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INDIVIDUAL GROWTH IN THE PATAGONIAN GASTROPOD
BUCCINANOPS COCHLIDIUM (NASSARIIDAE):
A FIELD TAGGING-RECAPTURE EXPERIMENT

Andres Averbuj^{1*}, Gabriela Escati-Peñaloza² & Pablo E. Penchaszadeh³

ABSTRACT

This study describes the growth of individuals in a population of *Buccinanops cochlidium* (Nassariidae) through the identification of the best-fitting growth model based on field tag-recaptured experimental data. A total of 48 individuals (8.6% of total tagged snails) were recaptured after 2 to 25 months, representing a remarkable proportion for a field experiment with infaunal organisms. The sex ratio was not different from 1:1. Males measured between 63.4 and 89.0 mm ($n = 25$), while females measured between 50.9 and 103.2 mm ($n = 23$) in shell length. The maximum annual length increment obtained was 35.74 mm, mean annual length increment was 4.51 and 8.43 mm for females and males, respectively. Because no statistically significant differences were found between male and female growth increments, a single growth model was fitted to the entire data set.

Regarding individual growth modeling, the inverse Logistic (iLog) model adequately described the pattern in the data, but showed heteroscedasticity. A refitting of iLog using weighted least squares, weighted inverse Logistic (iLog*), better fit the data (and agrees with biological knowledge of *B. cochlidium*) than the inverse Logistic (iLog), exponential (Exp), von Bertalanffy (vB) and Gompertz (Gz) models. Estimated parameters for the iLog* model were Max ΔL : 27.83, L_{50} : 69.89, L_{95} : 93.36. The results of this study are valuable for assessment of snail fisheries in Patagonia and suggest fisheries management policies for a sustainable future of this potential stock prior to extensive exploitation.

Key words: growth models, inverse logistic, edible snail, Nassariidae, fisheries, shells.

INTRODUCTION

Research about population parameters is a necessary first step in fisheries management (Botsford et al., 1998). Among them, growth models are a key component of stock assessments (Quinn & Deriso, 1999). Particularly for such difficult-to-age species as gastropods (Helidoniotis et al., 2011), crustaceans (Duran et al., 2013) and echinoderms (Russell & Meredith, 2000), size-based assessment models may be used to describe population dynamics instead of age-based models (Zhang et al., 2009).

Many organisms with calcareous parts, as mollusc shells, exhibit conspicuous growth band patterns. This may be due to annual cycles, although each case needs to be validated (Brey & Mackensen, 1997). However, in

many cases, observing and accurately counting these bands is very difficult; this is particularly true in some marine gastropods where bands are hidden by new shell growth or erased by sediment erosion. Tag-recapture experiments are a valuable approach to estimate growth parameters, but they are rarely used in invertebrates, including marine gastropods, despite the importance of growth characteristics as bioindicators, food resources, etc. (Appeldoorn, 1990; Henry & Jarne, 2007; Vasconcelos et al., 2006).

Among several individual growth functions, the von Bertalanffy (vB) growth model has been used historically as the default model in fisheries assessment (Beverton & Holt, 1959; Brey, 1999; Eveson et al., 2007; Frank, 1969). The vB model predicts a linear decline in growth rate as individuals get larger. Alternatively, the

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Gompertz (Gz) model predicts growth rates that initially rise for small individuals and then decline (Helidoniotis et al., 2011). However, these predictions are often not supported by data from juveniles. For some gastropod species, growth rate in juvenile stages was reported to remain constant rather than rising or dropping (Day & Fleming, 1992; Prince et al., 1988). The vB and Gz are deterministic growth functions that are probably not the best option for describing the growth of these size classes. The inverse Logistic (iLog) model was developed based on a modal analysis of length frequencies, and it suggests a constant growth rate for juvenile sizes. This model has been proposed as being biologically more appropriate for individual growth studies of some invertebrate species (Haddon et al., 2008; Helidoniotis et al., 2011; Ling et al., 2009; Starr et al., 2009). Previous studies on the individual growth of marine temperate gastropods tend to use vB model or exclude the iLog from the analysis (Arrighetti et al., 2012; Bigatti et al., 2007; Kideys, 1996; Vasconcelos et al., 2006; Zabala et al., 2013; among others).

The neogastropod *Buccinanops cochlidium* (Dillwyn, 1817) is endemic along the South American Atlantic coast between 23°00'S and 42°30'S. It reaches 110 mm in shell length and can weigh more than 100 g, which makes it the largest species of the genus and one of the largest members of the family Nassariidae (Abbott & Dance, 1986; Cernohorsky, 1984). Snail fisheries in Argentina have been focused mainly on volutid snails (Bigatti & Ciocco, 2008); *B. cochlidium* appears as a highly potential fisheries resource. The Argentinean *B. cochlidium* stock is abundant in sandy bottoms of shallow waters of North Patagonian gulfs, and is being commercially exploited at a small scale by artisanal fishermen for local consumption. However, extensive marine snail fisheries, including *Buccinanops* species, are starting to develop in response to international market requirements (Averbuj et al., 2010, 2014; Narvarte, 2006).

Most studies on *B. cochlidium* biology have mainly focused on its reproductive biology (Averbuj et al., 2010; Averbuj & Cremonte, 2010; Averbuj & Penchaszadeh, 2010; Penchaszadeh, 1971, 1973). Hatching size is only 4 mm in shell length (Averbuj & Penchaszadeh, 2010). Juveniles up to 25 mm are known to stay close to adults and take advantage of carrion generated by their predation to feed (Averbuj et al., 2012). Individuals reach reproductive

sizes at 60 mm (males) and 80 mm (females) in shell length (Averbuj et al., 2010). There are no studies on its growth. The sympatric species *B. globulosus* (Kiener, 1834) is presently commercially exploited (Narvarte, 2006); between 20 and 9,200 kg/year (2000–2004) of this species are captured in the San Matías Gulf (40°45'S, 64°00'W). It is locally consumed, as well as commercialized at small scale in Buenos Aires, Argentina, and is recently being exported to China (Averbuj et al., 2014).

