) (precision  $\pm 0.1$  mm), and determined total mass without epibionts (TM), shell mass (SM), shell-free wet mass (SFWM), gonadal mass (GM), adductor muscle mass (AMM) and epibionts mass (EM; all parameters with precision  $\pm 0.01$  g).

To compare the morphometric relationships between different beds, a full interaction ANCOVA model with subsequent Tukey multiple comparison tests (Zar, 1999) were used to evaluate effects on the relation between shell height (SH), length (SL), width (SW) and shell mass when assumptions of normality, homoscedasticity and parallelism were proved (Zar, 1999). To enhance overall data set homogeneity, we restricted the statistical analysis to the size range  $\geq 24$  to  $< 66$  mm shell height present at all beds. No comparisons were performed between other mass variables given the intra-annual variability in these parameters inside each bed (see Lasta et al., 2001).

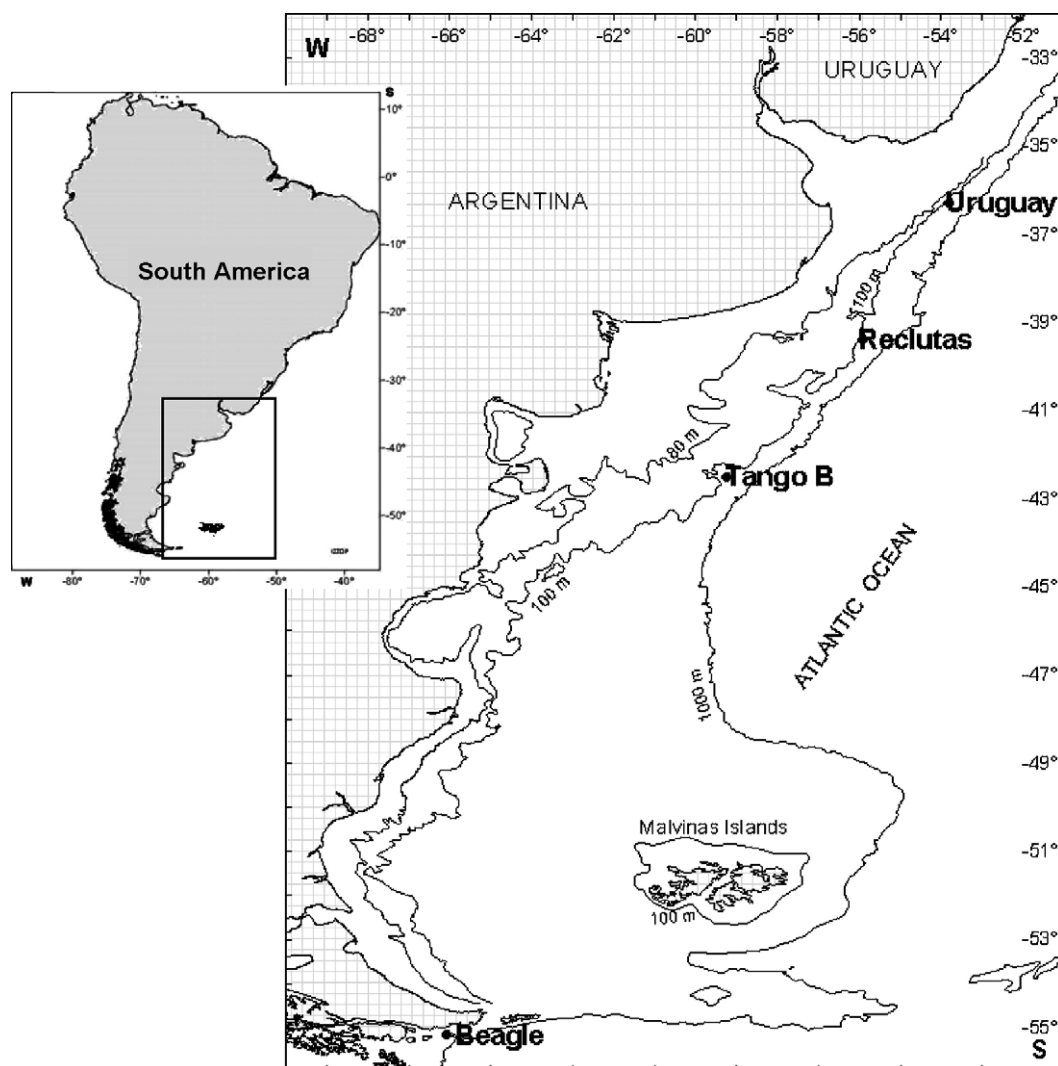


Fig. 1. Spatial distribution of the Patagonian scallop *Z. patagonica* bed sampled on the Uruguay-Argentine Continental Shelf, SW Atlantic.

