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Exploring the causes of differences in growth rate of the Patagonian scallop *Zygochlamys patagonica* along its commercial bed distribution in the SW Atlantic

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ABSTRACT

Comparisons of maximum age and growth rates of the Patagonian scallop *Zygochlamys patagonica* from seven beds across most of its distribution range (39°30'S to 46°47'S; SW Atlantic) were studied in relation with physical parameters and Chlorophyll *a* concentration. The estimated maximum age varies between 19 and 25 years across different beds. Differences in the von Bertalanffy parameters were found between beds located at 39°37'S (San Blas) and 42°15'S (Valdes) increasing H_{∞} , and decreasing k from North to South. These latitudinal trends are correlated with a meridional difference of spring *Chl a* concentration and the timing of the thermocline decreasing from North to South. Thus, with the available information we hypothesize that differences in scallop growth parameters between beds are due to hydrographical processes that influence primary productivity.

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1. Introduction

The growth of bivalves can be positively or negatively affected by environmental factors that alter the rates of ingestion, absorption, excretion or oxygen uptake (Thompson and MacDonald, 2006). Such environmental drivers could be variations in temperature (Dekker and Beukema, 1999; Jones et al., 1990; Laing, 2000), salinity (Kube et al., 1996; Laing, 2002; Vincent et al., 1994), substrate characteristics (Pratt, 1953; Pratt and Campbell, 1956; Silina and Zhukova, 2007), and food availability and quality (Beukema and Cadée, 1991; Beukema and Desprez, 1986; Kube et al., 1996; Lodeiros and Himmelman, 2000; Navarro et al., 2000). Moreover, density-dependence (Dekker and Beukema, 1999; Gutiérrez and Defeo, 2003; Maguirre and Burnell, 2001; Shriver et al., 2002; Vincent et al., 1994; Weinberg, 1998) and different community compositions and thus interactions such as predation (Bologna and Heck, 1999), and presence of fouling organisms (Lodeiros and Himmelman, 2000), could also affect growth rate of individuals inhabiting different latitudes. In general, bivalve mollusks from low latitudes grow faster, attain a smaller maximum size, and have a shorter lifespan than do co-specifics from higher latitudes (see Heilmayer, 2003; Newell, 1964). Latitude is often a proxy for total amount of and seasonality in solar energy input, which mainly

translates into temperature but also into primary production related parameters and food supply (Roy et al., 1998).

The Patagonian scallop *Zygochlamys patagonica* is an important economic SW Atlantic resource (e.g., Lasta and Bremec, 1998). This species 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 to 200 m (Defeo and Brazeiro, 1994; Gutiérrez and Defeo, 2003, 2005; Lasta and Zampatti, 1981; Waloszek and Waloszek, 1986; occasionally down to 960 m, Waloszek, 1991). In the Pacific, grounds occur in relatively 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; Fig. 1) matching the location of three major oceanic frontal systems (Bogazzi et al., 2005). From fish management purposes, each bed is considered a management unit (MU) which is located within two administrative sectors (south and north 39°30'S) inside Argentinean waters.

Most growth studies of *Z. patagonica* were based on observations of external growth rings (Defeo and Gutiérrez, 2003; Gutiérrez and Defeo, 2005; Lasta et al., 2001; Waloszek and Waloszek, 1986). These results show substantial discrepancies on the estimates of maximum age when compared with estimations based on analysis of internal structures such as chondrophores and ligaments (Bizikov and Middleton, 2002; Lomovasky et al., 2007, 2008). This discrepancy may in part be due to the poor readability of external rings as individuals get older (see Bizikov and Middleton, 2002; Lomovasky et al., 2007, 2008). In *Z.*

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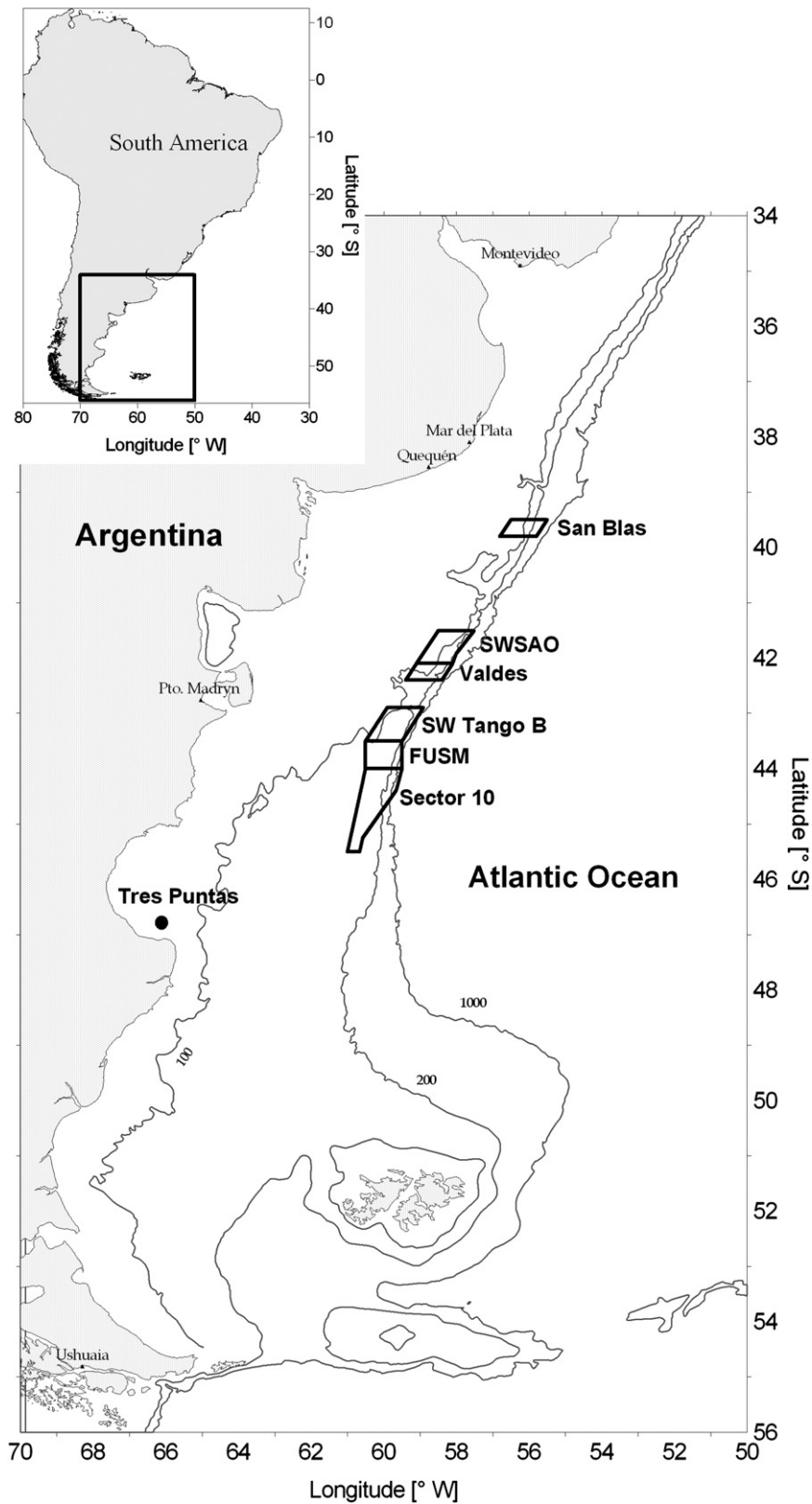


