Marine Biology Research

ISSN: 1745-1000 (Print) 1745-1019 (Online) Journal homepage: http://www.tandfonline.com/loi/smar20

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**To cite this article:** V. Bökenhans, G. Bigatti, M. García Asorey & A. Averbuj (2018): Age and growth differences in two populations of the edible marine gastropod Buccinanops globulosus, Marine Biology Research, DOI: 10.1080/17451000.2017.1406667

**To link to this article:** https://doi.org/10.1080/17451000.2017.1406667

MARINE BIOLOGY RESEARCH, 2018
https://doi.org/10.1080/17451000.2017.1406667

ORIGINAL ARTICLE

# Age and growth differences in two populations of the edible marine gastropod *Buccinanops globulosus*

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**ABSTRACT**
*Buccinanops globulosus* is an edible marine gastropod that is being captured by artisanal fishermen without management regulations. As basic knowledge on population features is required in case a sustained commercial exploitation of this species is established, we estimated and compared the age and growth of *B. globulosus* in two populations separated by 16 km, inhabiting similar physical environments but different anthropic influence. Our results, based on stable oxygen isotope analysis and best fitted models by likelihood ratio tests, detected differences in age and growth between both samplings. Maximum shell marks suggest one year difference between populations. Richards was chosen as the best fitting model for both sampling sites and significant differences were observed between them. Human activities could be causing the age reduction among other irreversible effects on the population under anthropic influence. This should be considered when developing sustainable management regulations for this fishery resource, especially those based on shell/age size.

**ARTICLE HISTORY**
Received 10 April 2017
Accepted 12 November 2017

**SUBJECT EDITOR**
Audrey J. Geffen

**KEYWORDS**
Artisanal fisheries; gastropod; growth functions; longevity; Nassariidae; stable oxygen isotope analysis

## Introduction

Annual catches of marine molluscs make them an important invertebrate fishery resource around the world (FAO 2016). In particular, gastropods represent around 2% of the marine molluscs captured worldwide; moreover, some species play important economic and social roles at a local level, having high economic values in the international market (Leiva & Castilla 2002). As valuable resources, it is important to establish baselines for the design of management strategies (Hilborn & Walters 1992; Jennings et al. 2009) that ensure the sustainability of any resource. Age and growth parameters are necessary background information in almost every aspect of fisheries, in order to provide useful management information (Brey 1999).

The individual age of many marine gastropod species is estimated on the basis of growth marks visible on hard structures, such as shell marks (Picken 1980; Cledón et al. 2005; Bigatti et al. 2007), statolith rings (Barroso et al. 2005b; Richardson et al. 2005; Chatzinikolaou & Richardson 2007; Galante-Oliveira et al. 2015) and opercula striae (Kideys 1996; Ilano et al. 2004; Vasconcelos et al. 2012). In particular, opercula striae have been used to study the nassariid gastropod *Buccinanops globulosus* age and growth (Narvarte et al. 2008; Avaca et al. 2013). However, these studies lack a rigorous validation of seasonality and are only based on the von Bertalanffy growth model; therefore, they reflect the need for proper age estimation in this species. As demonstrated by Bökenhans et al. (2016), shell marks in *B. globulosus* are much more reliable than opercula striae for accurate age determination, using previous validation of shell mark seasonality by oxygen stable isotope analysis, to avoid age misinterpretations. During shell deposition, the ratio of oxygen stable isotopes ($^{18}O$ and $^{16}O$) within $CaCO_3$ is inversely proportional to water temperature (Epstein et al. 1951). This relationship is almost linear between 5° and 30°C (Epstein et al. 1953; Epstein & Lowenstam 1953). The oxygen isotopic ratio reflects seawater temperature fluctuations, thus validating the environmental seasonality that allows reliable estimation of the individual age (Epstein et al. 1951; Epstein & Lowenstam 1953).

Oxygen stable isotope analyses have been used to determine growth rates for several marine gastropod species (Geary et al. 1992; Giménez et al. 2004; Cledón et al. 2005; Bigatti et al. 2007; Arrighetti et al. 2011, 2012; Zabala et al. 2013; Bökenhans et al. 2016).

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Size at age data may be used to model growth functions reliably (Kirkwood 1983; Lopez et al. 2000), with which it is possible to understand individual growth through a non-linear process with multiple parameters (Brey 1999). This is particularly relevant in species of commercial interest due to the necessity of successful management of a potentially valuable resource (Brey 1999). The von Bertalanffy growth model has been used commonly as the default model, when studying individual growth of marine gastropods. However, other growth functions may be more appropriate for this purpose (Haddon et al. 2008; Helidoniotis et al. 2011; Averbuj et al. 2015), and thus, should be considered in growth studies.

*Buccinanops globulosus* inhabits shallow coastal waters from the South-western Atlantic Ocean, in a latitudinal range from Uruguay (34°S) to Santa Cruz Province (48°S) in Patagonia, Argentina (Scarabino 1977). The species completes embryogenesis inside egg capsules attached to the adult female shell, without free larval stages (Averbuj & Penchaszadeh 2010). This developmental modality together with the limited spatial distribution typical of *Buccinanops* species (Narvarte et al. 2008; Averbuj & Penchaszadeh 2016; Averbuj et al. 2014), is usually related to a genetic structure that suggests lack of mutual flux (migrations) between populations (Johannesson 1988; Grant & Da Silva-Tatley 1997). In such species, life history (including age and growth) could be differentially affected in populations inhabiting areas with contrasting anthropic influence (Avaca et al. 2015; Márquez et al. 2016).

