



Full length article

Growth variability in a metapopulation: The case of the southern geoduck (*Panopea abbreviata*)

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ARTICLE INFO

Article history:

Received 17 March 2015

Received in revised form 10 August 2015

Accepted 10 August 2015

Keywords:

Southern geoduck

Growth

Patagonia

Multimodel inference

ABSTRACT

Oceanographic conditions modulate the growth of bivalves. In Northern Patagonia, Argentina, seasonal thermohaline fronts define 3 oceanographic domains in the San Matías Gulf (SMG) and the San José Gulf (SJG), which create different environmental conditions for growth. We studied the variability of the growth pattern in a metapopulation of the geoduck clam *Panopea abbreviata* within and between oceanographic domains. *P. abbreviata* forms spatially disjunct subpopulations in the SMG and the SJG. Growth patterns were determined using size-at-age data from counts of inner shell layers for two subpopulations in each oceanographic domain. We used a multimodel inference approach to describe the growth pattern, fitting five candidate growth models (von Bertalanffy, logistic, Gompertz, Richards, and Schnute-Richards). Growth was fast during the first 8–10 years and slowed in later years. This pattern was consistent with the pattern described in studies for other *Panopea* species. Larger individuals of *P. abbreviata* were more abundant in mud-sandy places (Punta Conos and Playa Fracasso, SJG's eastern coast) than in locations with sand sediment (Punta Colorada and Puerto Lobos, SMG's western coast). Multimodel inference is a robust way to estimate growth parameters for this species. We found differences among locations, independent of the domains. The results suggest that local environmental conditions are greater growth modulators than general oceanographic conditions. The differences in growth observed among locations should be considered when developing biological reference points specific for each location.

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1. Introduction

Growth is an important aspect of stock production. Ignoring migration, the increment of biomass of populations is a mixture of the recruitment of new individuals to the population and the growth of the individuals already in the population (Urban, 2000). The growth parameters are necessary inputs for fisheries assessment models (Haddon, 2001). Therefore, the study of growth is important for the sustainable management of fishery resources.

Southern geoduck *Panopea abbreviata* (Valenciennes, 1839) is endemic to the southwest Atlantic and is distributed from Rio de Janeiro (23°S) to Nuevo Gulf (48°S) (Ageitos de Castellanos, 1967; Signorelli and Fernández Alfaya, 2013) (Fig. 1). *P. abbreviata* is distributed in spatially disjunct subpopulations parallel to the coastline in waters ranging from shallow to 75 m deep, and investigations of this species recently began off northern Patagonia. Since

1999, the fishery has been experimental in two locations in the San Matías Gulf (SMG): El Sótano (NW) and Puerto Lobos (SW). During the first year of exploitation, geoduck landings reached 5.7 t, and in the subsequent years, fishery productivity varied between 1.8 and 15.6 t (Morsan et al., 2010). Currently, no management exists for the southern geoduck fishery.

Bivalves have indeterminate growth (Sebens, 1987). This pattern consists of a first phase of continuous growth and a second phase in which the growth stops. The second phase occurs when the individual reaches its maximum length. However, the individuals preserve growth potential – in case of a change in environmental conditions – throughout life. In species with indeterminate growth, environmental conditions determine the maximum length and growth rate. Studies on the growth of marine bivalves have described the relations between them and environmental characteristics (e.g., MacDonald and Thompson, 1988; Tanabe and Oba, 1988; Witbaard, 1996). Brown (1988) and Cranfield et al. (1996) found that several environmental factors simultaneously govern the growth of marine bivalves, and among these, food availability is one of the most important; at the same time, multiple environmental factors also affect growth, –e.g., temperature, salinity, depth

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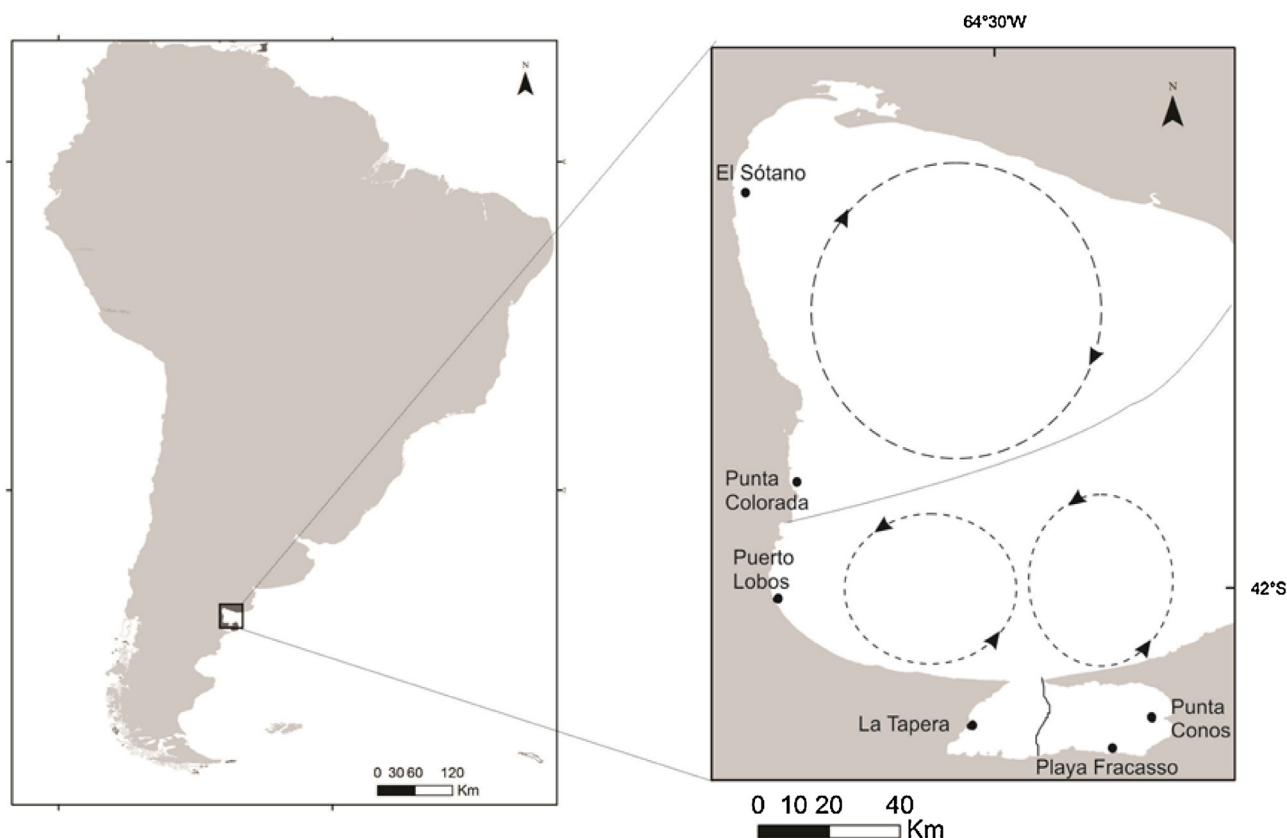