The aim of this study was to describe the individual growth in a population of *Buccinanops cochlidium* through the identification of the best fitting growth model based on field tag-recapture experimental data. Goodness-of-fit tests and model selection techniques were used in order to provide some of the basic parameters of population dynamics. The results provide valuable information for assessment and future successful management of this valuable resource in North Patagonian Argentinean waters.

MATERIAL AND METHODS

Site Selection

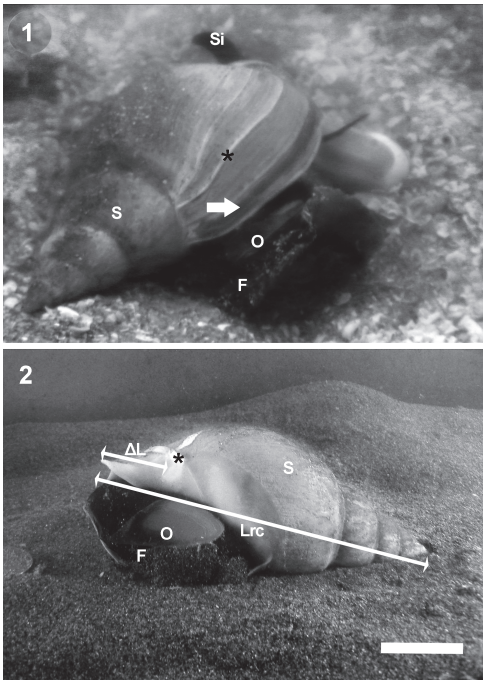
The study was carried out at Playa Villarino, in Golfo San José (42°25'S, 64°31'W). All *Buccinanops cochlidium* individuals were captured by SCUBA diving at 5 to 10 m depth (low tides), approximately 1 km off the coastline.

A total of 561 individuals of *B. cochlidium* were captured during 2006, in two sampling events: 261 snails in March and 300 snails in December. Each time, the Sampling Effort (SEf) was three divers (with a 12 l tank each, ~ 1 hour dives). All these snails were tagged and returned to field.

Tag-Recapture Experiment

Prior to tagging, colonizing algae and/or encrusting organisms (mainly *Antholoba aches* anemones) were removed from the shells with a hard brush and the largest whorl of the shell was gently smoothed with fine sandpaper, rinsed in seawater and clean dried with absorbent paper.

Subsequently, the specimens were tagged by painting a line transverse to the growth direction, in the exterior of the outer lip of the shell's aperture, occupying the whole whorl wide at the latest CaCO₃ deposit of the shell (Fig. 1). Common nail paint was used to tag the shell



FIGS. 1, 2. *Buccinanops cochlidium*. FIG. 1: Individual with tagged shell; FIG. 2: Measurements made to the tagged individual at recaptured after 4 months. Abbreviations: Arrow - tag; F - foot; O - operculum; S - shell; Si - siphon; ΔL - length increment; L_{rc} - length at recapture; * - shell mark. Scale bar = 2 cm.

(Henry & Jarne, 2007), using red and white for differentiation of the two tagging events, in March and December 2006 respectively. After allowing the paint to dry completely, tagged individuals were rinsed in seawater to avoid desiccation or potential contamination due to paint residues, and returned to the field. Immediately after returning the tagged snails to the field and the following day, diving observations showed no tagged dead specimens in the area, indicating that the experiment treatment was not harmful to the snails. Previous aquarium assays (aerated seawater, conditioned at 35‰ salinity, and temperature ranging between 12°C and 14°C (spring temperature) on a 12:12 h light: dark photoperiod, similar to field measurements) showed that snails tagged with this technique survived for more than one year in conditioned aquaria, showing no eye visible adverse effect on the snails and good durability of the paint.

Recapture of tagged specimens was undertaken periodically after that, approximately at two-month intervals (depending on weather conditions), by hand gathering of three SCUBA divers, with a SEF equivalent to that of the original captures (at tagging). Recaptured specimens were measured in shell length (SL) (Fig. 2) with a digital calliper to the nearest 0.1 mm. The SL was considered at tagging, L_c (to the external edge of the nail paint tag) and recapture, L_{rc} (to the maximum size). Each individual was sexed by the presence or absence (female or male, respectively) of vagina and reproductive accessory glands. All recaptured individuals were kept for later studies, without returning them to the field, avoiding a second recapture of any individual.

Growth Data

Because time at liberty was variable between individuals, we used individual length increments standardized by annual increment.

The sex ratio was analyzed with the Chi-square (χ^2) test. Difference in mean length at tagging ($\overline{L_c}$), at recapture ($\overline{L_{rc}}$) and mean length increments ($\overline{\Delta L}$) between sexes was evaluated through Two Sample t-test using the *t.test* function implemented in R (R Development Core Team, 2009).

The data set used in this study can be found in Appendix A.

Growth Models

Four non-nested candidate growth models were fitted to individual tag-recapture data (annual length increment; $n = 48$ individuals) to identify the optimal model, in terms of statistical fit and parsimony, as descriptor of the individual growth process:

von Bertalanffy (vB): This model implies that growth increments are a linear function of initial size.

Gompertz (Gz): This model predicts a humped growth rate curve, with increasing growth rate for juveniles until a maximum and a decreasing growth rate for adult stage.