### 2.3. Internal growth patterns and growth rings determination

Sub samples were obtained from each bed for growth and band formation analyses to reflect the size-range at each site (Uruguay:  $n=91$ ; Reclutas:  $n=322$ ; Tango B:  $n=90$ ; Beagle:  $n=95$ ). Growth pattern was inferred from internal shell growth bands of left valves of specimens from the different beds. Each valve was embedded in polyester resin and sectioned along the axis of maximum growth in shell height (SH) using a saw with a diamond blade. The cross-sections were polished on lapidary wheels using grits of 400, 600, 1200, and 2400 grade, and then etched between 23 and 30 min using 0.5% DE-CAL agent. Acetate peels were made of the cross-sectioned surfaces to allow microscopic examination (following Rhoads and Lutz, 1980) and were examined for the presence of internal growth bands.

Internal growth bands can be identified as translucent and opaque bands (Jones et al., 1990). Translucent bands are narrow dark while opaque bands are wide white. To confirm during

which season translucent and opaque bands (Jones et al., 1990) formed, and validate the external ring formation (annual formation confirmed by stable isotopes analysis; Lomovasky et al., 2007) with the internal bands formation, the stage of terminal growth in cross-section shells was identified within either the translucent band or the opaque band (see Arnold et al., 1998) and the correspondence with an external ring. At least 16 specimens per month were analyzed from the Reclutas bed, monthly growth stage data were pooled into seasonal groups and a proportion comparison test was performed (Zar, 1999).

The number of internal translucent bands and the corresponding shell height were recorded as age-shell height data (following Lomovasky et al., 2007) and fitted to the general von Bertalanffy growth model. For this purpose we used

$$H_t = H_\infty(1 - e^{-k(t-t_0)}) \text{ [mm, years]} \quad (1)$$

where  $H_\infty$  is asymptotic height,  $k$  the growth constant,  $t$  the age and  $t_0$  is age at zero height.

Table 1  
Morphometric relationships in *Zygochlamys patagonica* from different beds as described by linear regression  $y = a + bx$  (all significant relationships,  $p < 0.05$ ); and Tukey test to compare the morphometric relationships between different beds

Variable $x$	Variable $y$	Bed	$a$	$b$	$r_2$	$n$	Tukey test
$H$	$L$	Uruguay	-6.79	1.11	0.98	105	a
		Reclutas	-4.24	1.06	0.99	1187	a
		Tango B	-6.44	1.09	0.98	120	b
		Beagle	-5.93	1.09	0.98	394	c
$H$	$W$	Uruguay	-3.69	0.35	0.92	105	a
		Reclutas	-1.70	0.30	0.96	1317	a
		Tango B	-3.15	0.33	0.95	119	b
		Beagle	-2.89	0.36	0.88	395	c
log( $H$ )	log(TM)	Uruguay	-10.62	3.28	0.95	99	Not analyzed
		Reclutas	-9.06	2.91	0.99	1187	
		Tango B	-9.79	3.10	0.98	174	
		Beagle	-10.10	3.25	0.98	266	
log( $H$ )	log(SM)	Uruguay	-11.08	3.19	0.95	99	a
		Reclutas	-9.73	2.83	0.98	991	b
		Tango B	-9.91	2.90	0.97	174	c
		Beagle	-11.19	3.33	0.95	395	d
log( $H$ )	log(SFWM)	Uruguay	-11.69	3.39	0.93	99	Not analyzed
		Reclutas	-10.54	3.15	0.97	991	
		Tango B	-10.89	3.25	0.98	174	
		Beagle	-10.49	3.18	0.97	266	
log( $H$ )	log(AMM)	Uruguay	-14.03	3.67	0.86	99	Not analyzed
		Reclutas	-11.33	3.07	0.96	1316	
		Tango B	-12.84	3.49	0.96	174	
		Beagle	-12.04	3.32	0.95	266	
log( $H$ )	log(GM)	Uruguay	-19.84	4.54	0.73	99	Not analyzed
		Reclutas	-18.56	4.38	0.79	1290	
		Tango B	-16.64	3.96	0.61	174	
		Beagle	-12.35	2.94	0.44	264	
log( $H$ )	log(EM)	Uruguay	-11.46	3.05	0.31	99	No differences
		Reclutas	-11.67	3.05	0.41	989	
		Tango B	-15.05	3.80	0.65	174	
		Beagle	-11.87	3.04	0.47	265	

$H$ : shell height,  $L$ : shell length,  $W$ : width; TM: total body mass; SM: shell mass; SFWM: shell-free wet mass; AMM: adductor muscle mass; GM: gonadal mass; EM: epibiont mass. Equal letters indicate no significant differences at  $\alpha = 0.05$ . The average ratio of dependent variable to covariate decreases in alphabetical sequence.