Fig. 1. Map of the San Matías Gulf (SMG) and San José Gulf (SJG) showing the study site. The solid lines indicate the thermohaline front that divides each Gulf (Gagliardini et al., 2004). The dotted lines indicate the movement within the San Matías Gulf given by Tonini (2010).

and current-modulated food availability (e.g., Brown, 1988; Kube et al., 1996; Lomovasky et al., 2008). Regarding the genus *Panopea*, previous studies have revealed that size and growth are related to environmental factors, such as flow speed, type of sediment, depth, and wave exposure (Breen and Shields, 1983; Goodwin and Pease, 1991; Gribben and Creese, 2005; Hoffmann et al., 2000).

Several mathematical equations have been proposed to model growth; some of these are based on purely empirical relationships, whereas others have a theoretical basis (Zeide, 1993). The most common method to describe the growth of one location or species is to choose one growth model based on the shape of the desired curve and biological assumptions and fitting it to the data (Katsanevakis, 2006). Another option is choosing the best model from a set of candidate models using the likelihood ratio test in the case of models nested or using information theory (i.e., Akaike's Information Criterion) for non-nested models. Information-theoretical approaches can be used to make more reliable inferences based on the entire set of candidate models (multimodel inference) (Burnham and Anderson, 2002). Multimodel inference using model averaging allows one to integrate model selection uncertainty with parameter estimation. Therefore, parameter estimation is more robust or stable because it is not conditional on a single model, but it also incorporates the information from several models (Katsanevakis, 2006). Most previous research about growth of *Panopea* species have used the first approach, considering only the von Bertalanffy growth model and disregarding other growth models (Breen et al., 1991; Campbell and Ming, 2003; Cortez-Lucero et al., 2011; Gribben and Creese, 2005; Hoffmann et al., 2000; Morsan and Ciocco, 2004; Morsan et al., 2010). Recent studies have used the multimodel approach to model growth of *Panopea globosa* and have found that it represented the most robust method for growth parameter estimation of this species (Cruz-Vásquez et al., 2012).

Morsan and Ciocco (2004) studied the growth of *P. abbreviata* in one location in Puerto Lobos in the San Matías Gulf (SMG). That study described growth using two versions of the von Bertalanffy growth model. They established that the southern geoduck grows rapidly during the first 9–12 years, acquiring 89–94% of its maximum size ($L_{\infty} = 106.5\text{mm}$). Growth is very slow thereafter. Morsan et al. (2010) compared growth in two locations in the SMG: El Sótano and Puerto Lobos. However, several discontinuous locations of variable extension and density have been found along the west coast of the SMG and in the San José Gulf (SJG) following the coastline (Morsan et al., 2010).

The aim of this paper was to study the variability of the growth pattern of *P. abbreviata* between and within different oceanographic domains. To achieve this, we described the growth pattern for two locations of *P. abbreviata* in each oceanographic domain.

2. Material and methods

2.1. Study area

The SMG and SJG are closely linked with a fluent exchange of water between them (Amoroso and Gagliardini, 2010).