Exponential (Exp): This model assumes a growth rate proportional to the initial length. An empiric function for individual growth increment data was used.

inverse Logistic (iLog): This model implies constant growth increments in small individuals, and decreasing growth rate for intermediate sizes, until the growth increments are close to zero at larger sizes.

TABLE 1. Two samples t-test. Comparisons between sexes for mean length at capture and at recapture (L_c , L_{rc}), and mean growth increment (ΔL), both in mm. Abbreviations: F - female; M - male; t - student statistic; df - degrees of freedom; CI - confidence intervals; S.D. - standard deviation; $\alpha = 0.05$.

Parameter	F (S.D.)	M (S.D.)	t	df	p-value	CI
\bar{L}_c (S.D.)	89.94 (10.93)	76.13 (7.77)	1.89	46	0.06	[8.34; 19.30]
\bar{L}_{rc} (S.D.)	91.97 (8.92)	80.16 (6.15)	5.29	46	< 0.001	[7.29; 16.32]
$\bar{\Delta L}$ (S.D.)	4.51 (2.63)	8.43 (3.35)	-1.55	45	0.13	[-9.02; 1.17]

Models were fitted to length increment data (n = 48) using the Gauss-Newton algorithm, implemented in the function *nls* of the R program (R Development Core Team, 2009). As the iterative algorithm used in *nls* is sensitive to starting values, we selected an initial set of values for each growth function. The selection of these values was based on a preliminary data inspection of the parameters (considering its biological interpretation) obtained from the ΔL vs L_c plot. This is a valid method when parameters of the proposed models have graphical interpretation (Pineiro & Bates, 2000). The following values were identified, approximately: 22 mm for ΔL_{Max} ; 70 mm for L_{50} ; 90 mm for L_{95} .

Selection among tested growth functions was based on two complementary criteria: (i) log-Likelihood or LL (best estimate); (ii) Akaike Information Criterion corrected for small sample size or AIC_c (adequate fit and parsimony (i.e., simple models are preferred to complex)).

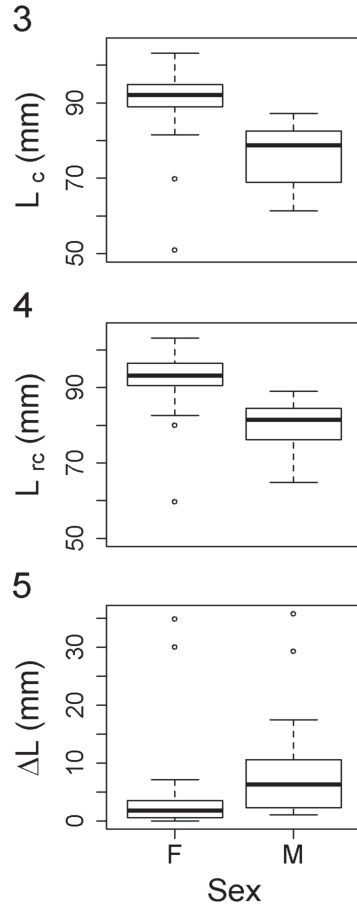
To deal with heteroscedasticity, the selected growth function was refitted using weighted least squares. The improvement was evaluated by values of residual standard errors, where lower values represent better model performance.

For further explanations for mathematical models, see Appendix B.

RESULTS

Tag-Recapture Experiment

A total of 48 individuals (8.6% of total tagged snails) were recaptured after 2 (first recapture event) to 25 months (last recapture event), throughout 11 events (including the second marking event). The sex ratio of the sampled population of *Buccinanops cochlidium* was not



FIGS. 3–5. Growth measures comparison among sexes. FIG. 3: Length-at-capture; FIG. 4: Length-at-recapture; FIG. 5: Mean growth increments. Boxplots showing median, first and fourth quartiles and extreme lower and upper whisker; dots indicate outliers. Abbreviations: L_c - length-at-capture; L_{rc} - length-at-recapture; ΔL - annual growth increments (all in mm).

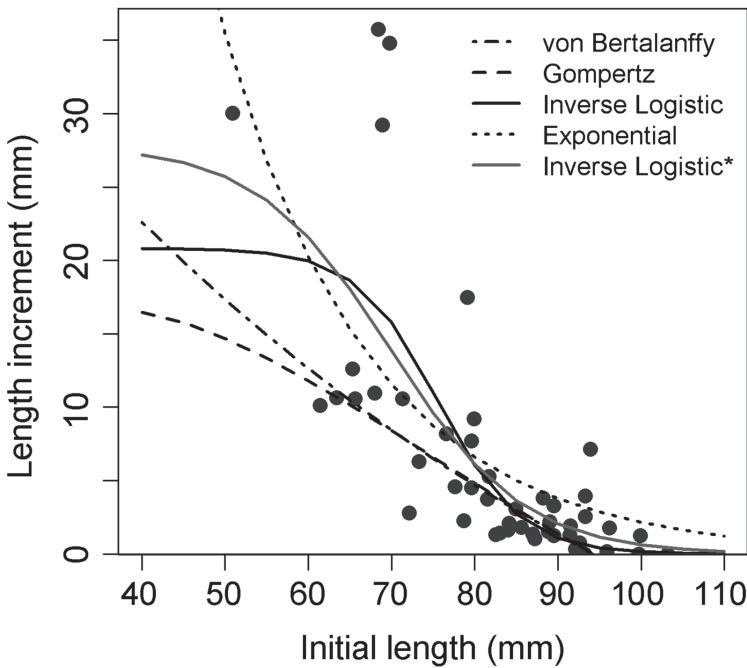


FIG. 6. The von Bertalanffy (vB), Gompertz (Gz), Exponential (Exp), inverse Logistic (iLog) and the weighted inverse Logistic (iLog*) growth models fitted to growth increment data as function of initial length. Tag-recapture growth data ($n = 48$ individuals); males (black spots) and females (grey spots) are plotted separately.

different from 1:1 ($\chi^2 = 0.5$, $df = 47$, $p > 0.05$, $n = 48$).