Fig. 1. Spatial distribution of the Patagonian scallop *Zygochlamys patagonica* sampled beds on the Argentine Continental Shelf, SW Atlantic. Each bed is considered a management unit (MU) within two administrative sectors (north and south of 39°30'S).

patagonica the shell growth marks are formed annually during periods of higher water temperature (austral winters) when the energy input to gamete proliferation is the cause of a decrease 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 populations (35°50'S to 36°50'S)

show differences in growth rates (Gutiérrez and Defeo, 2005; Lomovasky et al., 2008), abundance, individual size and muscle weight related to environmental variables (Gutiérrez et al., 2008) decreasing towards the northern limit of the species distribution. Argentinean populations showed evidence of variation in growth in three beds (Reclutas, 39°20'S; Tango B, 42°30'S; and Beagle, 55°10'S) along the species SW Atlantic distribution range, where a significant increase in H_{∞} 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 (Lomovasky et al., 2008). However, the cause of those differences has not been evaluated yet. Thus the purpose of this work is to evaluate if there are differences in maximum age and growth rates between the seven beds along the extended latitudinal distribution of this species, and determine the relationship between these parameters and oceanographic parameters (sea temperature and Chlorophyll a concentration) in the SW Atlantic.

2. Material and methods

2.1. Sampling sites

Samplings of *Z. patagonica* ($n = 2429$) were performed in 7 beds that are also Argentinean fishing Management Units (MU), which from North to South are: San Blas (MU3), SWSAO (MU5), Valdes (MU6), SW Tango B (MU8), FUSM (MU9), Sector 10 (MU10) and Tres Puntas (Fig. 1, Table 1), which do not necessarily match biological units. The surveys were conducted using a 2.5 m wide dredge in most beds with the exception of some trawls from Valdes, SW Tango B, FUSM and Sector 10, which were sampled with commercial ships using a bottom otter trawl (foot rope of 22 m, net and cod-end of 10 cm mesh size). Previous information suggests no differences in scallop size-selectivity between both fishing gears (Ciocco et al., 2006). A total of 27 trawls were made between March 2002 and June 2006 in the different beds. The initial and final positions using GPS

(precision: ± 60 m) and depth using depth sounder (precision: ± 1 m) of each trawl were registered. Individuals were collected, frozen at -20 °C, and epibionts were removed by brushing the shell surface.

2.2. Physical parameters

The oceanographic data used in this study consists of 499 hydrographical (bottle, and CTD) stations obtained between 1963 and 2010. This information is available in the "Base Regional de Datos Oceanograficos (BaRDO) – INIDEP" oceanographic database that includes Southern Ocean Database (SODB) data (http://woces.oatlas.tamu.edu/Sites/html/atlas/SOA_DATABASE.html). About 96% of total data consist of high-resolution CTD (conductivity, temperature, depth) records collected by INIDEP with a Meerestechnik Elektronik sonde and Seabird profilers (SBE911 and SBE19 series), which were calibrated by measuring water samples with a salinometer and reversing thermometers. Discrete water bottle samples represent only 4% of the total data used.

To characterize the annual regime of temperature in each bed, data were selected using boxes of 0.5° of latitude (centered in each of the sampling point inside each bed) and according to the depth range where the fishing grounds are located. Sea-bottom temperatures represent the average temperature of the bottom layer (70–120 m depth) for each hydrographic station. Given that temperature dominates the vertical structure of density fields, seasonally averaged temperature profiles were used to characterize the stratification cycle in the water column to each area. The data were grouped according to: summer (January to March), autumn (April to June), winter (July to September) and spring (October to December).

In addition, we used the Sea Surface Temperature (SST) data derived from satellite data from the Advanced Very High Resolution Radiometer (AVHRR) processed by the Pathfinder project version 5.0 (available at <http://data.nodc.noaa.gov/pathfinder/>). The monthly climatology data used consists of twelve composite images, for the 1985–2001 periods, with a resolution of about 4 km. We calculate a seasonal average and its standard deviation of SST over each of the 0.5° boxes.