The SMG is a semi-enclosed basin partially link with the open sea through a shallow sill (60 m depth) (Rivas and Beier, 1990). An intense thermohaline front – oriented SW to NE – divides the two water masses with different oceanographic conditions during spring and summer (Fig. 1): relatively cold-fresh waters similar to the open shelf waters (with a high concentration of nitrates and phytoplankton dominated by diatoms) lie south of the front, whereas warm salty waters (with low nitrate concentration and phytoplankton dominated by dinoflagellates) lie north of the front (Piola and Scasso, 1988; Williams, 2011). Sand dominates the bot-

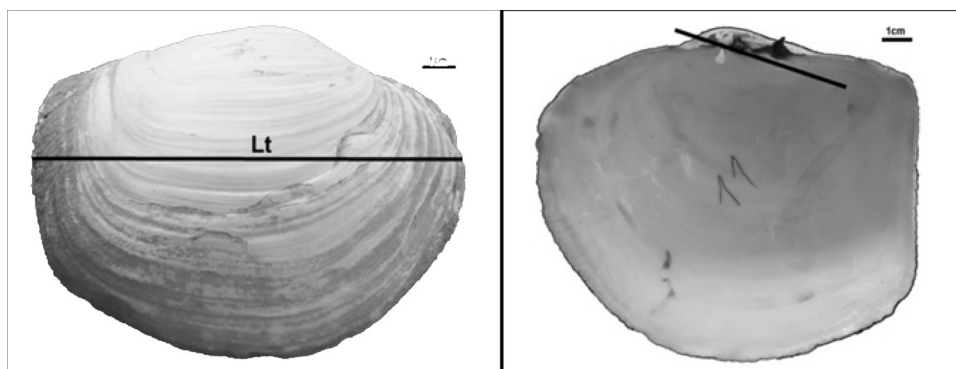


Fig. 2. Image of a *Panopea abbreviata* shell. The line indicates the position of the cut. Lt—length of the valve.

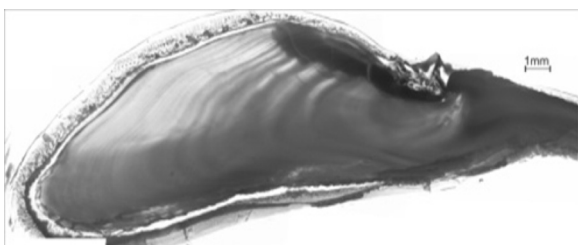


Fig. 3. Thin section of shell in which the growth bands can be observed.

tom sediment near the coastline and gradually mixes with shell hash, gravel, and mud. The SJG is divided into two areas by a well-defined thermal front for most of the year. The west of the SJG is directly influenced by high-nutrient waters from the continental platform (Carreto et al., 1974). This area is strongly influenced by water exchange with the south area of the SMG (Amoroso and Gagliardini, 2010). The east of the SJG has a closed circulation of water during the summer (Gagliardini and Rivas, 2004). During this time, the eastern SJG acts as a nutrient trap and larval retention zone (Amoroso and Gagliardini, 2010).

This configuration defines 3 oceanographic domains that potentially have different conditions for growth: (1) the north-western SMG, (2) the southern SMG and western SJG, and (3) the eastern SJG. (Fig. 1)

2.2. Sampling

Six locations were sampled randomly along the coast of the SMG and the SJG between 2000 and 2006 (Fig. 1): El Sótano (40°56'S to 41°S); Punta Colorada (41°44'S); Puerto Lobos (42°00'S); La Tapera (42°21'S, 64°33'O); Playa Fracasso (42°41'S y 65°03'O) and Punta Conos (42°20'S y 64°06'O). At each sampling site, between 300 and 500 geoducks were obtained by SCUBA divers using a water jet pump. The shell length of all individuals was measured using Vernier calipers (Fig. 2).

2.3. Age

Right valves were used for aging purposes, applying the methodology developed by Shaul and Goodwin (1982) and used by Morsan and Ciocco (2004) in *P. abbreviata*. Thin sections were obtained by cutting the valves with a low-speed diamond saw across the hinge plate (Fig. 3).

The internal section of the valve obtained from the first cut was ground and polished on a platform with variable speed, using very fine grain sandpaper (4000 grit). The polished surface was mounted on a microscope slide, using cyanoacrylate adhesive. A

thin section of 0.5 mm was obtained from a second cut. The thin section was ground and polished again with medium grain (1000 grit) and very fine grain (4000 grit) sandpaper until the adequate thickness and texture were reached. Small individuals with fragile valves were embedded in epoxy resin before proceeding as described previously. The preparation thus obtained was observed under a stereoscopic microscope with transmitted light to establish the optic pattern of the internal growth bands. The sections were observed twice, and recorded in case of coincidence. When the two observations were not coincident, we performed a third observation. If it was equal to one of the previous two observations, we used this as our result, and if the third observation was different from the two previous observations, we discarded the individual.

The seasonality of the internal growth bands was validated for this species according to Morsan and Ciocco (2004). Based on the degree of transparency of the shell margins of young (<8 years old) geoducks, which were sampled in different months during the year, those authors established that the periodicity of deposition of the internal translucent (winter) and opaque (spring–fall) bands corresponds to one year. Our age interpretation is based on the assumption that this pattern remains stable within the studied geographic range.

2.4. Growth pattern

Growth patterns were determined using size-at-age data (total length and total age) from counts of the inner shell layers. A set of 5 candidate models was used for each site to model growth of the the southern geoduck:

- The von Bertalanffy growth model considers animal growth as a result of the combination of two opposite processes: anabolism and catabolism. The rate of anabolism is proportional to the surface area of an organism, and the rate of catabolism is proportional to the organism size (Zeide, 1993). This model does not have an inflection point. The equation of von Bertalanffy growth model is:

$$L_t = L_\infty (1 - e^{-k_1(t-t_0)})$$

where k_1 is a relative growth rate parameter (with units yr^{-1}), L_∞ is the asymptotic length (L_∞ has the same meaning in all the models described below), and t_0 is interpreted as the age when an individual has zero length, assuming the equation to be valid at all ages.