The 25 recaptured males measured between 63.4 and 89.0 mm, while the 23 females measured between 50.9 and 103.2 mm in shell length. Total shell size was significantly different

between males and females, both at tagging and at recapture (Table 1; Figs. 3, 4). The mean annual length increment was 4.51 mm and 8.43 mm for females and males, respectively. Because no significant differences were found between male and females for growth increments (Table 1; Fig. 5), a single growth model was fitted to the entire data set. The maximum annual length increment obtained was 35.74 mm.

Growth Models

Length increment data showed maximum and more variable values at smaller sizes (50–68 mm), followed by a decrease in the growth rate for intermediate sizes (70–92 mm) and a minimum for larger sizes (Fig. 6).

Among the four evaluated models, the iLog showed the best fit to data based on AIC_c and LL criteria (Table 2). This model captured well the pattern of the data: a constant growth rate in juvenile size classes followed by a non-linear

TABLE 2. Information criteria associated with statistical model selection. Five growth functions: von Bertalanffy, Gompertz, Exponential, inverse Logistic and weighted Inverse Logistic. Abbreviations: AIC_c , Akaike's Information Criterion corrected by small samples.

Model	LL	AIC_c
<i>von Bertalanffy</i>	-168.00	342.28
<i>Gompertz</i>	-168.18	342.63
<i>Exponential</i>	-156.59	319.45
<i>inverse Logistic</i>	-153.80	316.15

TABLE 3. Residual error criterion for Inverse Logistic and weighted Inverse Logistic models.

Model	Residual error (df)
<i>inverse Logistic</i>	6.16 (45)
<i>weighted inverse Logistic</i>	2.26 (45)

TABLE 4. Growth parameters for 48 length increment data (in mm) for the selected weighted Inverse Logistic growth model (iLog*). Abbreviations: S.E., standard error.

Parameter	Estimate (S.E.)
$Max\Delta L$	27.83 (11.5)
L_{50}	69.89 (7.29)
L_{95}	93.36 (3.64)

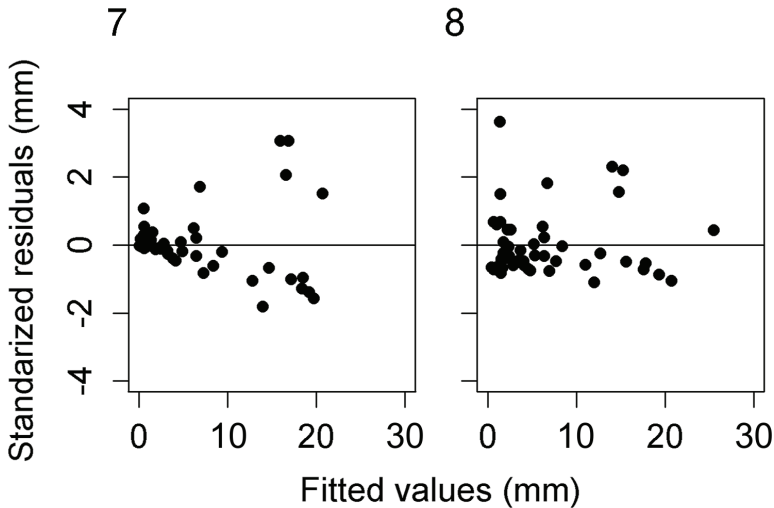
declining growth towards largest sizes (Fig. 6). The other growth models fitted the data and their biological interpretation worse. The Exp growth model fitted values slightly worse than those on iLog (Table 2); in addition, it predicted a maximum increment value of 583.28 mm. Gompertz and von Bertalanffy growth models failed to show a declining straight line, thus predicting negative increments for largest sizes (Fig. 6).

A residual graphical inspection over the selected iLog growth model showed heteroscedasticity in error terms (Fig. 7). The refit of the iLog growth function using weighted data (iLog*) solved the heteroscedasticity problem and improved the fit (Table 3, Fig 8). Finally, from the selected version of the weighted iLog* growth model, the estimated parameters predicted a

maximum annual length increment (ΔL_{Max}) of 27.83 mm; the initial length at which decline in growth rate is most rapid (L_{50}) was 69.89 mm; and the lengths where growth increments become small (L_{95}) was 93.36 mm. These parameters and their Standard Errors are included in Table 4.

DISCUSSION

Of 561 tagged individuals of *Buccinanops cochlidium* in this study, 48 were recaptured. This is a high recapture rate (~ 10%) for a subtidal marine open water study of infaunal mobile snails. Experiments in ponds or rocky



FIGS. 7, 8. Residuals analysis of the inverse Logistic model. FIG. 7: Variance assumed homogeneous; FIG. 8: Variance parameterized as inverse of squared predicted values from the original selected growth function.

shores have generated higher recapture rates (20–30%), including multiple recaptures (Vasconcelos et al., 2006; Eversole et al., 2008).

The pattern observed in the data shows that different processes occur through individual lifetimes in the analysed period. A non-linear growth pattern was evident: maximum growth increments occur at smaller sizes, then decrease at intermediate sizes, and minimum growth increments are observed at larger sizes. The weighted inverse Logistic (iLog*) model most adequately described the growth pattern. L_{95} (initial length at 0.05 times ΔL_{Max}) estimation of the iLog* is consistently close to the larger adult shell lengths in the studied population (Averbuj et al., 2010) where growth increments become small. L_{50} (initial length at 0.5 times ΔL_{Max}) of the iLog* model represented the initial shell length at which the decline in growth rate turned most rapid (Haddon et al., 2008). Declines in growth rate are associated with the onset of maturity as energy is transferred from somatic growth to reproductive effort and a reduction in growth rate is expected (Lester et al., 2004). A strong correlation was found in abalone between size at maturity and L_{50} by Helidoniotis et al. (2011). This change occurred in *B. cochlidium* at ~ 60 mm (for males) and ~ 80 mm (for females) in shell length (Averbuj et al., 2010; Averbuj & Penchaszadeh, 2010). The L_{50} size from the iLog* is 69.89 mm, which corresponds to an intermediate value between both supporting the use of the iLog* model. These consistencies between the known and observed values with iLog* model estimates support the use of the selected model as an adequate descriptor of the individual growth for *B. cochlidium* of Playa Villarino.