To simplify the fitting procedure, the model was forced to have a  $t_0$  estimate by the following equation:

$$t_0 = \frac{1}{k} \ln \left( \frac{H_\infty - H_0}{H_\infty} \right) \quad (2)$$

where  $H_0$  is considered as size at settlement and was fixed to 0.2 mm, inferred from the change in sculpture in the transition from prodissoconch to dissoconch in shell of adult individuals (Waloszek and Waloszek, 1986).

The maximum Likelihood method was used to fit the model to the data for each bed (following Edwards, 1992; Hilborn and Mangel, 1997).  $k$  and  $H_\infty$  parameters of the four beds were compared by pair-wise comparisons using the Likelihood ratio test (Cerrato, 1990; Haddon, 2001), and bivariate confidence limits (CI) for  $k$  and  $H_\infty$  parameters were constructed using profile Likelihood (see Hilborn and Mangel, 1997). In both cases (Likelihood ratio test and construction of confidence limits intervals) Bonferroni corrections were applied to avoid type I error inflation due to multiple comparisons (see Rice, 1989). Additionally,

the growth index  $\phi' = 2 \log_{10} H_\infty + \log_{10} k$  (Pauly and Munro, 1984) was calculated and used to assess growth performance.

### 3. Results

#### 3.1. Morphometric relationship

Exponential relationships between animal total body mass, shell mass, shell-free wet mass, adductor muscle mass, gonadal mass and epibiont mass as dependent variables and shell height as the independent variable were found in each bed. There were linear relationships between shell length and width with shell height (SH;  $p < 0.01$ ; Table 1) in all beds.

Tukey's multiple comparisons of SL/SH ratios indicated that Uruguay and Reclutas beds were similar with lower values than Tango B and Beagle beds ( $p < 0.05$ , Table 1). There were similar results for the relationship between SW/SH. There were also differences between beds for log(SM) as dependent variable and log(SH) as the independent variable with lower

values in the northern beds and higher at southern beds (Tukey multiple comparisons,  $p < 0.05$ ). However, there were no differences between beds for the relationship of  $\log(\text{EM})/\log(\text{SH})$  (ANCOVA,  $F = 0.71$ ,  $p = 0.54$ ).

### 3.2. Internal growth patterns and growth bands determination

Under reflecting light, acetate peels from the polished shell cuts showed a pattern of alternating broad opaque and narrow translucent growth bands (Figs. 2 and 3). In the Reclutas bed, the internal growth bands in the umbo were clearly observed (Fig. 2b). It was possible to follow each translucent internal growth bands from the umbo all along the shell section to the point where they cross the outer shell layer to form an external ring on the shell surface (Fig. 3c). The most recent translucent bands were often clearly visible at the point where they cross

the outer shell layer and each growth break (observed as an external ring) is formed by a group of internal shell growth bands (thereafter named “cluster of translucent bands, CTB”; Fig. 3b–d). For the first two or three bands, which were always very difficult to observe along the shell section, the pattern was different from other growths bands (Fig. 3a). At the last portion of the valve (the most recent bands), the internal growth bands were closer to the shell edge and proximate to each other (individuals  $> 50$  mm SH). They were clearly visible in acetate peels but very difficult to identify on the exterior shell surface.

The shell terminal stage analyzed across the year in Reclutas bed showed that the CTB, and thus external rings were clearly identified and developed between fall and winter (April to September) in 70% of all the individuals forming translucent bands, with only 10% of individuals in summer developing a “CTB” ( $p < 0.05$ ), but the formation of simple translucent bands