- The logistic growth model assumes that the relative growth rate (the rate of increase of the growth over the growth itself) is a linear function in the case of age and that the inflection point is

situated at the half of the asymptotic length. (Zeide, 1993). The logistic growth model equation is:

$$L_t = L_\infty(1 + e^{-k_2(t-t_1)})^{-1}$$

where k_2 is a relative growth rate parameter (with units yr^{-1}), and t_1 corresponds to the inflection point of the sigmoidal curve.

- In the Gompertz growth model, the relative growth rate is an exponential function of age. For this model, the inflection point is controlled only by the asymptotic length, and it occurs when length equals the asymptotic length over L_∞/e (Zeide, 1993). The Gompertz growth model equation is:

$$L_t = L_\infty \times e^{\left(-\frac{1}{k_3} \times e^{-(t-t_2)}\right)}$$

where:

$$t_2 = \frac{1}{k_3} \ln \lambda$$

and where λ is the theoretical initial relative growth rate at zero age (with units yr^{-1}) and k_3 is the rate of the exponential decrease of the relative growth rate with age (with units yr^{-1}).

- Richards growth model:

$$L_t = L_\infty \left(1 - \frac{1}{D} e^{-k_4(t-t_0)}\right)^D$$

where k_4 is a relative growth rate parameter (with units yr^{-1}), t_0 is interpreted as the age when an individual has zero length, assuming the equation to be valid at all ages, and D is a shape parameter that can make the Richards equation equivalent to the von Bertalanffy, Logistic or Gompertz growth models (Karkach, 2006).

- Schnute-Richards model:

$$L_t = L_\infty (1 + \delta e^{-at^c})^{\frac{1}{b}}$$

where δ , b , and c are dimensionless parameters and have units yr^{-c} ; altering the parameters, this model can take the form of a wide range of curves including the aforementioned models (Haddon, 2001).

The five models were fitted to each data set, with non-linear least squares (nl-LS) with iterations by means of Levenberg–Marquardt’s algorithm and using package ‘minpack.lm’ in R (Elzhov et al., 2013) (R Development Core Team, 2012).

Model selection and the estimation of model selection uncertainty were based on the information theory approach (Burnham and Anderson, 2002). The small-sample, bias-corrected form AIC_c was used for model selection because in some populations the ratio of sample size to the number of parameters of the model was small (<40) (Burnham and Anderson, 2002).

$$AIC_c = AIC + \frac{2z(z+1)}{n-z-1}$$

where

$$AIC = n \times \log(\sigma^2) + 2z$$

and

$$\sigma^2 = \frac{RSS}{n}$$

where RSS is the residual sum of squares, n the number of observations, and z is the total number of estimated regression parameters

including σ^2 (i.e., the number of parameters in the model equation plus 1). Normally distributed deviations with constant variance were assumed. For each location, the model with the smallest AIC_c value ($AIC_{c,min}$) was selected as the ‘best’ among the models tested. The AIC_c differences, $\Delta_i = AIC_{c,i} - AIC_{c,min}$, were computed over all candidate models g_i . According to Burnham and Anderson (2002), models with $\Delta_i > 10$ have essentially no support and might be omitted from further consideration; models with $\Delta_i < 2$ have substantial support, whereas considerably less support exists for models with $4 < \Delta_i < 7$. To quantify the plausibility of each model, given the data and the set of five models, the ‘Akaike weight’ w_i of each model was calculated:

$$w_i = \frac{\exp(-0.5\Delta_i)}{\sum_{k=1}^5 \exp(-0.5\Delta_k)}$$

The ‘Akaike weight’ is considered as the weight of evidence in favor of the model i being the actual best model of the available set of models (Burnham and Anderson, 2002). The ‘average’ model results were determined by averaging the predicted response variable $L(t)$ across models, using the corresponding w_i ’s as weights (Burnham and Anderson, 2002). For each age t :

$$\tilde{L}_t = \sum_{i=1}^5 w_i \times \hat{L}_{t,i}$$

For each of the 5 models, the expectation \hat{L}_∞ , asymptotic standard error $se(\hat{L}_\infty)$ and 95% confidence interval (CI) of the asymptotic length were estimated. The asymptotic 95% CI was estimated as $\hat{L}_\infty \pm t_{df,0.975} se(\hat{L}_\infty)$. Following the multimodel inference (MMI) approach, the model-averaged asymptotic length \tilde{L}_∞ was estimated as a weighted average using all five models with the prediction of each model weighted by w_i . Thus, the model-averaged asymptotic length is:

$$\tilde{L}_\infty = \sum_{i=1}^5 w_i \times \hat{L}_{\infty,i}$$

The unconditional standard error of L_∞ was estimated as (Burnham and Anderson, 2002):

$$se(\tilde{L}_\infty) = \sum_{i=1}^5 w_i \left(\text{var}(\hat{L}_{\infty,i}|g_i) + (\hat{L}_{\infty,i} - \tilde{L}_\infty)^2 \right)^{1/2}$$

where $\text{var}(\hat{L}_{\infty,i}|g_i)$ is the variance of the estimated asymptotic length according to the model g_i and is conditional on the model.

To compare the growth between locations, the model with the better performance between the Richards growth model and the Schnute-Richards model was chosen. Only these two models were considered because they were the most general models. The likelihood ratio test was then used to compare growth curves between locations (Cerrato, 1990; Kimura, 1980). The null hypothesis was as follows:

$$H_0 : \theta_1 = \theta_2$$

where θ was the vector of parameters, and 1 and 2 denote the two statistical populations being compared. Under the null hypothesis, the test statistic $-2\log(\Lambda)$ converges asymptotically to a $\chi^2_{(g)}$ distribution with g degrees of freedom (equal to the number of fixed parameters).