The Exponential (Exp) growth model is too simplistic to describe those processes. It assumes a constant decline growth rate that was not observed in the data. Furthermore, the residual analysis showed higher heteroscedasticity values in error terms, which were more difficult to statistically deal with, compared to iLog, as stated above (Escati-Peñaloza et al., 2010; Eveson et al., 2007). In the cases of von Bertalanffy (vB) and Gompertz (Gz), L_{∞} represents the initial shell length where the predicted mean increment is zero, thus these models failed in the representation of the asymptotic maximum shell length which exhibited minimum growth increments (Ratkowsky, 1986). Instead, L_{∞} represents the mean of the

distribution of maximum lengths for the population as a whole (Sainsbury, 1980). The vB and Gz growth models erroneously predicted negative growth increments at larger sizes. For further explanations of mathematical models see Appendix B.

Several studies have explored individual growth of marine snails, including a pioneering paper by Frank (1969) that focused on several tropical gastropods species. He tested the von Bertalanffy (vB) model, which explained correctly most of them. Most works since then have explained snails individual growth on the basis of vB function (Arrighetti et al., 2012; Frank, 1969; Ilano et al., 2004; Kideys, 1996; among others). Recently, alternative models explained better growth data of different gastropod species (Bigatti et al., 2007; Helidoniotis et al., 2011; Zabala et al., 2013). Among studies of marine gastropods growth based on tag-recapture data are scarce and commonly fitted vB model (Eversole et al., 2008; Vasconcelos et al., 2006). Nevertheless, studies of individual growth are essential for assessment and management of commercially exploited populations. Estimates of growth parameter are necessary as input parameters in many production models and stock assessments (Parma & Deriso, 1990; Quinn & Deriso, 1999).

The use of vB growth model is widely accepted in fisheries applications (Beverton & Holt, 1959; Brey, 1999; Eveson et al., 2007), frequently implemented by default without any previous analysis; thus, its adequacy has been questioned (Helidoniotis et al., 2011; Rogers-Bennett, 2003). Using the iLog (or iLog*) growth model avoid negative increments predictions without requiring complicated probability density functions (*pdf*) (Eveson et al., 2007; Helidoniotis et al., 2011).

Obtaining a statistically optimum model can be possible by several arbitrary ways, for example by a polynomial function (Picado, 2009). Since often in ecology or fisheries management there is interest in understanding the mechanisms of the processes, the biological interpretation of the selected model becomes important. Exponential and inverse Logistic models had close values of selection criteria (iLog and iLog* are both best fitted according to AIC_c and LL). However, the iLog* model shows a set of parameters that are biologically easier to understand, as explained above, that adds support to their use. Moreover, iLog (or its modified weighted inverse Logistic) model

showed the best fit, even through AIC_c criterion that penalizes the parameter number attending model parsimony.

Our study spanned the total range of individual sizes, although tagged juveniles (including small individuals under reproductive maturity up to 50 mm) were proportionally underrepresented in the growth analysis. Growth information from juvenile marine snails is difficult to obtain because small individuals are cryptic (Penchaszadeh et al., 2009), and also recapturing tagged juveniles becomes problematic owing to their mobility and high mortality rates (Gosselin & Pei-Yuan, 1997; Rogers-Bennett, 2003; among others). Despite this, the $iLog^*$ growth model better represented the individual growth behavior than the other growth models evaluated, as it incorporated constant growth rate in juvenile size classes. Lacking data of those juvenile size classes may influence parameter estimations and, thus, time to enter the fishery; in particular, bias toward faster growth rates could lead to less precautionary management than should be considered (Rogers-Bennett, 2003).

Our data also show high variability at initial sizes, which could reveal an important feature of the studied population. Smaller individuals exhibit high variability in individual growth that could probably be related to the high plasticity of the organisms at these early stages. Saunders et al. (2009) demonstrate plasticity in growth traits of abalone, mainly related to food availability. Early life represents the most fragile stage in marine invertebrate life-history, in gastropods particularly, mortality rates are usually > 90% (Gosselin & Pei-Yuan, 1997). Survivorship depends on juveniles reaching critical sizes at which vulnerability to physical and biological constraints is substantially reduced (Gosselin & Pei-Yuan, 1997). Among survivors, food availability and other constraints would affect growth performance that may be expressed as a high variability at initial sizes. Juveniles of *B. cochlidium* feed on remains of prey captured by adults, thus facilitating food availability and survivorship (Averbuj et al., 2012).

The results of this study represent a valuable and original output as a first approach for assessment of nassariid snail fisheries in Patagonia. Also, the use of an alternative growth model may be a precedent for future studies in other regions that may benefit of our results.