Argentinean marine gastropods are exploited mostly as a target of artisanal fishery and as by-catch of industrial fisheries. Resources captured by small-scale fisheries are not immune to overexploitation (Castilla & Fernandez 1998). *Buccinanops globulosus* shows increasing commercial importance, consumed in the North Patagonian gulfs (Narvarte 2006) and sold in various markets in Argentina and exported to Asia (Averbuj et al. 2014; Bigatti et al. 2015).

The main objective of this work is to estimate and compare the age and growth of *B. globulosus*, through the identification of the best fitting growth model, in two populations which inhabit environments with different anthropic influence in Golfo Nuevo, North Patagonia. For this purpose, we test the hypothesis that individuals living on a beach with high anthropic influence will achieve shorter ages and present a faster growth than those living on a beach with low anthropic influence. This work is also relevant because its methods are proved to be the most reliable for *B. globulosus*, which is frequently used as a case study organism in the region.

## Material and methods

### Sampling

Specimens of *B. globulosus* were collected monthly during 2012, on two sandy beaches with similar environmental conditions (16 km in the Golfo Nuevo, Patagonia) but presenting different human activity as tourism, maritime traffic and pollution: Puerto Madryn (PM) city (42°8′S, 65°5′W) and Cerro Avanzado (CA) (42°49′ S, 64°52′W) (Figure 1). PM is one of the most tourist crowded cities on the Atlantic Patagonian coast, with a stable population of about 100,000 people but receiving ~250,000 tourists per year, while sub-aquatic tourism areas (STA) receive about 7000 divers per year (Bravo et al. 2015). Tourists that visit PM during summer stay mostly at the sandy beaches of the city, including the PM site (Mendez et al. 2017). As a consequence of human recreational activities, adults of *B. globulosus* are selectively extracted for food or as souvenirs. Moreover, trucks and tractors remove cast seaweed along the PM beach in the summer season, over the zone that these gastropods inhabit. The city has two ports, ~1 km away from the PM sampling site, which receive cruise and fishing ships, which implies high maritime traffic. Approximately 720 ships per year were reported for the area in 2013 (Primost et al. 2015b). Population and maritime industries have incremented pollution in Nuevo Gulf harbour since the 1970s, promoting morphological changes in marine gastropods including *B. globulosus* (Bigatti et al. 2009; Márquez et al 2011; Márquez et al. 2016). Del Brio et al. (2016) found the highest concentrations of butyltins (TBT, DBT and MBT) in sediments and in *Odontocymbiola magellanica* gastropods in the harbour area near the PM site, decreasing with distance to the harbour and in areas with less maritime traffic. At the PM site, 100% of *B. globulosus* females presented imposex, indicating the presence of TBT (Bigatti et al. 2009; Primost et al. 2015c). Polyaromatic hydrocarbons (PAHs) and toxic metal levels were also found in PM sediment and *B. globulosus* foot tissue (Lozada et al. 2008; Torres et al. 2013; Primost et al. 2015c; Primost et al. 2017).

The CA beach is 16 km out of the PM city, there is no urbanization in the zone, and it has little tourist recreational activity (mainly in summer) and low maritime traffic (occasional small boats for recreational activities). Butyltins and PAHs were not found in sediments and no females presented imposex at the CA beach (Torres et al. 2013; Primost et al. 2015c). Higher maximum sizes of *B. globulosus* were observed in the CA population compared with PM in previous studies (Primost et al. 2015b).

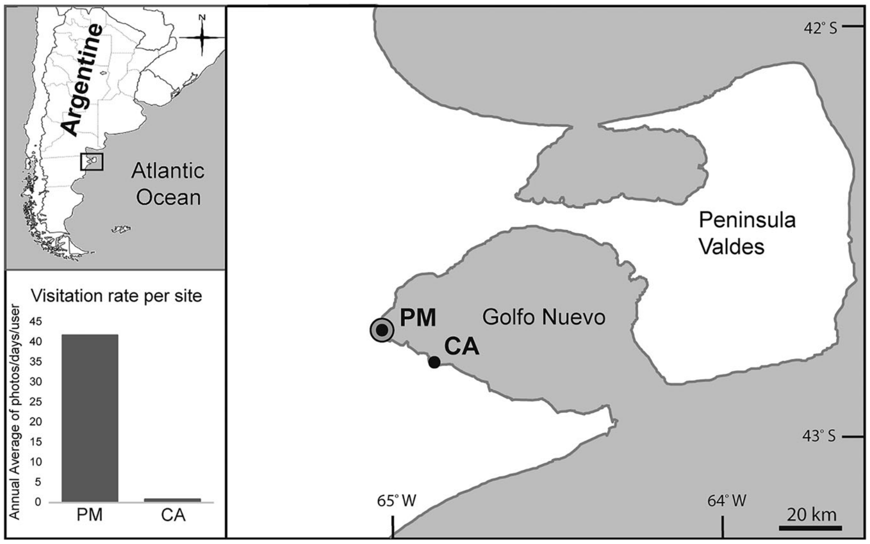

**Figure 1.** Sampling sites. Map showing Puerto Madryn and Cerro Avanzado sites in Golfo Nuevo, Patagonia, Argentina. Bar chart shows the visitation rate per site, according to the InVEST recreation model, which is ∼50 times higher at PM than at CA. PM: Puerto Madryn, CA: Cerro Avanzado.

PM and CA visitor rates were estimated with the InVEST recreation model (Sharp et al. 2016) as described by Wood et al. (2013). The InVEST recreation model uses the location of the photographs uploaded on social media as a proxy of the visitor rate at each location. The model assumes that the number of visits can be approximated by the total number of annual person-days of photographs uploaded to the photo-sharing website Flickr (https://www.flickr.com/).