2.3. Chlorophyll a

The satellite derived surface *Chl a* estimation data used correspond to Standard Mapped Images (SMI) of satellite derived concentrations (CSAT). We used CSAT seasonal climatology (summer: 21 December through 20 March; autumn: 21 March through 20 June; winter: 21 June through 20 September and; spring: 21 September through 20 December) from the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) for the periods 1997–2010 provided by the NASA Goddard Space Flight Center's Ocean Data Processing System (<http://oceancolor.gsfc.nasa.gov/cgi/l3>). The SMIs are derived from Level-3 seasonal binned data products of a two dimensional array of an Equidistant Cylindrical projection of the globe of 9 km resolution. CSAT estimated concentrations (mg m^{-3}) are processed by NASA with the OC4v4 algorithm (O'Reilly et al., 1998), and are generally in good agreement with in situ bio-optical observations in the SW Atlantic (Dogliotti et al., 2009). The global SMI data were sub-sampled to the region limited by 39–48°S and 55–70°W.

Simple correlations (r) between *Chl a* and sea temperatures were evaluated by linear models (Zar, 1999).

2.4. Internal growth patterns and growth ring determination

For growth and band formation analyses, sub-samples were obtained from each bed to reflect the size-range at each site (all $n = 604$; see Table 2). Growth pattern was inferred using internal shell growth bands (Rhoads and Lutz, 1980). Each left valve was

Table 1
Area, depth and number of individuals sampled in the present study.

Beds	Latitude	Longitude	Area (km ²)	Depth (m)	N
San Blas	39°30'	55°30'	2895	103–109	401
	39°30'	56°30'			
	39°48'08	56°48'32			
	39°48'08	55°48'36			
SW SAO	41°30'29	57°30'71	5116	107–110	255
	41°30'29	58°30'18			
	42°05'83	59°05'84			
	42°05'83	58°06'12			
Valdes	41°55'	58°00'	2877	103–109	594
	42°05'83	59°05'84			
	42°05'83	58°06'12			
	42°23'89	58°24'32			
SW TangoB	42°23'89	59°23'91	5368	100–112	504
	42°53'86	59°54'20			
	42°53'86	58°54'49			
	43°30'	59°30'			
FUSM	43°30'	60°30'	4516	104–108	400
	43°30'	60°30'			
	44°00'	60°30'			
	44°00'	59°30'			
Sector 10	44°00'	60°30'	9228	105	200
	44°00'	59°30'			
	44°23'19	59°39'71			
	45°14'80	60°35'			
Tres Puntas	45°30'	60°40'	104	75	
	45°30'	61°00'			
	46°47'	66°07'			

Table 2

Parameters of the general von Bertalanffy growth function with confidence limits (CI) at alpha 0.05 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 ϕ' estimated for each bed.

Beds	H_∞ (mm) (CI)	k (year ⁻¹) (CI)	t_0 (year)	n	H_{\max} (mm)	Age _{max}	ϕ'
San Blas	60.41 (58.82, 62.01)	0.2442 (0.2197, 0.2736)	-0.014	91	75.28	25	2.95
SW SAO	64.23 (62.19, 66.26)	0.1907 (0.1739, 0.2102)	-0.016	96	75.36	24	2.90
Valdes	67.31 (65.79, 68.82)	0.1782 (0.1611, 0.1945)	-0.017	116	79.42	24	2.91
SW TangoB	61.79 (59.91, 63.67)	0.2146 (0.1922, 0.2418)	-0.015	93	73.93	23	2.91
FUSM	64.77 (62.68, 66.87)	0.2220 (0.2029, 0.2437)	-0.014	118	76.94	24	2.97
Sector 10	59.98 (56.88, 63.09)	0.2094 (0.1749, 0.2609)	-0.016	24	67.74	19	2.88
Tres Puntas	56.77 (55.73, 57.81)	0.4145 (0.3238, not possible)	-0.016	66	65.56	23	3.13

embedded in polyester resin, sectioned along the axis of maximum growth in shell height (SH) using a saw with a diamond blade, and the cross-sections polished on lapidary wheels using grits of 400, 600, 1200, 2500, and 4000 grade, and then etched between 23 and 30 min using 0.5% DE-CAL agent. Acetate peels were made of the cross-sectioned surfaces of 20 individuals from each bed to allow for microscopic examination for the presence of internal growth bands following Lomovasky et al. (2007, 2008).

Additionally, analyses of ligament and condrophores were carried out and compared with the acetate peel technique (both readings) in order to find a quick method to be extensive in future stock evaluations. Umbo sections with ligament and condrophore were taken and embedded in polyester resin, polished on lapidary wheels and etched (as described above), and were examined for the presence of internal growth bands under binocular stereomicroscope. Internal growth bands can be identified as translucent and opaque bands (Jones et al., 1990), where translucent bands are narrow and dark and opaque bands are wide and white.

The general von Bertalanffy growth model was used to fit the number of internal translucent bands and the corresponding shell height recorded as age-shell height data (following Lomovasky et al., 2007, 2008). For this purpose we used:

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

where H_∞ is asymptotic height, k is the growth rate, t is age and t_0 is age at zero height.

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

$$t_0 = 1 / k * \ln((H_\infty - H_0) / H_\infty) \quad (2)$$

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 the shells of adult individuals (Waloszek and Waloszek, 1986).

To fit the model to the data for each bed the maximum likelihood method was used (following Edwards, 1992; Hilborn and Mangel, 1997). The von Bertalanffy k and H_∞ parameters of the seven 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_∞ parameters were constructed using profile likelihood (see Hilborn and Mangel, 1997). Bonferroni corrections were applied to avoid type I error inflation due to multiple comparisons in the likelihood ratio test and in the construction of confidence limit intervals (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.

Simple correlations between growth parameters and mean oceanographic variables were carried out by linear models (Zar, 1999).