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LITERATURE CITED

- ABBOTT, R. T. & S. P. DANCE, 1986, *Compendium of seashells*, 3rd printing ed., American Malacologists inc., Melbourne, FL., USA, 411 pp.
- APPELDOORN, R. S., 1990, Growth of juvenile queen conch *Strombus gigas* L., of La Parguera, Puerto Rico. *Journal of Shellfish Research*, 9: 59–62.
- ARRIGHETTI, F., V. TESO, T. BREY, A. MACKENSEN & P. E. PENCHASZADEH, 2012, Age and growth of *Olivancillaria deshayesiana* (Gastropoda: Olividae) in the southwestern Atlantic Ocean. *Malacologia*, 55: 163–170.
- AVERBUJ, A., G. BIGATTI & P. E. PENCHASZADEH, 2010, Gametogenic cycle and size at first maturity of the Patagonic edible snail *Buccinanops cochlidium* from Argentina. *Marine Biology*, 157: 2229–2240.
- AVERBUJ, A. & F. CREMONTE, 2010, Parasitic castration of *Buccinanops cochlidium* (Gastropoda: Nassariidae) caused by a leprocreadiid digenean in San José Gulf, Argentina. *Journal of Helminthology*, 84: 381–389.
- AVERBUJ, A., G. PALOMO, M. I. BROGGER & P. E. PENCHASZADEH, 2012, Diet and feeding of the nassariid *Buccinanops cochlidium* from northern Patagonia, Argentina. *Aquatic Biology*, 17: 261–268.
- AVERBUJ, A. & P. E. PENCHASZADEH, 2010, Reproductive seasonality, oviposition and development of the nassariid whelk *Buccinanops cochlidium* (Dillwyn, 1817) in Patagonia, Argentina. *Journal Molluscan Studies*, 76: 25–32.
- AVERBUJ, A., M. ROCHA & M. S. ZABALA, 2014, Embryonic development and reproductive seasonality of *Buccinanops globulosus* (Nassariidae) (Kiener, 1834) in Patagonia, Argentina.

- Invertebrate Reproduction and Development*, 58: 138–147.
- BEVERTON, R. & S. HOLT, 1959, A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. Pp. 142–180, in: *Ciba Foundation Symposium – The lifespan of animals (Colloquia on Ageing)*, Vol. 5. Wiley Online Library, xii + 342 + 46 pp.
- BIGATTI, G. & N. F. CIOCCO, 2008, Volutid snails as an alternative resource for artisanal fisheries in northern Patagonic gulfs: availability and first suggestions for diving catches. *Journal of Shellfish Research*, 27: 417–421.
- BIGATTI, G., P. E. PENCHASZADEH & M. CLEDÓN, 2007, Age and growth in *Odontocymbiola magellanica* (Gastropoda: Volutidae) from Golfo Nuevo, Patagonia, Argentina. *Marine Biology*, 150: 1199–1204.
- BOTSFORD, L. W., C. L. MOLONEY, J. L. LARGIER & A. HASTINGS, 1998, Metapopulation dynamics of meroplanktonic invertebrates: the Dungeness crab (*Cancer magister*) as an example. *Canadian Special Publication of the Journal of Fisheries and Aquatic Science*, 125: 295–308.
- BREY, T., 1999, Growth performance and mortality in aquatic benthic invertebrates. *Advances in Marine Biology*, 35: 153–223.
- BREY, T. & A. MACKENSEN, 1997, Stable isotopes prove shell growth bands in the Antarctic bivalve *Laternula elliptica* to be formed annually. *Polar Biology*, 17: 465–468.
- BURNHAM, K. P. & D. R. ANDERSON, 2002, *Model selection and multi-model inference: a practical information-theoretic approach*, 2nd ed. Springer, New York, 488 pp.
- CERNOHORSKY, W. O., 1984, *Systematics of the family Nassariidae (Mollusca: Gastropoda)*. Auckland Institute and Museum, Auckland, New Zealand, 356 pp.
- DAY, R. & A. FLEMING, 1992, The determinants and measurement of abalone growth. Pp. 141–168, in: S. A. SHEPARD, M. J. TEGNER & S. A. GUZMAN DEL PROO, eds., *Abalone of the world: biology, fisheries and culture*. Wiley-Blackwell, Cambridge, Massachusetts, 624 pp.
- DILLWYN, L. W., 1817, *A descriptive catalogue of Recent shells arranged according to the Linnaean method, with particular attention to the synonymy*. John & Arthur Arch, London, 1122 pp.
- DURAN, J., M. PALMER & E. PASTOR, 2013, Growing reared spider crabs (*Maja squinado*) to sexual maturity: The first empirical data and a predictive growth model. *Aquaculture*, 409: 79–97.
- ESCATI-PEÑALOZA, G., A. M. PARMA & J. M. ORENSANZ, 2010, Analysis of longitudinal growth increment data using mixed-effects models: Individual and spatial variability in a clam. *Fisheries Research*, 105: 91–101.
- EVERSOLE, A. G., W. D. ANDERSON & J. J. ISELY, 2008, Age and growth of the knobbed whelk *Busycon carica* (Gmelin 1791) in South Carolina subtidal waters. *Journal of Shellfish Research*, 27: 423–426.
- EVESON, J. P., T. POLACHEK & G. M. LASLETT, 2007, Consequences of assuming an incorrect error structure in von Bertalanffy growth models: a simulation study. *Canadian Journal of Fisheries and Aquatic Science*, 64: 602–617.
- FABENS, A. J., 1965, Properties and fitting of the von Bertalanffy growth curve. *Growth*, 29: 265–289.
- FRANK, P. W., 1969, Growth rates and longevity of some gastropod mollusks on the coral reef at Heron Island. *Oecologia*, 2: 232–250.
- GOSSELIN, L. A. & Q. PEI-YUAN, 1997, Juvenile mortality in benthic marine invertebrates. *Marine Ecology Progress Series*, 146: 265–282.
- HADDON, M., C. MUNDY & D. TARBATH, 2008, Using an inverse-logistic model to describe growth increments of blacklip abalone (*Haliotis rubra*) in Tasmania. *Fishery Bulletin*, 106: 58–71.
- HELIDONIOTIS, F., M. HADDON, G. TUCK & D. TARBATH, 2011, The relative suitability of the von Bertalanffy, Gompertz and inverse logistic models for describing growth in blacklip abalone populations (*Haliotis rubra*) in Tasmania, Australia. *Fisheries Research*, 112: 13–21.
- HENRY, P. & P. JARNE, 2007, Marking hard-shelled gastropods: tag loss, impact on life-history traits, and perspectives in biology. *Invertebrate Biology*, 126: 138–153.
- ILANO, A. S., A. ITO, K. FUJINAGA & S. NAKAO, 2004, Age determination of *Buccinum isaotakii* (Gastropoda: Buccinidae) from the growth striae on operculum and growth under laboratory conditions. *Aquaculture*, 242: 181–195.
- JOHNSON, J. B. & K. S. OMLAND, 2004, Model selection in ecology and evolution. *TRENDS in Ecology and Evolution*, 19: 101–108.
- KIDEYS, A. E., 1996, Determination of age and growth of *Buccinum undatum* L. (Gastropoda, Prosobranchia) off Douglas, Isle of Man. *Helgolander Meeresuntersuchungen*, 50: 353–368.
- LESTER, N., B. SHUTER & P. ABRAMS, 2004, Interpreting the von Bertalanffy model of somatic growth in fishes: the cost of reproduction. *Proceedings of the Royal Society B, Biological Sciences*, 271: 1625–1631.
- LING, S. D., C. R. JOHNSON, K. RIDGWAY, A. J. HOBDAY & M. HADDON, 2009, Climate-driven range extension of a sea urchin: inferring future trends by analysis of recent population dynamics. *Global Change Biology*, 15: 719–731.
- NARVARTE, M. A., 2006, Biology and fishery of the whelk *Buccinanops globulosum* (Kiener, 1834) in northern coastal waters of the San Matías Gulf (Patagonia, Argentina). *Fisheries Research*, 77: 131–137.
- PARMA, A. M. & R. B. DERISO, 1990, Dynamics of age and size composition in a population subject to size-selective mortality: effects of phenotypic variability in growth. *Canadian Journal of Fisheries and Aquatic Science*, 47: 274–289.