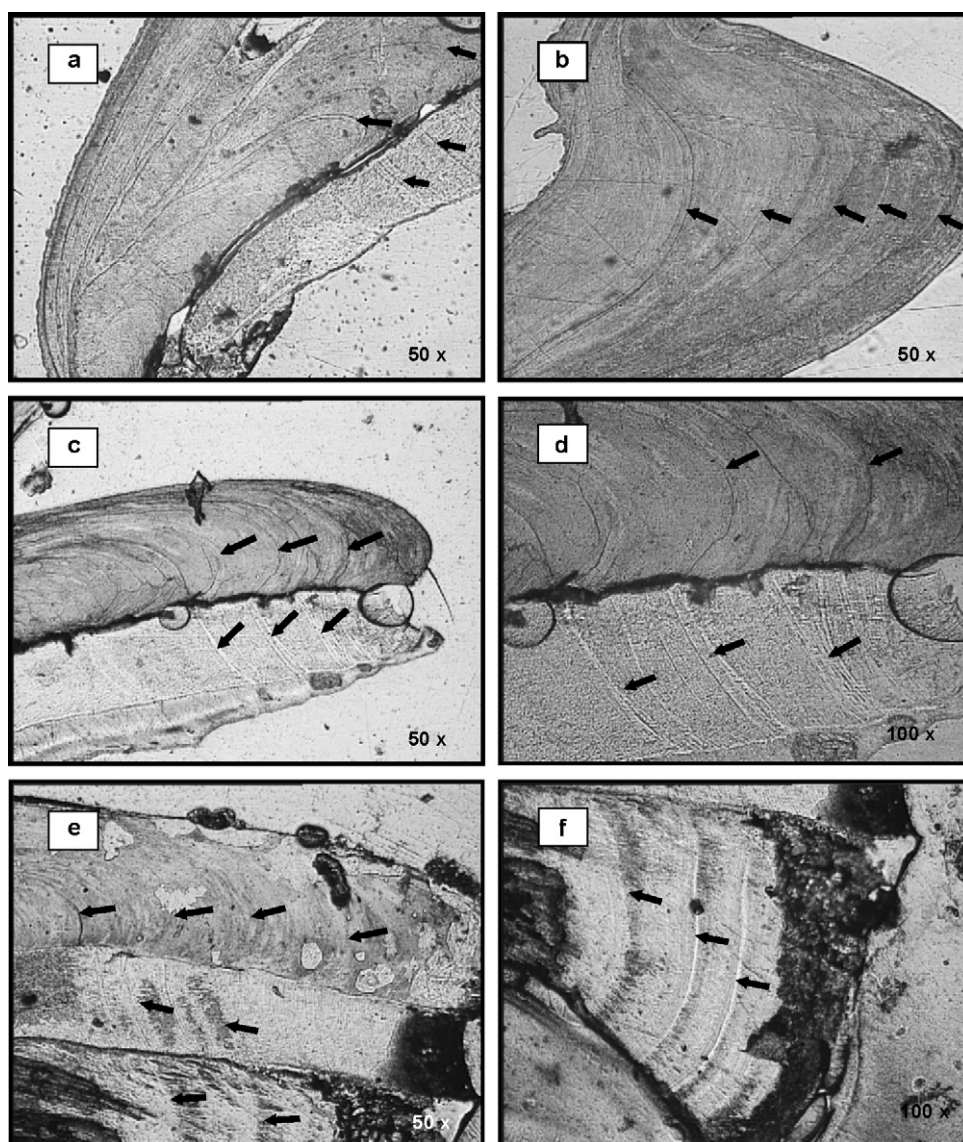


Fig. 2. Acetate peels of shell cross-sections of *Z. patagonica* from (a) umbos of the Uruguay and (b) the Reclutas beds; (c and d) umbo and ligament of the Tango B and (e) the Beagle and; (f) ligament of individuals from the Beagle bed showing the internal translucent growth bands (black arrows) representing period of very slow or even halted shell growth.