3. Results

3.1. Physical parameters

Some differences in the seasonal cycle of sea-bottom temperature and vertical structure of water column were observed between beds (Fig. 2). The annual sea-bottom temperature variation was between 5° and 7 °C, decreasing 0.5 °C from San Blas to Sector 10 (39°30'S to 45°30'S). The maximum temperatures (6.5 °C ± 0.4) occur from May to June in San Blas, June to July in SW SAO, extending to the period from May to August in Valdes, SW TangoB and FUSM, and from July to August in Sector 10. The minimum temperatures (5.6 °C ± 0.4) also present a distinct timing occurring between beds during September in San Blas, in October for Valdes and from October to November in Sector 10. Tres Puntas bed presented highest annual sea-bottom temperature variation (6 °C) reaching its maximum from March to May (11 ± 1 °C) and lowest values from August to October (7.6 ± 0.8 °C).

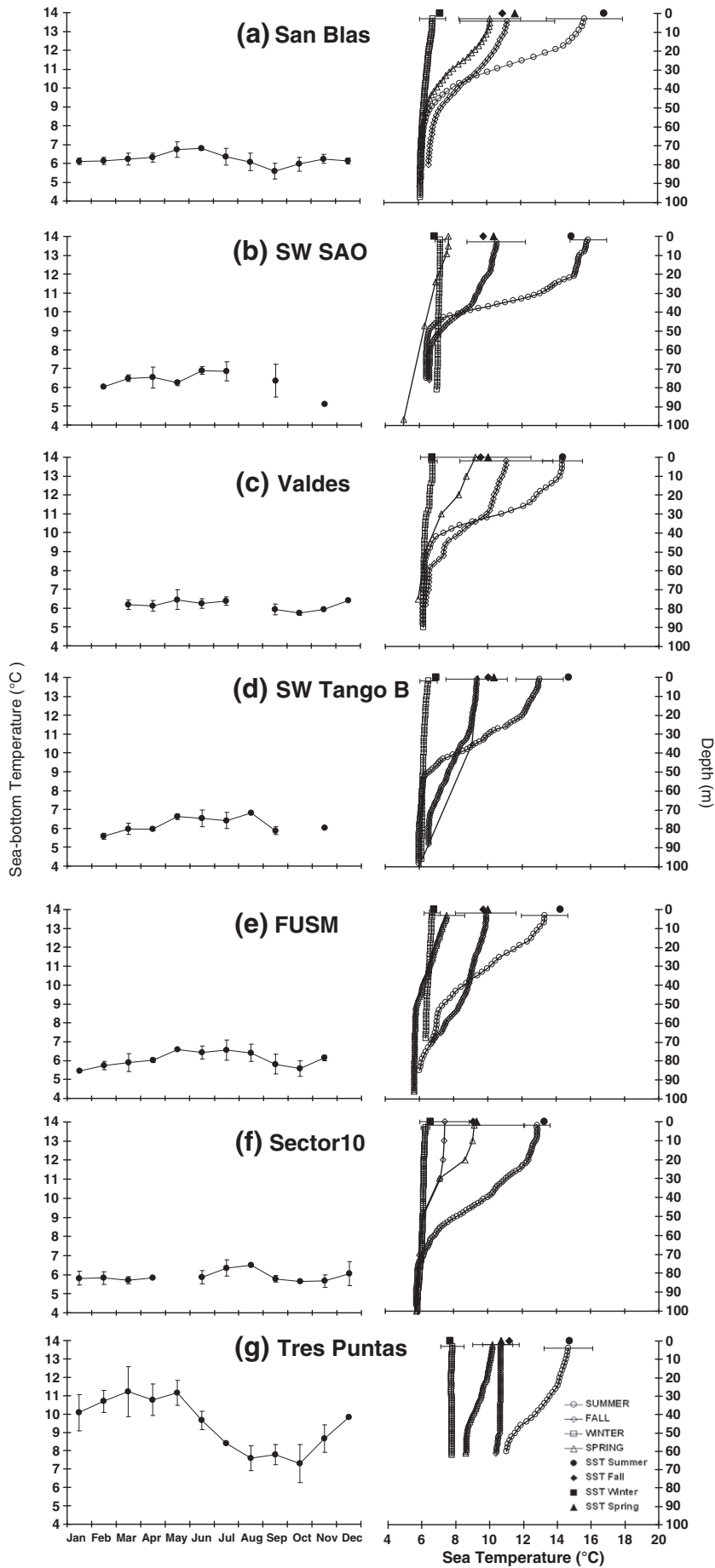
The analysis of the water column temperatures showed that the surface layer undergoes large seasonal temperature changes (Fig. 2 – profiles). In situ temperature measurements correlated with SST estimates (Baldoni, personal communication). In San Blas the amplitude of the sea surface temperature cycle exceeded 11 °C and decreased to 7 °C in Sector 10. There was a large change in the vertical stratification, from strongly stratified summer conditions, with an established thermocline between 30 m and 50 m depth, to a homogeneous winter condition. The transition states of development and breakdown of seasonal thermocline during spring and autumn, respectively, were represented by a weaker stratification in temperature profiles. A gradual decrease of seasonal stratification was observed with increasing latitude, reaching minimum values in Tres Puntas (46°47'S) where the turbulence generated by high tidal currents keeps the coastal waters well-mixed.

3.2. Chlorophyll *a*

Mean seasonal CSAT distribution (Fig. 3) presented highest concentration (2.5–3.0 mg m⁻³) in spring and lowest values in autumn and winter (0.5–1.5 mg m⁻³). This seasonal CSAT cycle showed differences between beds. In summer San Blas maintains values of about 2.5 mg m⁻³ while in the rest of the beds the values decay to 2.0 mg m⁻³. Likewise the lowest concentrations observed during autumn and winter diminish from San Blas (1–1.5 mg m⁻³) to Sector 10 (0.5–1 mg m⁻³). The values observed in Tres Puntas present lower seasonal variations maintaining CSAT concentrations between 1 and 2.5 mg m⁻³ throughout the year. The winter *Chl a* (minimum concentration) were positively correlated with winter SST ($p < 0.05$; $r = 0.86$).