- PENCHASZADEH, P. E., 1971, Aspectos de la embriogénesis de algunos gasterópodos del género *Buccinanops* d'Orbigny, 1841 (Gastropoda, Prosobranchiata, Buccinidae). *Physis*, 30: 475–482.
- PENCHASZADEH, P. E., 1973, Nuevas observaciones sobre la reproducción de *Buccinanops gradatum* (Deshayes, 1844) (Gastropoda: Prosobranchiata, Dorsaninae). *Physis Sección A*, 32: 15–18.
- PENCHASZADEH, P. E., C. SANCHEZ ANTELO, M. S. ZABALA & G. BIGATTI, 2009, Reproduction and imposex in the edible snail *Adelomelon ancilla* from northern Patagonia, Argentina. *Marine Biology*, 156: 1929–1939.
- PICADO, J., 2009, Seashells: the plainness and beauty of their mathematical description. Pp. 1–18, in: J. C. PINHEIRO, & D. M. BATES, 2002, *Mixed-effects models in S and S-PLUS*, 2nd ed. *MAA Mathematical Sciences Digital Library*. Springer-Verlag, New York.
- PRINCE, J. D., T. L. SELLERS, W. B. FORD & S. R. TALBOT, 1988, Recruitment, growth, mortality and population structure in a southern Australian population of *Haliotis rubra* (Mollusca: Gastropoda). *Marine Biology*, 100: 75–82.
- QUINN, T. J. & R. B. DERISO, 1999, Growth and fecundity. Chapter 4, in: T. J. QUINN & R. B. DERISO, eds., *Quantitative fish dynamics*. Oxford University Press, New York, 542 pp.
- R DEVELOPMENT CORE TEAM, 2009, *R: A language and environment for statistical computing*. ISBN 3-900051-07-0. R Foundation for Statistical Computing. Vienna, Austria, 2013. Online at <http://www.r-project.org>.
- RATKOWSKY, D., 1986, Statistical properties of alternative parameterizations of the von Bertalanffy growth curve. *Canadian Journal of Fisheries and Aquatic Science*, 43: 742–747.
- ROGERS-BENNETT, L. D., 2003, Modeling red sea urchin growth using six growth functions. *Fishery Bulletin*, 101: 614–626.
- RUSSELL, M. P. & R. W. MEREDITH, 2000, Natural growth lines in echinoid ossicles are not reliable indicators of age: a test using *Strongylocentrotus droebachiensis*. *Invertebrate Biology*, 119: 410–420.
- SAINSBURY, K. 1980, Effect of individual variability on the von Bertalanffy growth equation. *Canadian Journal of Fisheries and Aquatic Science*, 37: 241–247.
- SAUNDERS, T., S. CONNELL & S. MAYFIELD, 2009, Differences in abalone growth and morphology between locations with high and low food availability: morphologically fixed or plastic traits? *Marine Biology*, 156: 1255–1263.
- STARR, P. J., P. A. BREEN, T. H. KENDRICK & V. HAIST, 2009, Model and data used for the 2008 assessment of rock lobsters (*Jasus edwardsii*) in CRA 3 200. *New Zealand Fisheries Assessment Report 2009/22*: 62 p.
- VASCONCELOS, P., M. B. GASPAS, A. M. PEREIRA & M. CASTRO, 2006, Growth rate estimation of *Hexaplex trunculus* based on mark/recapture experiments in the Ria Formosa lagoon. *Journal of Shellfish Research*, 25: 249–256.
- ZABALA, M. S., P. E. PENCHASZADEH, O. PANARELLO, M. I. BROGGER & G. BIGATTI, 2013, Life history parameters in the edible snail *Adelomelon ancilla* from patagonian waters. *Malacologia*, 56: 215–229.
- ZHANG, Z., J. LESSARD & A. CAMPBELL, 2009, Use of Bayesian hierarchical models to estimate northern abalone, *Haliotis kamtschatkana*, growth parameters from tag-recapture data. *Fisheries Research*, 95: 289–295.