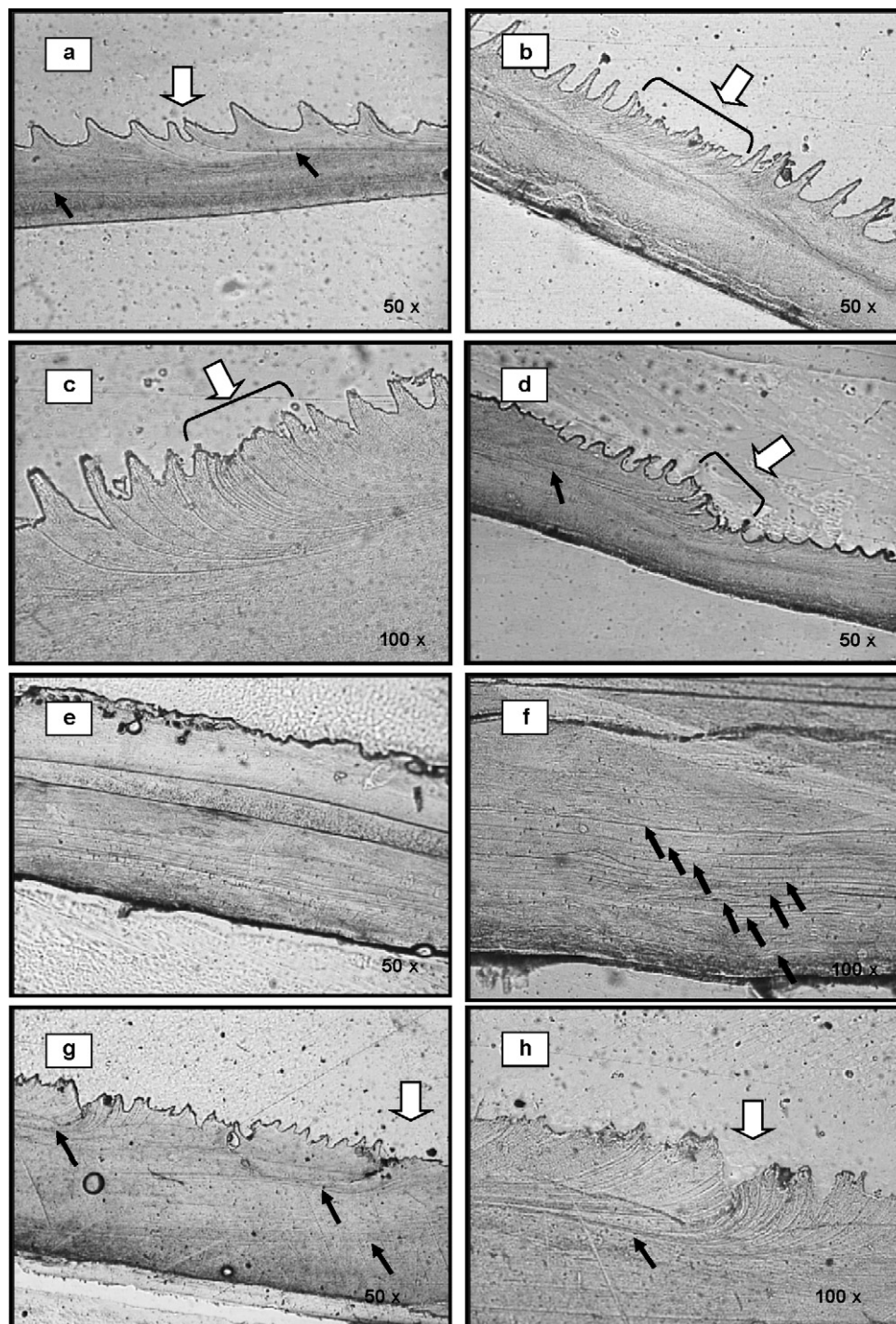


Fig. 3. Acetate peels of the shell cross-sections of *Z. patagonica* from (a) the Reclutas bed showing the internal growth bands of the first years all the way along a cross-shell section; (b) point where translucent growth bands cross the outer shell layer to form a “cluster of translucent growth bands, CTB” corresponding with an exterior ring on the shell surface from individuals of the Uruguay bed, (c) the Reclutas bed and (d) the Tango B bed; (e and f) individuals from the Beagle bed showing: all the way along a cross-shell section (notice the higher shell thickness) and (g and h) point where translucent growth bands cross the outer shell layer to form an exterior ring on the shell surface formed with a simple internal translucent growth bands (non-CTB). Black arrows: translucent growth bands; white arrows: exterior rings.

was not different between seasons (winter: 40%,  $n = 53$ ; spring: 27%,  $n = 183$ ; summer: 33%,  $n = 57$ ; fall: 26%,  $n = 58$ ;  $\chi^2 = 4.02$ ;  $p = 0.26$ ).

The pattern of internal growth bands in the umbo was similar in all beds analyzed (Fig. 2) and was used to determine the num-

ber of translucent growth bands and thus, their correspondence with chronological age.