3. Results

3.1. Age structure

A total of 2289 geoducks were aged from 6 sampled locations. Age ranged from 1 to 60 years, but the ranges differed between the locations. The maximum age recorded for each location varied between the gulfs. The oldest geoduck from the locations in the SMG ranged from 42 to 60 years old, whereas no geoducks older than 30 years old were found in the locations in the SJG. Despite the fact that differences in maximum ages were found, 5- to 20-year-old individuals predominated in all locations.

3.2. Growth modeling

The values of the parameters of the growth models estimated for each location can be found, in the online supplementary material (Appendix 1). For each data set and for each model, the corresponding AIC_c, Δ_i, w_i and $\hat{L}_{\infty,i}$, are given in Table 1, as well as the values of \hat{L}_{∞} , se(\hat{L}_{∞}) and the 95% confidence limits of \hat{L}_{∞} . The von Bertalanffy growth model was found to be the best fit among all candidate models for Puerto Lobos, La Tapera, and Punta Conos. The logistic growth model was found to be the best fit for Punta Colorada, and this model also had substantial support for La Tapera, Playa Fracasso, and Punta Conos. The Gompertz growth model was not the best model for any location. However, this model had substantial support for five of the six locations (Punta Colorada, Puerto Lobos, La Tapera, Playa Fracasso, and Punta Conos). The Richards growth model was found to be the best among all candidate models for El Sótano. This model had substantial support for all other locations, except for Playa Fracasso. The Schnute-Richards growth model was the best model for Playa Fracasso. Moreover, this model had substantial support for El Sótano.

For most locations, the best model had a w_i lower than 0.4, and all models had support. The only exception was El Sótano, where the best model had w_i = 0.67. In this location, only two models had much support because, although several models have support, the shapes of the different models were similar. Fig. 4 compares the results at two locations from the five models.

The \hat{L}_{∞} estimated for the 6 localities, had a wide range (95.33–446.96 mm). The highest estimate was for Playa Fracasso, where the estimated size was much larger than the maximum recorded size (137.18 mm). Only the \hat{L}_{∞} of Schnute-Richards growth model (130.54 mm) (best model for this location) was similar to the maximum size found, whereas \hat{L}_{∞} estimates of the other growth models were very large (318.81–868.85 mm). The \hat{L}_{∞} for El Sótano, Punta Colorada, Puerto Lobos, La Tapera, and Punta Conos were different (Fig. 5).

All models showed fast growth during early life and slower growth in later years for El Sótano, Punta Colorada, Puerto Lobos, and La Tapera. Individuals at these locations reached more than 80% of \hat{L}_{∞} at 6 years of age, regardless of the model. In the case of Playa Fracasso, all models seemed to be straight, which suggests that the growth rate in the first 20 years was uniform. As shown previously, L_{∞} for this location differed substantially among models. In an average model, 10-year-old individuals achieved 22.15% of \hat{L}_{∞} , whereas in the Schnute-Richards growth model (best model for this location), 10-year-old individuals achieved 76.26% of \hat{L}_{∞} (Fig. 6).

The Richards growth model was used to compare the growth between locations. This model was chosen because it had better performance than the Schnute-Richards model for all populations ($\sum \Delta_i = 10.5$ for the Richards growth model vs. 14.9 for

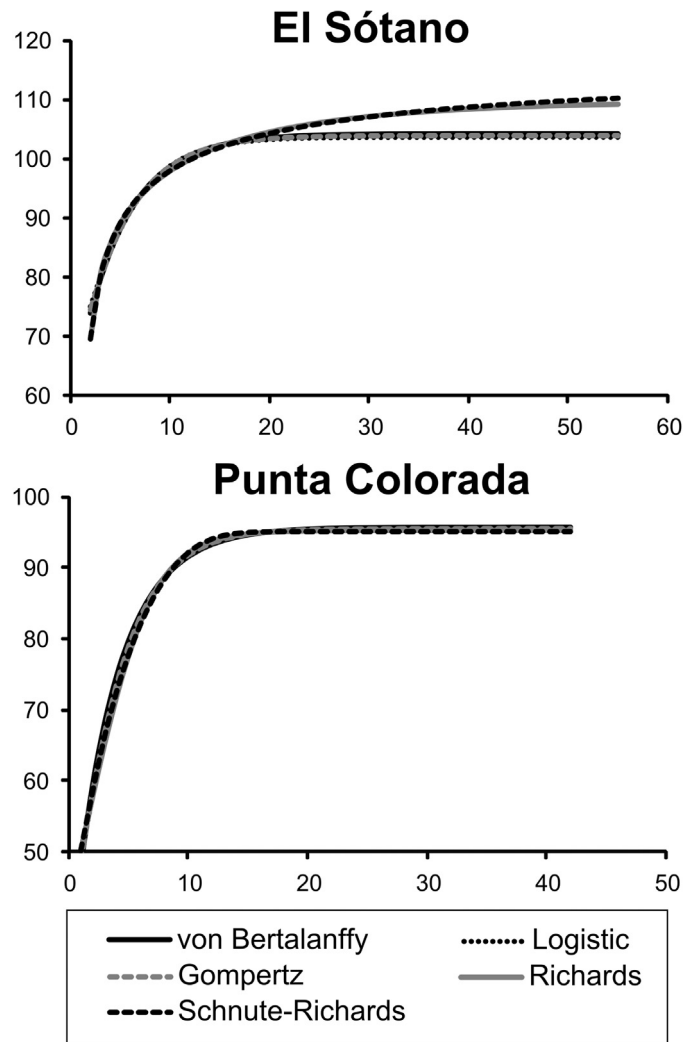


Fig. 4. Results at two locations from the 5 models.