3.3. Internal growth pattern and growth band determination

The patterns of internal growth bands in the ligament and condrophore were similar in all beds analyzed, showing alternating



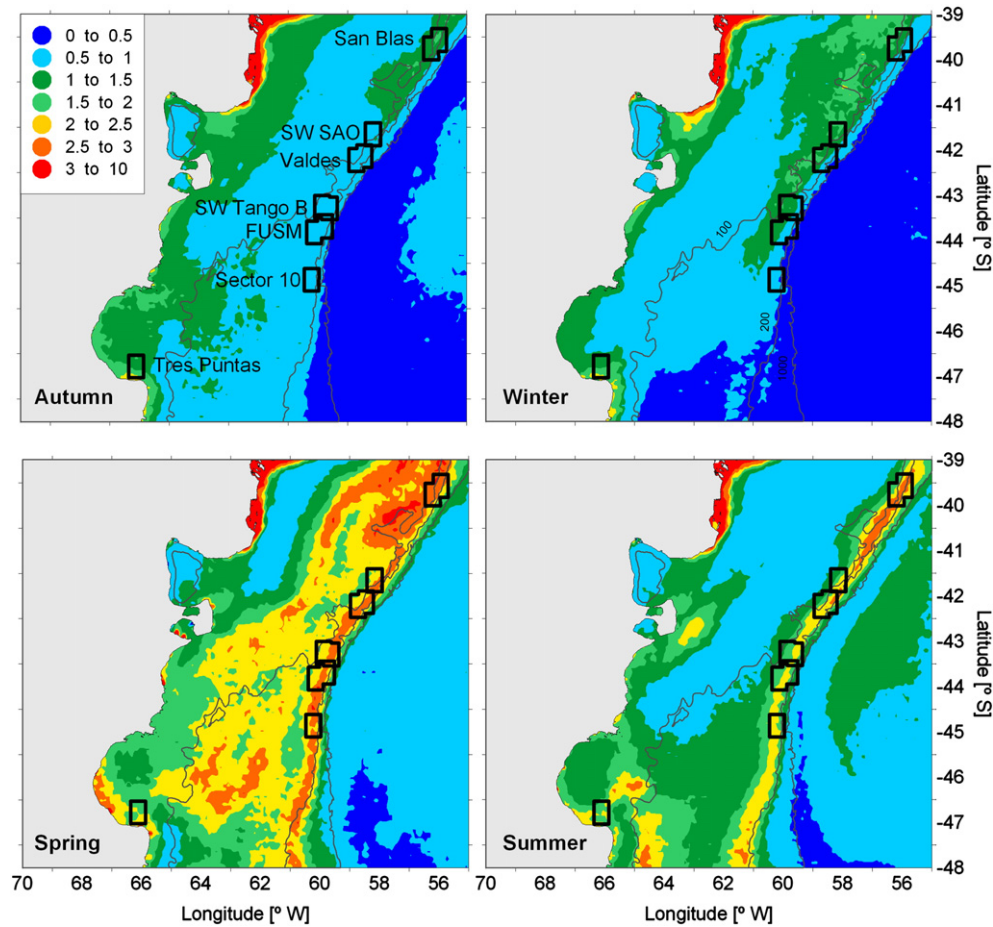


Fig. 3. SeaWiFS derived surface *Chl a* (mg m^{-3}) in (a) austral autumn (Apr to Jun), (b) winter (Jul to Sep), (c) spring (Oct to Dec), and (d) summer (Jan to Mar) in the western South Atlantic between 39–48°S and 55–70°W.

broad opaque and narrow translucent growth bands; they corresponded to identical numbers of internal growth bands in the shell, and were thus used to determine the number of translucent growth bands and the inferred chronological age. Given the association between external rings and internal translucent bands in the shell (annual formation confirmed by oxygen isotope analyses, see Lomovasky et al., 2007) and internal growth bands in the ligament (this study), thereafter we referred to age instead of number of translucent growth bands.

The maximum age of *Z. patagonica* across beds was between 19 and 25 years (Table 2).

Size-age data analyzed per bed showed a good fit to the general von Bertalanffy growth model with values of H_{∞} and k with confidence limits (CI) at alpha 0.05 (Table 2, Fig. 4). Likelihood ratio tests (Table 3) and surface confidence limits (Fig. 5) show that k and H_{∞} parameters were different between San Blas and Valdes. Given the lack of animals younger than 6 years old for the Sector 10 and Tres Puntas beds, no comparison with bivariate confidence limits (CI) for k and H_{∞} parameters was constructed for these areas in relation with the rest. The growth performance ϕ' varied from 2.95 to 3.13 (from northern to southern beds respectively; Table 2).

Positive linear correlations were observed between the scallop growth rates and the spring surface *Chl a* concentrations ($r = 0.77$).

Negative linear correlations were found between H_{∞} and spring surface *Chl a* ($r = -0.89$; $p < 0.05$; Fig. 6).

4. Discussion

A comparison of maximum age and growth rates of the Patagonian scallop from seven beds along most of the species distribution range in the south administrative sector (south 39°30'S) shows no difference in the maximum age between beds. However, there are differences in the von Bertalanffy parameters between San Blas (39°37'S) and Valdes (42°15'S) increasing H_{∞} , and k decreases from North to South. Growth rates were positively correlated with spring *Chl a*.

The internal shell growth bands in the ligament, condrophore and umbo of *Z. patagonica* were similar between beds, and the pattern in the shell was similar to that observed in shells from the Tango B (42°30'S) and Beagle beds (55°10'S) (South administrative sector), with less defined internal growth band patterns in the “cluster of translucent bands” (Lomovasky et al., 2008). In bivalves, the presence of translucent growth bands indicate a 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

Fig. 2 Annual variation in sea-bottom temperature between 90 and 120 m depth (mean \pm SD) and seasonal sea temperature profiles from 0 to 100 m depth in: (a) San Blas, (b) SW SAO, (c) Valdes, (d) SW TangoB, (e) FUSM, (f) Sector 10 and, (g) Tres Puntas.