There was a similar pattern of internal growth bands in Uruguay and Reclutas beds (see above, Fig. 3b and c). In the Tango B internal growth bands along the cross-section were sim-

Table 2  
Parameters of the general von Bertalanffy growth function in *Zygochlamys patagonica* from different beds along a latitudinal gradient using fixed  $H_0$  of 0.2 mm  $H$  (Waloszek and Waloszek, 1986) and the growth performance index  $\phi'$  estimated for each bed

Beds	$H_\infty$ (mm)	$k$ (year <sup>-1</sup> )	$t_0$ (year)	$n$	$H_{max}$ (mm)	Age <sub>max</sub>	$\phi'$
Uruguay	56.17	0.38	-0.0094	91	65.31	13	3.08
Reclutas	55.43	0.39	-0.0092	322	64.25	14	3.08
Tango B	64.01	0.34	-0.0093	90	72.9	20	3.14
Beagle	65.28	0.31	-0.0099	95	76.8	21	3.12

ilar but it was difficult to observe the point where the translucent bands cross the outer shell layer to form an exterior ring. The CTB of these exits were less defined (Fig. 3d). Shells from the Beagle bed showed a higher shell thickness along the cross-shell section (Fig. 3e and f) generating heavier shells (see above), where it was possible to see all the internal growth bands. The point where the translucent growth bands form an exterior ring did not have a CTB; it was a simple translucent growth band (Fig. 3g and h).

There was an increase in the maximum number of translucent growth bands of *Z. patagonica* following a N–S latitudinal beds, from Uruguay and Reclutas beds with 13 and 14 bands, respectively, followed by the Tango B with 20 bands and the Beagle bed with 21 bands (Table 2). Given the correspondence between external rings (annual formation confirmed by oxygen isotope analyses) and internal translucent bands, thereafter we referred to age instead of number of translucent growth bands.

Size-age data were independently analyzed by beds, always showing a good fit to the general von Bertalanffy growth model (Table 2, Fig. 4). The values of  $H_\infty$  were Uruguay: 56.17 mm (CI=54.86–57.47), Reclutas: 55.43 mm (CI=54.52–56.34), Tango B: 64.01 mm (CI=61.91–66.10) and, Beagle: 65.28 mm (CI=63.63–66.94). The values of  $k$  were Uruguay: 0.38 year<sup>-1</sup> (CI=0.35–0.42), Reclutas: 0.39 year<sup>-1</sup> (CI=0.37–0.42), Tango B: 0.34 year<sup>-1</sup> (CI=0.29–0.39) and, Beagle: 0.31 year<sup>-1</sup> (CI=0.28–0.35). Likelihood ratio test (Table 3) and surface confidence limits (Fig. 5) show that  $k$  and  $H_\infty$  parameters were similar between Uruguay and Reclutas beds and between Tango B and Beagle beds. The growth performance  $\phi'$  varied from 3.08 to 3.12 (northern and southern beds, respectively; Table 2).

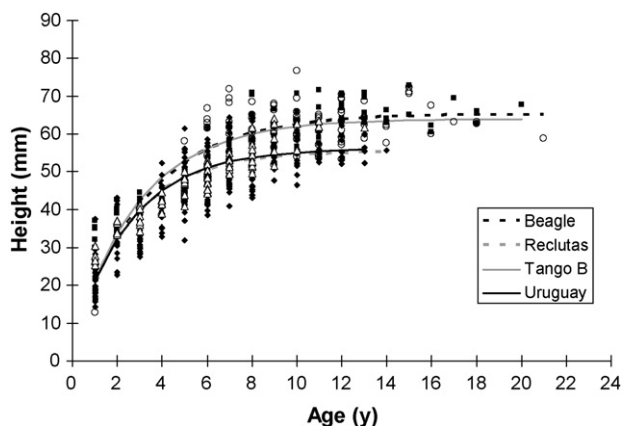


Fig. 4. von Bertalanffy growth curves of *Z. patagonica* based on internal rings from specimens of different beds. (Δ) Uruguay,  $n=91$ ; (◆) Reclutas,  $n=322$ ; (■) Tango B,  $n=90$ ; (○) Beagle,  $n=95$ .

Table 3  
Results of Likelihood ratio test for pair-wise comparison for  $k$  and  $H_\infty$  parameters between different beds

Beds compared	Minimum negative log-Likelihood		Likelihood ratio test	
	Null hypothesis	Alternative hypothesis	$\chi^2$ (d.f. = 2)	$p$ -Value
Uruguay vs. Reclutas	680.08	679.83	0.51	0.7734
Uruguay vs. Tango B	327.27	312.40	29.74	<0.0001
Uruguay vs. Beagle	320.05	302.20	35.69	<0.0001
Reclutas vs. Tango B	755.48	721.21	68.53	<0.0001
Reclutas vs. Beagle	758.86	712.94	91.84	<0.0001
Tango B vs. Beagle	340.78	340.50	0.57	0.7528

The Bonferroni correction for multiple testing did not modify the outcome of statistical tests.