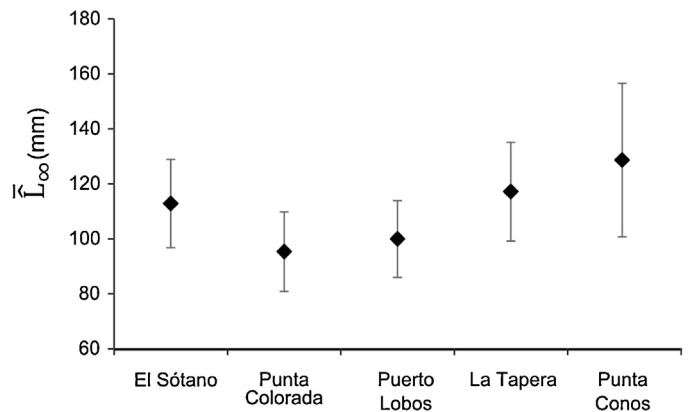


Fig. 5. \hat{L}_{∞} of *Panopea abbreviata* estimated for 5 locations.

the Schnute-Richards model). Substantial differences were found among all locations (Fig. 7).

4. Discussion

In almost all locations, the growth pattern was similar, showing fast growth until 8–10 years and very slow growth in later years, regardless of the growth model. This pattern was consis-

Table 1
For each dataset and for each candidate model z is the total number of estimated regression parameters in the model the small-sample bias corrected form of Akaike's information criterion AIC_c , Akaike differences Δ_i , Akaike weights w_i , and the estimation of asymptotic length L_∞ . Model-averaged asymptotic length \bar{L}_∞ with the corresponding asymptotic standard error (**se**), and 95% confidence limits (**CL**) is also given (unconditional estimations). The models are sorted from best to worst.

El Sótano				
Models	z	Δ_i	w_i	L_∞ (mm)
Richards	5	0.00	0.67	109.71
Schnute-Richards	6	1.48	0.32	119.33
von Bertalanffy	4	11.69	0.00	104.20
Gompertz	4	14.30	0.00	103.89
Logistic	4	16.84	0.00	103.63
Model-averaged				
\bar{L}_∞	se	95% CL		
112.80	8.16	Lower	Upper	
		96.77	128.83	
Punta Colorada				
Models	z	Δ_i	w_i	L_∞ (mm)
Logistic	4	0.00	0.40	95.29
Gompertz	4	0.92	0.25	95.45
Richards	5	1.89	0.16	95.19
von Bertalanffy	4	2.82	0.10	95.64
Schnute-Richards	6	3.05	0.09	95.04
Model-averaged				
\bar{L}_∞	Se	95% CL		
95.33	7.35	Lower	Upper	
		80.87	109.78	
Puerto Lobos				
Models	z	Δ_i	w_i	L_∞ (mm)
von Bertalanffy	4	0.00	0.41	99.82
Richards	5	1.15	0.23	100.17
Gompertz	4	1.62	0.18	99.62
Schnute-Richards	6	2.59	0.11	100.61
Logistic	4	3.65	0.07	99.47
Model-averaged				
\bar{L}_∞	Se	95% CL		
99.93	7.09	Lower	Upper	
		85.99	113.87	
La Tapera				
Models	z	Δ_i	w_i	L_∞ (cm)
von Bertalanffy	4	0.00	0.32	117.81
Gompertz	4	0.08	0.31	116.92
Logistic	4	0.73	0.22	116.27
Richards	5	2.05	0.11	117.44
Schnute-Richards	6	4.13	0.04	117.62
Model-averaged				
\bar{L}_∞	Se	95% CL		
117.15	9.12	Lower	Upper	
		99.17	135.12	
Playa Fracasso				
Models	z	Δ_i	w_i	L_∞ (cm)
Schnute-Richards	6	0.00	0.39	130.54
Logistic	4	0.40	0.32	868.85
Gompertz	4	1.86	0.15	318.81
von Bertalanffy	4	2.98	0.09	395.98
Richards	5	3.73	0.06	655.28
Model-averaged				
\bar{L}_∞	Se	95% CL		
446.96	291.86	Lower	Upper	
		-126.55	1020.47	