Baited traps (using decomposed lamb meat) were used to attract *B. globulosus*, at depths less than 5 metres during low tides. Seasonally, 200 individuals were randomly collected from the traps at each sampling site and taken to the laboratory, where the shell lengths (SL) were measured with a Vernier calliper to the nearest 0.1 millimetre. Length frequency distribution histograms were performed for each sampling site, with a size interval of 1 mm. A Chi-square test was done in order to test for differences between them. Spiral growth trajectory (SG) was copied by following it with a thread which was extended to be measured to the nearest millimetre. A linear regression analysis was used to describe the relationships between SL and SG.

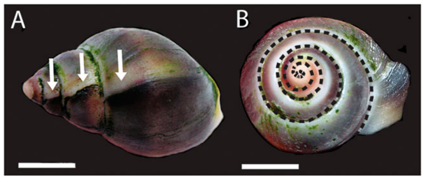

**Figure 2.** *Buccinanops globulosus*. A: Shell marks externally visible (white arrows). B: Spiral growth trajectory (SG) of an individual (dashed black line). Scale bars: 1 cm.

Additionally, 40 individuals were randomly taken from the sampled gastropods, after discarding those with high levels of erosion or damage. A total of 199 and 218 data pairs were used for the growth model analysis at PM and CA, respectively (Figure 2). In the laboratory the total number of shell marks was counted as described by Bökenhans et al. (2016), and the SG at each visible shell mark was measured and analysed.

### *Oxygen stable isotopes*

Two representative specimens of *B. globulosus* were used for stable isotope analysis in Cerro Avanzado (Individual CA #1: 48.85 mm and Individual CA #2: 23.02 mm) and four in Puerto Madryn (Individual PM #1: 37.67 mm, Individual PM # 2: 27.40 mm, Individual PM #3: 25.34 mm and Individual PM #4: 19.87 mm). After softly cleaning the shells with a brush and fine sandpaper, carbonate samples were taken from the shell by using a Dremel, until 10 mg of sample was collected. Samples were drilled from the external visible growth lines and between them. The SG data for each sample of stable isotope analysis was converted into SL data by the linear equations relating both variables. Isotopic ratios were determined (Brey 1999; Zabala et al. 2013). Oxygen isotope analyses were carried out in the INGEIS-UBA laboratories in a Finnigan MAT Delta S, triple collector, double inlet system, mass spectrometer. The results were reported as deviation per mil (dδ) relative to the VPDB (Vienna Pee Dee

Belemnite) standard and the analytical error was 0.1 δ for $\delta^{18}O$.

The seasonality of growth mark formation was analysed in each of the six individuals from both sites by means of oxygen stable isotope analysis ($\delta^{18}O$). In this study area, where there is a constant salinity and a cyclical annual oscillation of temperature, we expect the $\delta^{18}O$ curve to reflect the environmental seasonality (Giménez et al. 2004; Cledón et al. 2005; Bigatti et al. 2007; Arrighetti et al. 2011; Zabala et al. 2013).

### Age and growth models

As growth marks were found to be formed regularly at low temperatures (winter) every year (Bökenhans et al. 2016), size-at-age data were obtained by data pairs of each growth mark and its corresponding SG.

*Buccinanops globulosus* growth was modelled based on the general model proposed by Schnute & Richards (1990). The Schnute–Richards growth model generalizes traditional growth models used in fisheries: Gompertz, von Bertalanffy, Richards and the Logistic model (Quinn & Deriso 1999; Haddon 2010). The basic form of this model is:

$$L_t = L_\infty (1 + \alpha\, e^{-kt^c})^{-\frac{1}{b}}$$

where $L_t$ is the length at age t, $L_\infty$ is the asymptotic length, k is a relative growth rate parameter (with units year$^{-c}$), and $\alpha$, c and b are dimensionless parameters (Quinn & Deriso 1999). By altering the value of the parameters c and b the model becomes equivalent to one of the traditional growth models (Gompertz when $b = 0$, $c = 1$; von Bertalanffy when $b = -1$, $c = 1$; Richards when b = free, $c = 1$ and Logistic when $b = 1$, $c = 1$).

The four candidate models were fitted using maximum likelihood methods (Hilborn & Mangel 1997) implemented in an Excel spreadsheet. A multiplicative error structure was assumed for the models because the residuals increased with increasing $L_t$, for which we used a normal probability density function with log-transformed data (observed and expected values) and we found the normal likelihood values (Quinn & Deriso 1999). The asymptotic length ($L_\infty$) was restricted not to exceed 65 mm for CA and 55 mm for PM growth functions, to constrain the estimation to more realistic value in biological terms. In our work, both studied populations showed marked differences when comparing maximum shell length, coinciding with previous reported data (Averbuj et al. 2014; Primost et al. 2015a).

First, differences in growth curves between sexes for the Schnute–Richards model were compared using likelihood ratio tests (LRT, Hilborn & Mangel 1997). As no significant differences between sexes were found, LRTs combined with Akaike's Information Criterion (AIC) were used to select the model that best describes the *B. globulosus* growth (Burnham & Anderson 2003), for each sampling site. AICs were computed as:

$$AIC = -2\ \ln(ML) + 2k$$

where, ML is the numerical value of the maximum likelihood and k is the number of parameters for the model. The AIC differences ($\Delta_i = AIC_i - AICmin$) were computed over all candidate models and were used to rank the support of the remaining models relative to the best-fit model. According to Burnham & Anderson (2003), models with $\Delta_i > 10$ have essentially no support and might be omitted from further consideration, models with $\Delta_i < 2$ have substantial support, while there is considerably less support for models with $3 < \Delta_i < 7$.