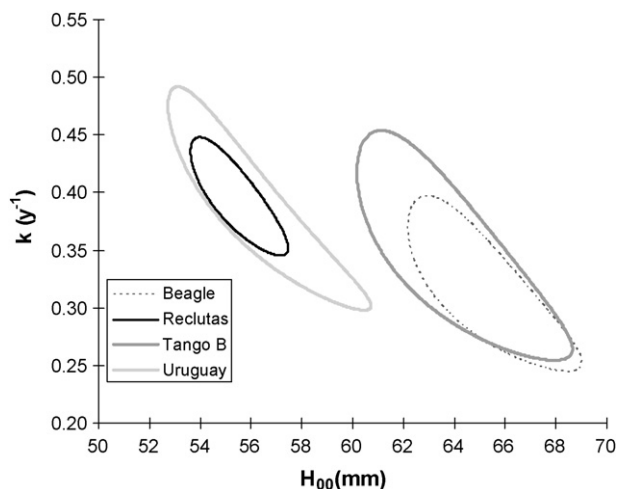


Fig. 5. Surface of confidence limits for  $k$  and  $H_\infty$  parameters. The line encompasses pairs of values for  $k$  and  $H_\infty$  parameters. Applying the Bonferroni correction, confidence limits were constructed at 1.25% in order to reach and overall 5% type I error.

#### 4. Discussion

Comparison of morphometry, internal shell growth patterns, growth rates and, maximum age of the Patagonian scallop from four beds across most of their distribution range showed a clear N to S pattern in increasing height, length, width, shell mass,  $H_\infty$ , and maximum age, and decreasing  $k$ .

The morphometric relationships of *Z. patagonica* differed between beds (Table 1). The individuals from southern beds showed higher size (height and length) and shell mass than the northern beds. The shell of *Z. patagonica* exhibits a number of surface marks, including growth rings (this study), and



repaired shell margin breaks (Lomovasky et al., 2005b). Shell cuts revealed alternating broad opaque and narrow translucent growth bands (Figs. 2 and 3) such as observed for other bivalve species (Richardson, 2001; Lomovasky et al., 2002, 2005a). In bivalves, the presence of translucent growth bands indicates period of very slow or even halted shell growth (Rhoads and Lutz, 1980; Richardson, 2001), which may be caused by low metabolic rates related to low environmental temperatures (Grizzle and Lutz, 1988; Jones et al., 1990), lack of food (Green, 1973; Beukema and Desprez, 1986; Beukema and Cadée, 1991), and/or by diversion of metabolic products into gamete production (Morton, 1978; Arneri et al., 1998; Lomovasky et al., 2002). In *Z. patagonica* the formation of “external rings” was coincident with higher temperatures (minimum  $\delta^{18}\text{O}$  isotopes) in all beds analyzed here (Lomovasky et al., 2007), and a higher gonadal condition index (gamete proliferation, following Campodónico et al., 2001) observed in the Reclutas bed in winter that coincide with higher percentage of individuals forming a “cluster of translucent bands” (this study), showing that the energy input to gamete proliferation could be the cause of decreased in shell growth (Lomovasky et al., 2007). This is likely given that food availability in this period is low (Rivas and Piola, 2002; Lomovasky et al., 2007).

The internal shell growth bands in the umbo of *Z. patagonica* were similar in all beds (Fig. 2) but, the patterns in the body differed between beds (Fig. 3). At Reclutas and Uruguay beds the translucent bands were clearly observed in the umbo and it was possible to follow each translucent internal growth band from the umbo all along the shell section to the point where it crossed the outer shell layer to form an external ring in the form of a CTB. Shells from the Tango B showed the same internal growth band pattern with less defined CTB. The pattern observed for the first two or three growth bands along this section was less defined than the other growths bands, with sizes of these individuals corresponding to first maturity (Campodónico et al., 2007). If juveniles and adults use different amounts of energy for growth and reproduction (see Griffiths and King, 1979; Héral and Deslous-Paoli, 1983; Smaal et al., 1997), the difference found in the first growth bands of *Z. patagonica* can be due to different energy allocation to shell production between juvenile and adult organisms. Similar differences were observed for other bivalves such as *Anomalocardia squamosa* (Morton, 1978), *Chlamys opercularis* (Richardson et al., 1982), *Donax trunculus* (Ramón et al., 1995), *Eurhomalea exalbida* (Lomovasky, 2002), *Euvola (Pecten) ziczac* (Lodeiros and Himmelman, 2000), *Macoma balthica* (Ankar, 1980), *Mercenaria mercenaria* (Peterson and Fegley, 1986) and, *Venus verrucosa* (Arneri et al., 1998) where there was no seasonal interruption of shell growth of juvenile individuals, but there was in adults.