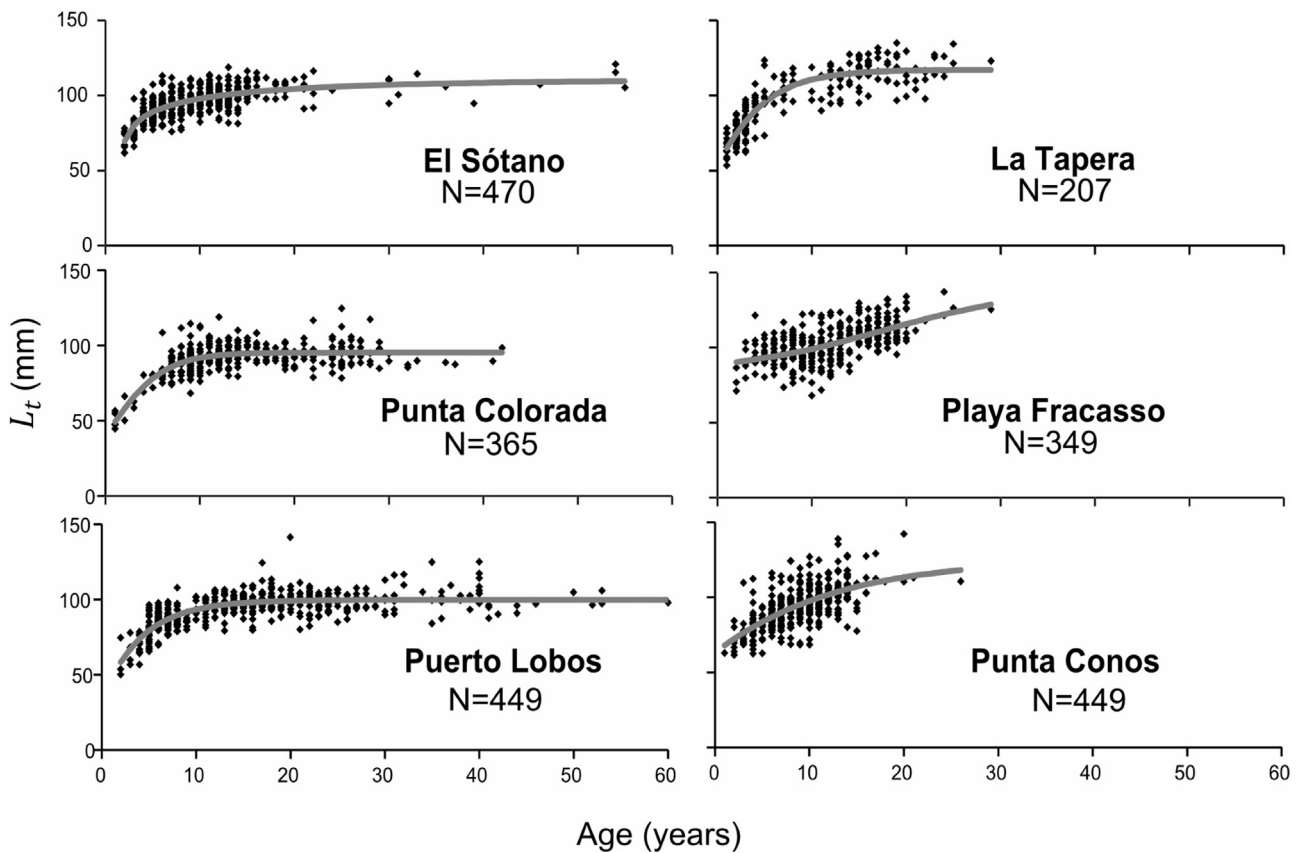


Fig. 6. Size-at-age and average growth model estimates for *Panopea abbreviata* at 6 locations.

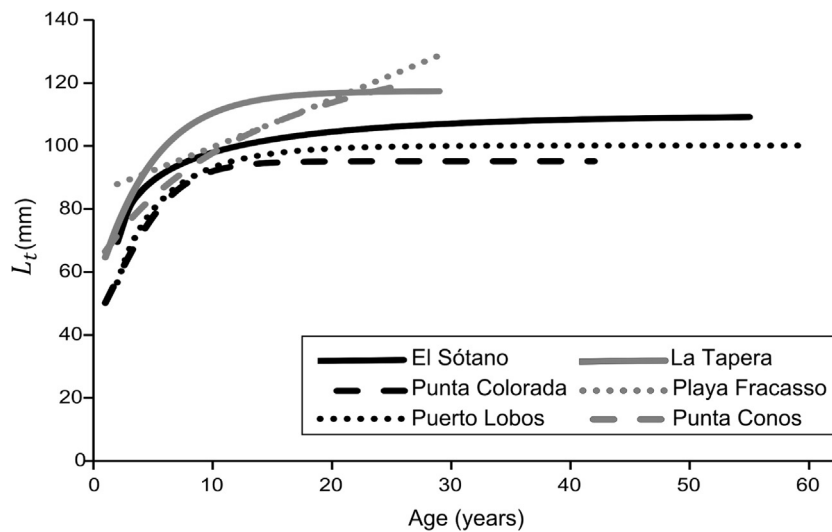


Fig. 7. Richards growth model estimates for *Panopea abbreviata* at 6 locations.

tent to those previously found in other studies of *P. abbreviata* and other species of the genus *Panopea* (Breen et al., 1991; Campbell and Ming, 2003; Cortez-Lucero et al., 2011; Cruz-Vásquez et al., 2012; Gribben and Creese, 2005; Hoffmann et al., 2000; Morsan and Ciocco, 2004; Morsan et al., 2010). Growth estimation for Playa Fracasso differs from this general pattern. In this location, all models were similar to a straight line which suggests no decreasing growth rate. Such estimations can be considered unrealistic. Modelling of growth depends largely on the age structure of the sample (Zivkov et al., 1999). The absence of an asymptotic size may be

due to the prevalence of individuals younger than 15 years old and wide variation in size-at-age data. The rapid growth in the early years can provide an advantage in competition for space (Arendt, 1997). On the other hand, the geoduck shows a correlation between the length of the valve and the length of the siphon. Larger siphons allow clams to burrow deeper in the sediment, which allows them to be more protected from predators. Therefore, rapid growth in the early years could provide an advantage.