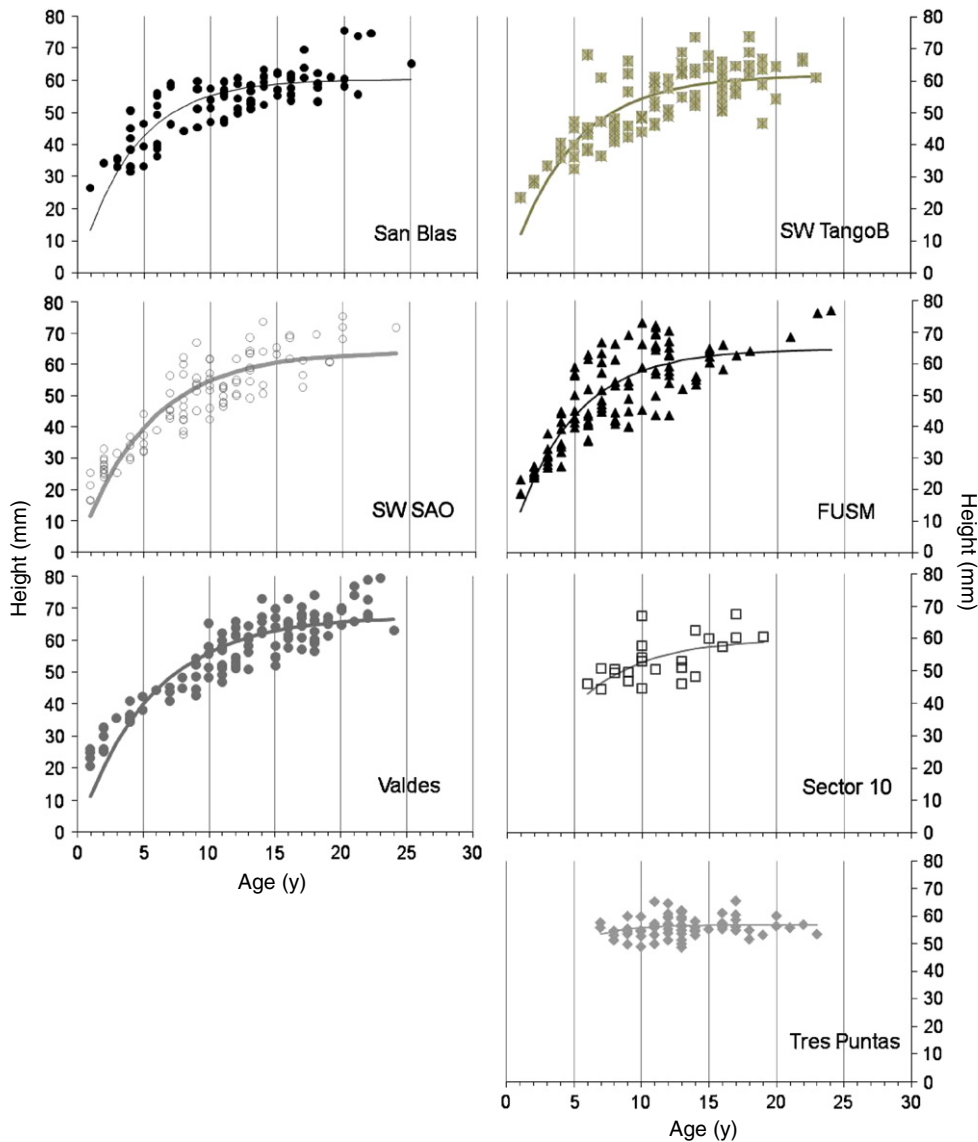


Fig. 4. von Bertalanffy growth curves of *Zygochlamys patagonica* based on internal growth lines from specimens of different beds.

(Beukema and Cadée, 1991; Beukema and Desprez, 1986), and/or a redistribution of a good part of metabolic products necessary for shell growth into gamete production (MacDonald and Thompson, 1986a,

Table 3

Results of Likelihood ratio test for pair-wise comparison for k and H_{∞} parameters between different beds. The Bonferroni correction for multiple testing modifies the outcome of statistical tests.

Beds compared	Minimum negative log-likelihood		Likelihood ratio test		
	Null hypothesis	Alternative hypothesis	χ^2 (df=2)	P-value	Bonferroni correction
San Blas – SW SAO	7 800.24	7 640.93	3.86	0.1452	No sig
San Blas – Valdes	7 984.61	7 444.88	14.49	0.0007 *	Sig **
San Blas – SW TangoB	7 664.14	7 616.45	1.15	0.5631	No sig
San Blas – FUSM	10 726.38	10 416.21	6.13	0.0466 *	No sig
SW SAO – Valdes	8 839.98	8 721.44	2.86	0.2390	No sig
SW SAO – SW TangoB	8 935.73	8 893.00	0.91	0.6357	No sig
SW SAO – FUSM	12 143.90	11 692.77	8.10	0.0174 *	No sig
Valdes – SW TangoB	9 074.78	8 696.95	8.89	0.0117 *	No sig
Valdes – FUSM	11 710.35	11 496.72	4.31	0.1160	No sig
SW TangoB – FUSM	12 075.57	11 668.28	7.24	0.0268 *	No sig

Asterisks with a significance $p < 0.05$.

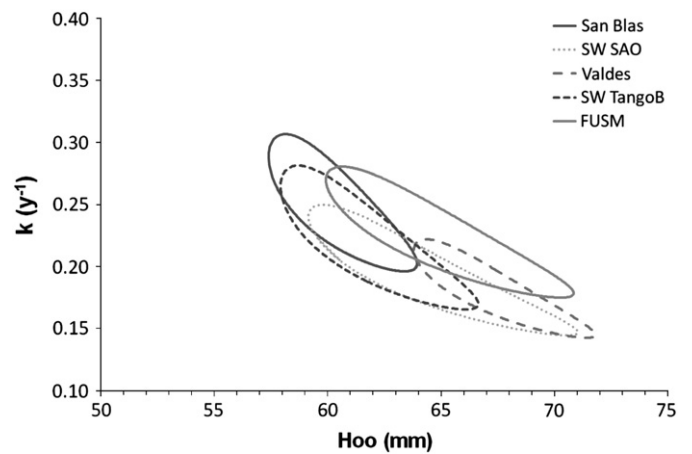


Fig. 5. Surface of confidence limits for k and H_{∞} parameters. The line encompasses pairs of values for k and H_{∞} parameters. Applying the Bonferroni correction, confidence limits were constructed at 1.25% in order to reach and overall 5% Type I error.