Finally, differences in growth curves between sampling sites for the best fitted model were compared using LRTs. Fifteen hypotheses were tested (Table II): a simultaneous test for all four parameters, a test for each single parameter, and a test for all possible combinations of parameters grouped in pairs and in triplets (Kimura 1980).

## Results

According to the InVEST recreation model, visitation rate is over 50-fold higher in PM than in CA, considering the annual averages (2004–2014) of photos/day/user (CA: 0.8, PM: 41.7) (Figure 1).

### Oxygen stable isotopes

The $\delta^{18}O$ profiles of *B. globulosus* shells showed a different oscillating pattern in all the individuals studied, that reflect a cyclical water temperature regime. The average $\delta^{18}O$ profiles ranged between −0.21‰ and 0.9‰ for the individuals of Cerro Avanzado (CA) and between −0.6‰ and 1.3‰ for those of Puerto Madryn (PM) (Figure 3). Visible shell growth marks coincided with the maximum values of $\delta^{18}O$ (corresponding to minimum temperature), i.e. one shell growth mark was formed each year when water temperature was minimal (end of winter).

### Age and growth models

A total of 791 and 792 specimens of *B. globulosus* were captured in CA and PM, respectively. Individuals from CA showed an average SL of 27.52 ± 7.94 mm, where

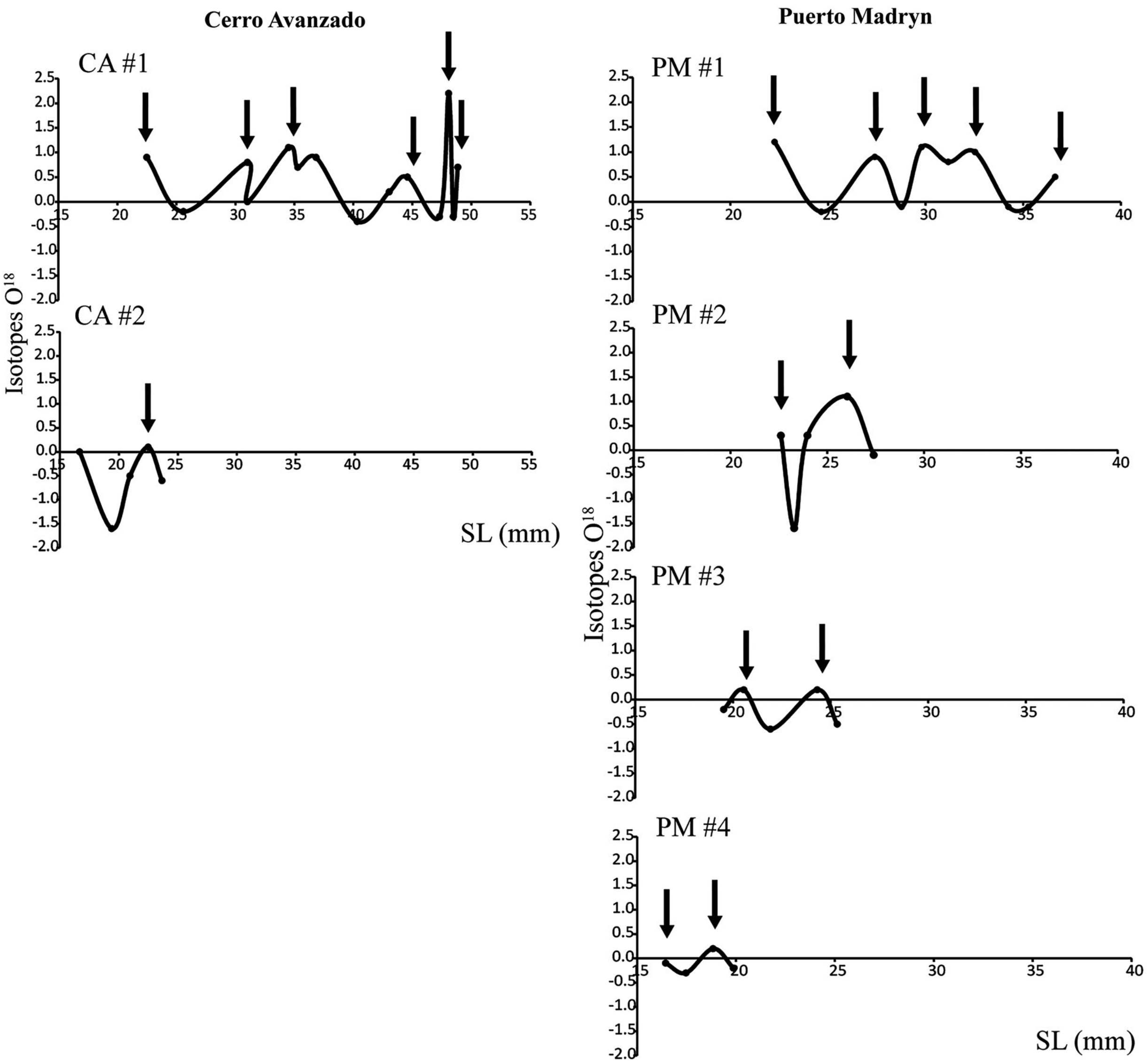

**Figure 3.** $\delta^{18}O$ profiles of *Buccinanops globulosus* plotted against corresponding shell lengths (SL) of individuals from Cerro Avanzado and Puerto Madryn. Black arrows correspond to the visible external shell marks.

females ranged from 17.53 to 58.18 mm and males ranged from 12.59 to 34.00 mm. Individuals from PM showed an average shell length (SL) of 23.16 ± 5.95 mm, where females ranged from 14.9 to 44.04 mm and males ranged from 12.4 to 33.47 mm. Size frequency distributions were significantly different between sampling sites ($\chi^2$ = 2125.125, d.f. = 60, $P <$ 0.01) (Figure 4).