The multimodel approach allowed the incorporation of the information from multiple models into the parameter estimation,

thereby integrating model selection uncertainty into the estimation (Katsanevakis, 2006). The best model was not strongly supported as a “clear winner” (with $w_i > 0.9$) for any of the six locations of the present study. In all cases, there was at least one additional model that was also supported by the data (with $\Delta_i < 7$). Most previous studies of growth in the genus *Panopea* used only the von Bertalanffy growth model (Breen et al., 1991; Campbell and Ming, 2003; Cortez-Lucero et al., 2011; Gribben and Creese, 2005; Hoffmann et al., 2000; Morsan and Ciocco, 2004; Morsan et al., 2010). In the present study, the von Bertalanffy growth model was the best model for three locations (Puerto Lobos, La Tapera, and Punta Conos), but in these locations, all models had support. In the remaining locations, the best models were the Richards growth model (El Sótano) and the logistic growth model (Punta Colorada). Using only one model, even if it is the best one, could cause biased point estimation and false evaluation of precision (Katsanevakis, 2006).

In this study, we chose to use multimodel inference to select the best L_∞ estimation and to compare it among the locations. We found that the L_∞ of the shell of the southern-geoduck *P. abbreviata* from the SMG and the SJG was between 95.33 and 128.69 mm (excluding Playa Fracasso). Previous estimations of L_∞ in 2 locations in the SMG (El Sótano and Puerto Lobos) (Morsan et al., 2010) are included within the range of this study. The values of L_∞ were similar to those found for *P. zelandica* and *P. globosa* and smaller than those found for *P. generosa* (Breen et al., 1991; Campbell and Ming, 2003; Cortez-Lucero et al., 2011; Cruz-Vásquez et al., 2012; Gribben and Creese, 2005; Hoffmann et al., 2000).

The L_∞ differed among El Sótano, Punta Colorada, Puerto Lobos, La Tapera, and Punta Conos. Sediment type influences the growth rate of infaunal bivalves (Newell and Hidu, 1982). Hernández-Otero et al. (2014) found that in the infaunal bivalve, *Ensis arcuatus*, of several environmental factors (e.g., temperature, salinity and concentration of chlorophyll) that affect growth, the mud percentage was the most related to size variability. Previous research on *P. generosa* revealed that there is a relation between the shell size and the type of sediment: individuals found in mud-sand or sand sediments were larger than those found in mud and pea gravel-gravel sediments (Goodwin and Pease, 1991). In contrast, larger individuals of *P. abbreviata* were more abundant in mud-sandy places (Punta Conos and Playa Fracasso, SJG's east coast) than in locations with sand (Punta Colorada and Puerto Lobos, SMG's west coast). Goodwin and Pease (1991) suggested that clams growing in low current areas (fine sediments) receive less food than those of high current areas; therefore, they are smaller. However, *P. abbreviata* showed an inverse pattern, which may result from the fact that the locations with low current (Playa Fracasso and Punta Conos) have high primary productivity (Amoroso and Gagliardini, 2010). To compare the growth among the locations, the likelihood ratio test was used in the Richards growth model, and it showed significant differences among all the locations.

Several studies have found latitudinal gradients in the rate of growth, such as those related to temperature (Beukema and Meehan, 1985; Cardoso et al., 2006; Gutiérrez and Defeo, 2003; Moura et al., 2013). In our work, we have found differences among all locations without latitudinal gradient, suggesting that growth is mainly governed by local environmental conditions, as occurs in other infaunal bivalve species (Gaspar et al., 2004; Gribben and Creese, 2005).

Recent research has proposed that management regulations for sedentary invertebrates could be fine-tuned to take into account growth variability at relatively fine spatial scales (Escati-Peñaloza et al., 2010; Lomovasky et al., 2008; Saunders et al., 2009). Hoffmann et al. (2000) studied the “managerial significance” of differences in growth parameters of the von Bertalanffy model (how much the growth parameters must change before

management decisions would be altered). They found that small differences (>0.03) in k have managerial significance. Therefore, the differences found in our work indicate that stock assessment for this resource should be conducted assuming that each location differs in terms of growth. This study was part of a series of studies on aspects of the life history and population dynamics of the *P. abbreviata* and serves to complement the stock assessment of this species in Northern Patagonia. When first begun, the fishery of *P. abbreviata* (2001) was subjected to a set of preventive measures, including mandatory on-board observers, control of landings, and fishing zone. Some years later the authorities relaxed the management measures, and at present, they are almost non-existent. The development of management measures that encourage a sustainable fishery for each location is necessary.

The aim of this work was to model the growth of *P. abbreviata* using several models and to study their variability among the oceanographic domains of the SMG and SJG and among the populations located in each domain. We conclude that multimodel inference represents the most robust method for evaluating growth parameters for this species, as was found by Cruz-Vásquez et al. (2012) in growth study in *P. globosa*. We found differences among all locations, independently of the domains. The differences observed in the growth among locations should be considered for developing biological reference points specific for each location.

Acknowledgments

This study was supported by PNUD Ar 02/018, PICT 2006-01674 (Agencia Nacional de Promoción Científica y Tecnológica) and M019 (Universidad Nacional del Comahue). The authors thank Silvina Van der Molen and Norberto De Garin for their help in survey data collection, the nautical and diving staff of CENPAT and IBMPAS for diving assistance, Socorro Doldan for her constructive comments, Matías Gaitan and Patricia Acosta for their technical assistance and Ayelén Fernandez and American Journal Experts for collaboration on the English version.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.fishres.2015.08.011>.

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