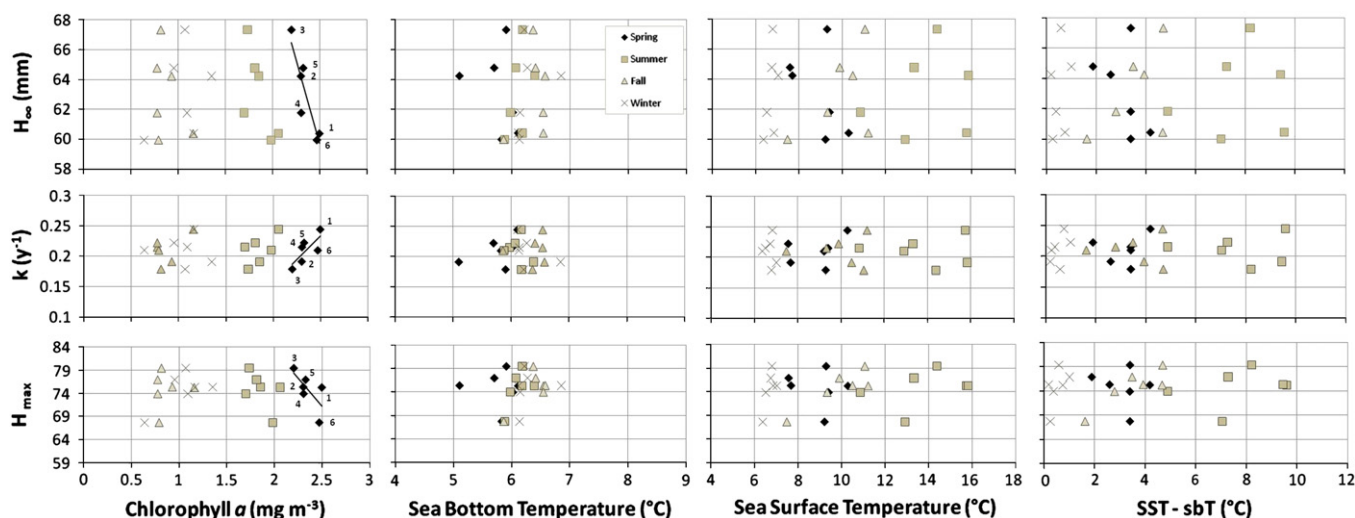


Fig. 6. Bivariate correlations between H_{∞} , growth rate k and H_{\max} and oceanographic variables (mean seasonal Chl a concentration, mean sea surface temperature (SST), mean sea bottom temperature (SBT) and mean difference between SST and SBT) in the different beds. Numbers inside represent different beds: (1) San Blas, (2) SW SAO, (3) Valdes, (4) SW Tango B, (5) FUSM and (6) Sector 10.

1986b, 1988; Thompson and MacDonald, 2006). In *Z. patagonica* the formation of “external rings” corresponded with internal growth bands and was coincident with higher temperatures (minimum $\delta^{18}\text{O}$ isotopes; Lomovasky et al., 2007), a lower adductor muscle condition index and a higher gonadal condition index (gamete proliferation, following Campodónico et al., 2008) showing that the energy input to gamete proliferation could be the cause of a decrease in shell growth in beds such as Reclutas (39°20’S) and Tango B (Lomovasky et al., 2007). Similar patterns in the shift from somatic to gonad growth have been observed in other pectinid species (e.g. Bricelj and Shumway, 1991; Richardson et al., 1982).

The maximum number of growth bands (or age) of *Z. patagonica* observed in this study was between 19 and 25 years old. These results are similar to those obtained for the Tango B (up to 20 years old) and Beagle (up to 21 years old) (Lomovasky et al., 2008) and for individuals captured near the Malvinas Islands (51°43’ S, 60°03’ W; Bizikov and Middleton, 2002), that were age estimated using acetate peels of shells and chondrophores and ligaments, respectively. Collectively, these beds represent the Argentinean South administrative sector (south 39°30’S). When compared with beds further north than 39°30’S, the maximum age decreases. For Uruguay (36°17’S) the species is aged up to 13 years old (internal growth lines; Lomovasky et al., 2008) and 7–9 years old (external rings; Defeo and Gutiérrez, 2003; Gutiérrez and Defeo, 2005); for Reclutas up to 14 years old (internal growth lines; Lomovasky et al., 2008) and 9 years-old (external rings; Lasta et al., 2001). Thus, we conclude that there is an increase in the maximum age of *Z. patagonica* on beds following a N–S latitudinal gradient, determined by the south and north of 39°30’S, given that management units do not necessarily match biological units. At this latitude the southward flowing Brazil Current and the northward flow of the Malvinas Current, circulating along the continental slope, encounter in a frontal region known as the Confluence Zone (Saraceno et al., 2004). The Confluence Zone is a highly dynamic region characterized by intense near surface velocities associated with a complex array of eddies, rings and filaments and high spatial-temporal variability (Garzoli and Giulivi, 1994), representing the limit between a subtropical (BC) and sub-Antarctic regime (MC). The different patterns of internal shell growth bands and maximum age between beds show differences in the regulation of shell growth along the beds (Lomovasky et al., 2007).