The SL was significantly related to the spiral growth trajectory (SG) by a linear regression on both sites (Cerro Avanzado: $R^2 = 0.932$, N = 791, F = 10,964.41, VC = 0; Puerto Madryn: $R^2 = 0.906$, N = 792, F = 7621.29, VC = 0) (Figure 5).

The maximum number of shell marks found in females was 9 in CA and 8 in PM, while in males it was 7 in CA and 6 in PM. No significant differences were found in Schnute–Richards growth curves between sexes for both sampling sites (CA: LRT $\chi^2$ = 8.59, d.f. = 6, $P = 0.1981$; PM: LRT $\chi^2$ = 8.81, d.f. = 6, $P = 0.1847$); therefore, individuals of both sexes were pooled when comparing sampling sites.

Based on AIC values and LRT, Richards was chosen as the best model for both sampling sites (Table I). In contrast, the Logistic models showed no empirical support for both sites (Table I). The other models showed less support than Richards when both sites were considered. While at the PM site the von Bertalanffy and Gompertz models had support and no significant differences were found between these models and the Schnute–Richards model (Table I), at the CA site the von Bertalanffy and Gompertz models did not show empirical support (Table I).

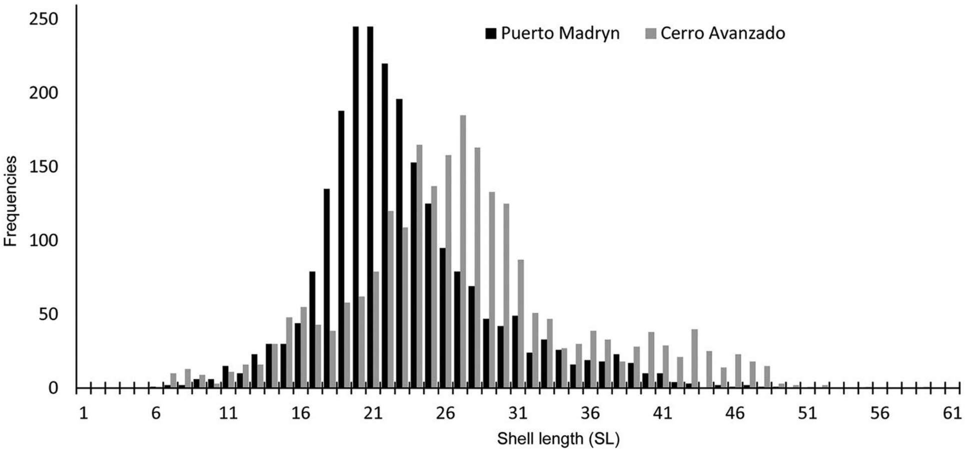

**Figure 4.** Shell length (SL) frequency distribution histogram of *Buccinanops globulosus* for Cerro Avanzado and Puerto Madryn.

Finally, comparison of the Richards growth curves between sampling sites (Figure 6) by LRTS showed significant differences among sampling sites when all four parameters were compared simultaneously ($P < 0.001$, Test 1, Table II), but no significant differences were found either when the parameters were compared one at a time (Tests 2–5, Table II), or for those combinations of parameters that did not include the $a$ and b parameters at the same time (Tests 6–15, Table II).

## Discussion

Traditional age estimation techniques in molluscs (e.g. shell marks, opercula striae) require suitable temporal validation (Kideys 1996; Brey & Mackensen 1997). This validation can be obtained by comparing the oxygen stable isotope ratio ($^{18}O$ and $^{16}O$) in mollusc shells with seawater temperature seasonality during shell formation (Brey & Mackensen 1997; Richardson 2001). As described by Bökenhans et al. (2016), oxygen stable isotopic analysis (SIA) in *B. globulosus* shells showed a clear annual pattern of seawater temperature, where each shell mark corresponds to a maximum $\delta^{18}O$ value (minimum seawater temperature). Therefore, each shell mark registered in this work was formed annually, implying a maximum age of nine years for the Cerro Avanzado (CA) population and eight years for the Puerto Madryn (PM) population. Results of oxygen SIA obtained at CA coincide with those studied previously by Bökenhans et al. (2016) in the same population. Longevity variation among populations of a single species that are geographically