Individuals from the Beagle bed showed thicker shells (with higher shell mass) and simple translucent growth bands form the exterior rings. The different patterns of internal shell growth bands between beds show differences in the regulation of shell growth along the four beds. These differences are restricted to differences in the maximum number of growth bands or age, asymptotic heights and growth rates as found in this study.

The maximum number of growth bands (or age) of *Z. patagonica* increase from beds located at the north to those located at the south (Uruguay up to 13 years old; Reclutas up to 14 years old; Tango B up to 20 years old; Beagle up to 21 years old). The maximum age found in this study for the northern beds was higher than the one previously reported for Uruguayan waters (7–9 years old; Defeo and Gutiérrez, 2003; Gutiérrez and Defeo, 2005), for the Reclutas bed (9 years old; Lasta et al., 2001) and, for the beds located between  $41^{\circ}50'S$  and  $54^{\circ}30'$  (7–8 years old; Waloszek and Waloszek, 1986; see Defeo and Gutiérrez, 2003). However, our results for the southern beds (Tango B and Beagle) are similar to those found for individuals captured near the Malvinas Islands (Bizikov and Middleton, 2002) a site located at almost the same latitude, estimations that were obtained using aging from the chondrophores and ligaments. The acetate peel technique gives the possibility to identify the internal shell growth bands closer to the shell edge (the most recent bands), which are very difficult to identify on the exterior surface of the shell. This pattern was already observed for the Malvinas Islands beds (Bizikov and Middleton, 2002), and our technique allows us to obtain new information on the maximum age of individuals. Thus, we conclude that there is an increase in the maximum age of *Z. patagonica* on the four beds following a N–S latitudinal gradient. If clusters of translucent bands are representative of annual rings (as suggested by our information), it can be concluded that *Z. patagonica* is a long-lived species similar to other species from deeper waters (up to 100–200 m) and moderate depth (up to 50–60 m; see Bricelj and Shumway, 1991).

Our study provides evidence of growth patterns variation in *Z. patagonica* in its SW Atlantic distribution range, where a significant increase in  $H_{\infty}$  from N to S beds was observed with similar results between Uruguay and Reclutas beds and between Tango B and Beagle beds (Tables 2 and 3; Fig. 4). These observations match the internal growth pattern observed in this study. The growth rates were different between the northern beds (Uruguay and Reclutas) and the southern beds (Tango B and Beagle), with a tendency to higher reduction of growth rate from year to year in the northern beds (lower latitudes) than the southern beds analyzed. Uruguayan water stocks located between  $35^{\circ}50'S$  and  $36^{\circ}50'S$  have also shown differences in growth rates decreasing toward the northern limit of the species distribution which was attributed to environmental limitation at the edge of the species geographical range (Gutiérrez and Defeo, 2005).

The large-scale aggregations of *Z. patagonica* on the south-western Atlantic do match the location of three major and different frontal systems (see Guerrero and Piola, 1997; Acha et al., 2004): (a) the Shelf-Break Frontal System, (b) the northern Patagonia Frontal System and (c) the Southern Patagonia Frontal System. Each one is functionally different but all correspond to areas of high productivity (see Bogazzi et al., 2005). Three of the beds analyzed in this study (Uruguay, Reclutas and Tango B, see Fig. 1) are located at the Shelf-Break Frontal System which present several processes that influence the circulation and water exchange (i.e., topographic waves, eddies, mid-level intrusions, turbulent exchange between interleaved layers of shelf and slope water), with difference in sea-bottom temperatures and

seasonality of waters mixing (Lomovasky et al., 2007) that may explain different seasonal enrichment and productivity across this front (see Rivas and Piola, 2002; Bogazzi et al., 2005). Different process occurred in the Beagle bed, which is characterized by a nearly homogenous water column (Sabatini et al., 2004; Lomovasky et al., 2007) by continuous vertically mixed water column with maximum temperatures during the warm season and minimum during winter. Thus, the observed difference in the morphological relationships, growth patterns, maximum age and, growth rates across beds may be related to hydrographic processes that influence primary productivity with concomitant effects on growth. In any case our results show that stock assessment for this resource should be done assuming that each bed is different in terms of growth patterns (i.e., bed-specific stock assessment).

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