Our study provides evidence of variation in growth patterns of *Z. patagonica* along part of its SW Atlantic distribution range, where an

increase in H_{∞} from San Blas (39°37’S) to Valdes (42°15’S) was observed with similar results between the rest of the beds with exception of Sector 10 (44°45’S) and Tres Puntas (46°47’S; Table 2; Fig. 4) which could not be compared given the lack of individuals younger than 6 years old. The k growth rate decreases to the South with a difference between San Blas and Valdes. Uruguayan water stocks located between 35°50’S to 36°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; Heilmayer, 2003). Individuals from the Tres Puntas bed that are influenced by coastal waters showed a trend similar to the North beds (see Fig. 1; Lomovasky et al., 2008) with lower H_{∞} and higher k .

The large-scale aggregations of *Z. patagonica* on the SW Atlantic match the location of three major frontal systems (see Acha et al., 2004; Guerrero and Piola, 1997). Each one is functionally different but all correspond to areas of high productivity (see Bogazzi et al., 2005). The beds analyzed in this study (from San Blas to Sector 10; see Fig. 1) are located at the Shelf-Break Frontal System which represents the transition between the Malvinas Current, advecting northward nutrient rich Subantarctic waters, and the diluted Subantarctic waters of the continental shelf, strongly governed by a seasonal cycle of thermocline formation and breakdown (Guerrero and Piola, 1997; Martos and Piccolo, 1988; Saraceno et al., 2004) which showed a gradual decrease of seasonal stratification with increasing latitude (San Blas to Sector 10). The sea bottom temperature showed that the maximum values were similar between beds (San Blas to Sector 10), but distinct warm periods were observed across beds. It lasted one month in San Blas, two in Sector 10, and four from Valdes to FUSM.

The Shelf-Break Frontal System presents a band of high Chl a concentration (García et al., 2008; Podestá, 1997; Romero et al., 2006; Saraceno et al., 2005) and is associated with several biological aggregations (Acha et al., 2004; Brunetti et al., 2000; Podestá, 1990; Thomson et al., 2001) including scallop beds (Bogazzi et al., 2005). The nutrient enrichment mechanisms of this high productivity area are poorly understood and several processes are proposed to influence the circulation and water exchange (i.e., topographic waves, eddies, intrusions, turbulent exchange between interleaved layers of shelf and slope water; see Podestá, 1990; Saraceno et al., 2005; Piola et al., 2010). Results from an oceanographic model suggest that the bottom friction, associated with the presence of the intense flow of the Malvinas Current over the slope, produce divergence and

upwelling over the shelf-break (Palma et al., 2008). The mixing of nutrient rich Subantarctic waters of the Malvinas Current and the vertical stratification over the continental shelf seems to be a relevant process in the enhanced phytoplankton growth over the continental shelf (Romero et al., 2006). We observed a difference in *Chl a* concentrations across the meridional gradient; maximum *Chl a* concentrations occurred in all beds in spring with values between 2.5 and 3.0 mg m⁻³ (see Fig. 3). The minimum values were observed in autumn–winter with a clear decreasing trend towards high latitudes from San Blas to Sector 10. This seasonal cycle presents substantial interannual variations, but the bloom locations are remarkably stable because it is associated with a bottom trapped front (Romero et al., 2006; Saraceno et al., 2004). Therefore it is expected that the topographic characteristics affect local dynamics and nutrient enrichment mechanisms.

Positive correlations were observed between the scallop growth rates and spring surface *Chl a* concentrations and negative relationships were found for H_{∞} and H maximum (see Fig. 6). Food availability at the bottom depends on the concentration of phytoplanktonic biomass at the surface and the benthopelagic coupling processes (Valiela, 1995). A high diatom sedimentation rate even occurred during stratification conditions (Hansen and Josefson, 2001) between spring and summer in the SW Atlantic, and the stomach contents analysis for individuals of this specie in November (spring) which showed the presence of subantarctic diatoms and dinoflagellates (Schejter et al., 2002), indicate that the phytoplankton is the main food source of this species and could be the cause of the difference in growth parameters observed between beds.

The Tres Puntas bed (this study) and the Beagle bed (Lomovasky et al., 2007; 2008) are characterized by an almost homogenous water column throughout the year, with maximum sea bottom temperatures during the warm season (January to May) and minimum at the end of the winter. Tres Puntas is under the influence of the Southern Patagonian Frontal System, a thermohaline front that represents the transition between tidally mixed low-salinity waters of the Patagonian Current and seasonally stratified more saline waters of the continental shelf. Enhanced vertical mixing due to the interaction of strong tidal currents with the sea bottom leads to much weaker stratification in coastal waters (Glorioso and Flather, 1995; Guerrero and Piola, 1997). The high *Chl a* observed in this near coastal site suggest that tidal induced mixing plays a major role in the redistribution of nutrients and in the maintenance of this productivity zone. Numerical simulations (Palma et al., 2004) suggest that tidal currents are important in preventing cross-isobaths flows and may lead to the development of upwelling and downwelling regions. The high annual *Chl a* concentration found in this bed (46°47'S) is close to that found in San Blas (39°37'S) which could explain the high values of growth rate found in this coastal bed.

The difference between beds (Lomovasky et al., 2008; this study) in the von Bertalanffy parameters increasing H_{∞} , and decreasing k from North to South is related to the difference in spring *Chl a* concentrations along the meridional gradient and the timing of the thermocline decreasing from North to South shown in this study. A decrease in abundance, individual size and muscle weight was found at the northern edge of the distribution of this species (Uruguayan waters) associated with a major temperature, showing the best scallop conditions associated with a higher *Chl a* concentration (Gutiérrez et al., 2008). At the MDQ bed (38°44' S), differences in scallop abundance and recruitment were found to strongly relate to the position of the Shelf Break Front and the associated high *Chl a* concentration (Mauna et al., 2008).

In both cases, food availability was determinant of the health of this species. Thus, the possible differences in oceanographic variables along a latitudinal gradient could be the cause of the differences observed in our study, as was previously suggested for this species (Lomovasky et al., 2008).

In conclusion, we hypothesize that the differences in growth parameters between beds of the Patagonian scallop are due to hydrographic processes that influence primary productivity.

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