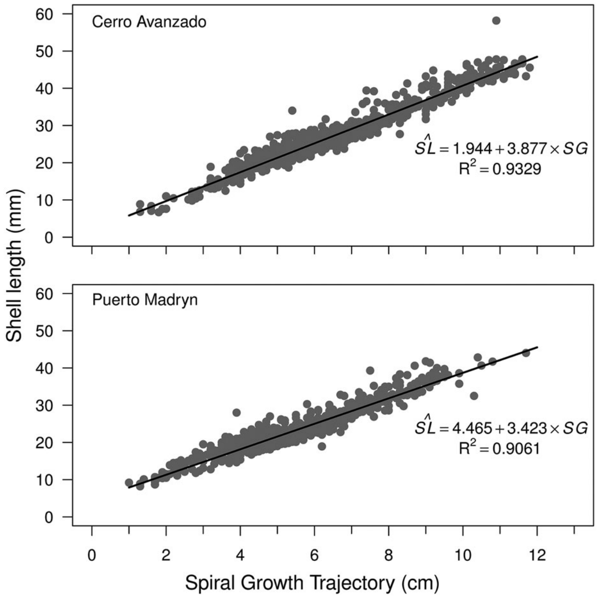

**Figure 5.** Linear regression between shell length and spiral growth trajectory of *Buccinanops globulosus*.

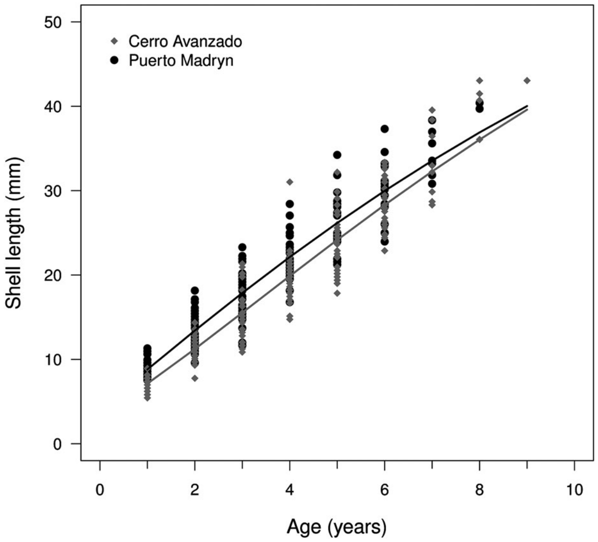

**Figure 6.** Richards model growth curves for both sampling sites.

**Table I.** Values obtained for the parameters of each growth model at both sampling sites. For each model, differences between *P* values acquired with the likelihood ratio tests (LRT) and Akaike's Information Criterion (AIC) are expressed; models with substantial support are in bold. Abbreviations: CA: Cerro Avanzado, PM: Puerto Madryn, $L_\infty$: asymptotic length, K: relative growth rate parameter, *a*, b and c are dimensionless parameters, #par: number of estimated parameters.

| | Model | #par | Log-lik. | AIC | delta | LRTs *P*-value | $a$ | K | $L_\infty$ | b | c |
|---|---|---|---|---|---|---|---|---|---|---|---|
| CA | Schnute–Richards | 5 | 127.863 | −245.727 | 1.72 | | −0.0059 | 0.3092 | 65.00 | −0.0020 | 0.7955 |
| | Von Bertalanffy | 3 | 121.900 | −237.799 | 9.65 | 0.0026 | −0.9740 | 0.0861 | 65.00 | −1 | 1 |
| | Logistic | 3 | 120.087 | −234.173 | 13.27 | 0.0004 | 7.0828 | 0.4941 | 39.39 | 1 | 1 |
| | Richards | 4 | 127.724 | −247.447 | 0.00 | **0.5968** | −0.7389 | 0.1388 | 65.00 | −0.4665 | 1 |
| | Gompertz | 3 | 125.839 | −245.678 | 1.77 | **0.1321** | 0.0000 | 0.2391 | 51.90 | 0 | 1 |
| PM | Schnute–Richards | 5 | 117.936 | −225.871 | 1.92 | | −0.1981 | 0.3002 | 55.00 | −0.0868 | 0.8394 |
| | Von Bertalanffy | 3 | 114.201 | −222.401 | 5.39 | 0.0239 | −0.9453 | 0.1155 | 55.00 | −1 | 1 |
| | Logistic | 3 | 112.758 | −219.517 | 8.27 | 0.0056 | 5.2722 | 0.5150 | 37.47 | 1 | 1 |
| | Richards | 4 | 117.896 | −227.791 | 0.00 | **0.7768** | −0.7061 | 0.1656 | 55.00 | −0.4991 | 1 |
| | Gompertz | 3 | 116.588 | −227.177 | 0.61 | **0.2682** | 0.0000 | 0.2724 | 45.88 | 0 | 1 |

separated is not uncommon, as was reported in the nassariid gastropod *Nassarius reticulatus*: 15 years on the Swedish coast (Tallmark 1980), 11 years on the Portuguese coast (Barroso et al. 2005a) and seven years on the UK coast (Chatzinikolaou & Richardson 2007). In the case of *B. globulosus*, the differences registered between PM and CA (separated only by 16 km and presenting the same physical environmental conditions), could be attributable to human activities, as gastropod extraction for food and souvenirs, daily cast seaweed removal during the summer season and pollution due to maritime traffic that leads to contamination such as TBT, PAHs and trace metals (Gil et al. 2006; Commendatore & Esteves 2007; Lozada et al.,

**Table II.** Likelihood ratio tests (LRT) comparing Richards parameter estimates for both sampling sites. In all cases, comparisons were made between each constrained model and unconstrained model. Abbreviations: CA: Cerro Avanzado, PM: Puerto Madryn, $L_\infty$: asymptotic length, K: relative growth rate parameter, *a*, b and c are dimensionless parameters, ns: not significant, ***: significant at the 0.1% level.

| Test | Model constraints | Site | $a$ | K | $L_\infty$ | b | Log-lik. | Df | LRT *P*-value | Signific. |
|---|---|---|---|---|---|---|---|---|---|---|
| | None | CA | −0.7404 | 0.1385 | 65.00 | −0.4683 | 240.751 | | | |
| | | PM | −0.7060 | 0.1656 | 55.00 | −0.4990 | | | | |
| 1 | $a_{CA} = a_{PM}$<br>$K_{CA} = K_{PM}$<br>$L_{\infty CA} = L_{\infty PM}$<br>$b_{CA} = b_{PM}$ | | −0.8117 | 0.1247 | 65.00 | −0.6005 | 162.713 | 4 | 0.0000 | *** |
| 2 | $a_{CA} = a_{PM}$ | CA | −0.7265 | 0.1404 | 65.00 | −0.4519 | 240.735 | 1 | 0.8575 | ns |
| | | PM | | 0.1627 | 55.00 | −0.5254 | | | | |
| 3 | $K_{CA} = K_{PM}$ | CA | −0.6522 | 0.1542 | 62.91 | −0.3768 | 240.276 | 1 | 0.3294 | ns |
| | | PM | −0.7780 | | 55.00 | −0.6004 | | | | |
| 4 | $L_{\infty CA} = L_{\infty PM}$ | CA | −0.7401 | 0.1386 | 65.00 | −0.4679 | 241.227 | 1 | 0.3294 | ns |
| | | PM | −0.8383 | 0.1191 | | −0.6831 | | | | |
| 5 | $b_{CA} = b_{PM}$ | CA | −0.7479 | 0.1375 | 65.00 | −0.4774 | 240.742 | 1 | 0.8904 | ns |
| | | PM | −0.6883 | 0.1680 | 55.00 | | | | | |
| 6 | $a_{CA} = a_{PM}$<br>$K_{CA} = K_{PM}$ | CA | −0.6469 | 0.1718 | 56.44 | −0.3795 | 239.398 | 2 | 0.2583 | ns |
| | | PM | | | 55.00 | −0.4323 | | | | |
| 7 | $a_{CA} = a_{PM}$<br>$L_{\infty CA} = L_{\infty PM}$ | CA | −0.7857 | 0.1320 | 65.00 | −0.5270 | 250.723 | 2 | 0.7983 | ns |
| | | PM | | 0.1282 | | −0.5902 | | | | |
| 8 | $a_{CA} = a_{PM}$<br>$b_{CA} = b_{PM}$ | CA | −0.1597 | 0.2622 | 43.46 | −0.0739 | 227.540 | 2 | 0.0000 | *** |
| | | PM | | 0.2265 | 55.00 | | | | | |
| 9 | $K_{CA} = K_{PM}$<br>$L_{\infty CA} = L_{\infty PM}$ | CA | −0.7923 | 0.1306 | 65.00 | −0.5370 | 240.860 | 2 | 0.8969 | ns |
| | | PM | −0.7732 | | | −0.5699 | | | | |
| 10 | $K_{CA} = K_{PM}$<br>$b_{CA} = b_{PM}$ | CA | −0.6254 | 0.1776 | 55.31 | −0.3613 | 238.589 | 2 | 0.1150 | ns |
| | | PM | −0.5736 | | 55.00 | | | | | |
| 11 | $L_{\infty CA} = L_{\infty PM}$<br>$b_{CA} = b_{PM}$ | CA | −0.7981 | 0.1299 | 65.00 | −0.5450 | 240.731 | 2 | 0.9805 | ns |
| | | PM | −0.7558 | 0.1329 | | | | | | |
| 12 | $a_{CA} = a_{PM}$<br>$K_{CA} = K_{PM}$<br>$b_{CA} = b_{PM}$ | CA | −0.4503 | 0.2087 | 48.32 | −0.2437 | 225.628 | 3 | 0.0000 | *** |
| | | PM | | | 55.00 | | | | | |
| 13 | $a_{CA} = a_{PM}$<br>$L_{\infty CA} = L_{\infty PM}$<br>$b_{CA} = b_{PM}$ | CA | −0.8557 | 0.1097 | 65.00 | −0.6741 | 222.418 | 3 | 0.0000 | *** |
| | | PM | | 0.1299 | | | | | | |
| 14 | $a_{CA} = a_{PM}$<br>$K_{CA} = K_{PM}$<br>$L_{\infty CA} = L_{\infty PM}$ | CA | −0.7803 | 0.1312 | 65.00 | −0.5224 | 240.641 | 3 | 0.9743 | ns |
| | | PM | | | | −0.5772 | | | | |
| 15 | $K_{CA} = K_{PM}$<br>$L_{\infty CA} = L_{\infty PM}$<br>$b_{CA} = b_{PM}$ | CA | −0.7860 | 0.1332 | 65.00 | −0.5250 | 240.438 | 3 | 0.8902 | ns |
| | | PM | −0.7389 | | | | | | | |

2008; Massara Paletto et al. 2008; Torres et al. 2013; Primost et al. 2017).

Moreover, we found female shell length (SL) to be larger than in males in both studied populations. These findings have previously been reported for *B. globulosus* (Avaca et al. 2012; Averbuj et al. 2014; Márquez & Averbuj 2016), denoting a sexual size dimorphism. Differences between sexes were also observed in this study when comparing maximum shell marks. However, no significant differences between sexes were found among growth functions. The larger number of shell marks in females suggests a longer lifespan for females than for males in the studied populations of *B. globulosus*.

Differences of average size among populations of *B. globulosus* inhabiting different areas of North Patagonian gulfs have previously been reported (Narvarte et al. 2008; Primost 2014). This variability was explained by Narvarte et al. (2008) by different local conditions, such as food availability or predation pressure, but later Primost (2014) related size variation to anthropic impact, mainly human extraction. Food limitation and specimen removal can cause a great impact at a population level, affecting size and structure of molluscs (Vermeij 1972; McQuaid 1982; Morton & Chan 2004). Primost et al. (2015c) found differences in terms of oxidative stress for PM and CA populations of *B. globulosus*, where those inhabiting PM suffered an increase of antioxidant defences along with oxidative damage to lipids, indicating a negative physiological effect inflicted by the presence of pollutants at the PM beach. This negative effect related to anthropic impact could be leading to size differences between populations, as reported in this study.

The von Bertalanffy growth function is one of the most often used growth models in fishery science and has been evaluated on numerous gastropod species (Frank 1969; Kideys 1996; Ilano et al. 2004; Arrighetti et al. 2012; Avaca et al. 2013). However, considering this unique growth function as the only possible model is not desirable, as alternative models have better explained growth data of different gastropod species (Bigatti et al. 2007; Helidoniotis et al. 2011; Zabala et al. 2013; Averbuj et al. 2015). In this study, the Richards growth model was selected as the best model in CA and PM. This model has not previously been selected as the best fit for gastropod growth. According to Richards (1959), this model is more flexible and depending on the presence and position of the inflection point, it could adopt similar shapes to the curves of the von Bertalanffy or Gompertz models. These two models have previously been used to fit the growth data of Argentinean marine gastropods, after oxygen SIA validation (Giménez et al. 2004; Bigatti et al. 2007; Arrighetti et al. 2011, 2012; Zabala et al. 2013). Additionally, the von Bertalanffy growth function was used to model *B. globulosus* growth (Narvarte et al. 2008; Avaca et al. 2013) and other nassariid species such as *Bullia rhodostoma* (McLachlan et al. 1979) and *Nassarius reticulatus* (Chatzinikolaou & Richardson 2007), but without validation by oxygen SIA. However, in neither of these cases was the growth model used questioned; the authors analysed the growth choosing only one model based on the shape of the size–age data patterns and/or on biological assumptions.

The estimation of growth function parameters is very sensitive to the distribution of sizes and ages in the sample (Cope & Punt 2007). Probably, older age specimens were under-represented in our sampling, which may have caused a higher $L_\infty$ estimation in relation to the expected values considering the maximum shell length of the species in the area (Bigatti et al. 2015). Although $L_\infty$ is the maximum theoretical size that a species tends towards, but never actually reaches, the use of biological constraints is suggested to improve parameter estimation in such cases, i.e. when relatively small and/or large individuals are under-represented in samples (Kritzer et al. 2001).

Significant differences observed in the Richards growth function among sampling sites are subtle and appear to be more related to the curve shapes (determined by the *a* and b parameters), than to biologically explainable parameters (such as k and $L_\infty$) that would facilitate an interpretation of the underlying process. However, these differences may be showing the effect of different environmental pressures on populations of *B. globulosus*. Environmental parameters such as salinity, temperature, sediment characteristics, wave action or hours of light are similar at the two sampled sites (separated by only 16 km) (Primost et al. 2017), while the anthropic influence in CA is markedly lower than in PM. The *B. globulosus* population of PM appears to be expressing only partially its phenotypic potentiality of size/age (growth) compared with that of CA. Populations facing great anthropogenic impacts manifest extreme phenotypic responses (Hendry et al. 2008), which may include reduced growth rate, age at maturation, body size and productivity, as an effect of constant extraction (Conover et al. 2009). These responses are seen in the PM population as a decrease in maximum size and a slight increase in growth rate. A decrease in the reproductive maturity size was also reported by Primost et al. (2015a: 25 mm) and Avaca et al. (2015: 26 mm) in contrast with 38 mm for CA (Averbuj unpublished data). Size-at-age maturity depends on changes of growth rates, adult mortality, juvenile mortality or both and how they interact (Stearns & Koella 1986). Avaca et al. (2015) also relate the lower size maturity in PM to a higher mortality risk at this location.

Consistent with our interpretation, Márquez et al. (2016) described a phenotypic plasticity of the shell shape for *B. globulosus* for the same study sites. Although both studied sites are within a relatively short geographical distance, migration between populations seems unlikely, thus impeding gene flow among them. Therefore, a change in the environment appears to be leading to an initial plastic response in the *B. globulosus* PM population that could be followed by hidden genetic changes (Hendry et al. 2008).

The direct anthropic effect on both populations of *B. globulosus* needs further investigation; however, it appears that long-term selective extraction of larger sized individuals may cause a reduction of the maximum ages and sizes and the reproductive maturity sizes, leading to an irreversible decrease of the population, as was detected in the bivalve *Donax hanleyanus* from northern coasts of Argentina, which are affected by tourist recreational activities during summer (Herrmann et al. 2009). This work provides a foundation upon which further hypothesis-driven studies of the effect of anthropic activities in the life history of marine gastropods could be carried out. Our results should be considered when developing sustainable management regulation for this artisanal fishery resource, which in addition to a small relative growth rate, an extended developmental period, the absence of free larval dispersal (Averbuj et al. 2014), and the low percentage of soft edible parts per individual (Bigatti et al. 2015) makes *B. globulosus* a fragile resource.

## Acknowledgements

The authors are members of CONICET. This is publication No. 83 of the Laboratorio de Reproducción y Biología Integrativa de Invertebrados Marinos (LARBIM). All research work including sampling and laboratory investigations comply with current Argentine laws. None of the authors have any competing interests in the manuscript.

## Disclosure statement

No potential conflict of interest was reported by the author(s).

## Funding

This research was partially supported by projects of FONCYT (PICT 0174, PICT 1476, PICT 2709, PICT 3696) and CONICET (PIP067).

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