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APPENDIX A. Data set used in this Study.

ID	L1	L2	T1	T2	inc	dT	Sex	Lm	dL	dT.a
1	65.6	69.6	1	139	4.0	138	M	67.60	0.02898551	0.37808219
2	76.6	79.7	1	139	3.1	138	M	78.15	0.02246377	0.37808219
3	79.6	81.3	1	139	1.7	138	M	80.45	0.01231884	0.37808219
4	81.7	83.7	1	139	2.0	138	M	82.70	0.01449275	0.37808219
5	84.9	87.2	1	274	2.3	273	M	86.05	0.00842491	0.74794521
6	72.1	74.2	1	274	2.1	273	M	73.15	0.00769231	0.74794521
7	68.0	76.2	1	274	8.2	273	M	72.10	0.03003663	0.74794521
8	78.7	80.7	1	324	2.0	323	M	79.70	0.00619195	0.88493151
9	83.0	84.5	1	383	1.5	382	M	83.75	0.0039267	1.04657534
10	84.1	86.3	1	383	2.2	382	M	85.20	0.00575916	1.04657534
11	77.6	82.4	1	383	4.8	382	M	80.00	0.01256545	1.04657534
12	61.4	72.0	1	383	10.6	382	M	66.70	0.02774869	1.04657534
13	87.2	88.3	1	383	1.1	382	M	87.75	0.00287958	1.04657534
14	84.0	85.7	1	383	1.7	382	M	84.85	0.00445026	1.04657534
15	73.3	79.9	1	383	6.6	382	M	76.60	0.01727749	1.04657534
16	87.0	89.0	1	544	2.0	543	M	88.00	0.00368324	1.48767123
17	82.5	85.3	1	771	2.8	770	M	83.90	0.00363636	2.10958904
18	79.1	81.4	274	322	2.3	48	M	80.25	0.04791667	0.13150685
19	68.4	73.1	274	322	4.7	48	M	70.75	0.09791667	0.13150685
20	63.4	64.8	274	322	1.4	48	M	64.10	0.02916667	0.13150685
21	71.3	74.4	274	381	3.1	107	M	72.85	0.02897196	0.29315068
22	79.9	82.6	274	381	2.7	107	M	81.25	0.02523364	0.29315068
23	68.9	82.2	274	440	13.3	166	M	75.55	0.08012048	0.45479452
24	79.6	83.1	274	440	3.5	166	M	81.35	0.02108434	0.45479452
25	65.3	76.5	274	598	11.2	324	M	70.90	0.0345679	0.88767123
26	93.3	94.8	1	139	1.5	138	H	94.05	0.01086957	0.37808219
27	93.9	96.6	1	139	2.7	138	H	95.25	0.01956522	0.37808219
28	88.8	89.5	1	169	0.7	168	H	89.15	0.00416667	0.46027397
29	85.6	87.2	1	324	1.6	323	H	86.40	0.00495356	0.88493151
30	91.5	93.2	1	324	1.7	323	H	92.35	0.00526316	0.88493151
31	88.2	92.2	1	383	4.0	382	H	90.20	0.0104712	1.04657534
32	93.3	96.4	1	442	3.1	441	H	94.85	0.00702948	1.20821918
33	89.5	91.8	1	666	2.3	665	H	90.65	0.00345865	1.82191781
34	91.4	94.1	1	771	2.7	770	H	92.75	0.00350649	2.10958904
35	92.6	92.7	274	322	0.1	48	H	92.65	0.00208333	0.13150685
36	99.7	99.7	274	322	0	48	H	99.70	0	0.13150685
37	103.2	103.2	274	322	0	48	H	103.20	0	0.13150685
38	99.7	99.7	274	322	0	48	H	99.70	0	0.13150685
39	93.2	93.2	274	322	0	48	H	93.20	0	0.13150685
40	69.8	80.0	274	381	10.2	107	H	74.90	0.0953271	0.29315068
41	50.9	59.7	274	381	8.8	107	H	55.30	0.08224299	0.29315068
42	92.1	92.2	274	381	0.1	107	H	92.15	0.00093458	0.29315068
43	81.5	82.6	274	381	1.1	107	H	82.05	0.01028037	0.29315068
44	89.0	90.0	274	440	1.0	166	H	89.50	0.0060241	0.45479452
45	89.5	91.0	274	440	1.5	166	H	90.25	0.00903614	0.45479452
46	95.9	96.0	274	477	0.1	203	H	95.95	0.00049261	0.55616438
47	99.9	101.0	274	598	1.1	324	H	100.45	0.00339506	0.88767123
48	96.2	98.6	274	769	2.4	495	H	97.40	0.00484848	1.35616438

APPENDIX B. Detailed Explanations of Mathematical Models.

Individual length increments standardized year

$$(1) \Delta L = \frac{L_{rc} - L_c}{\Delta t_a}; \quad \Delta t_a = (t_{rc} - t_c)/365$$

were ΔL is the standardized length increment, L_{rc} the length at recapture, L_c the length at tagging, Δt_a represent the time at liberty relative to an annual period with t_{rc} as time at recapture and t_c the time at tagging.

von Bertalanffy (vB). This model implies that growth increments are a linear function of initial size. A re-parameterized version for tag-recaptured data was used (Fabens, 1965),

$$(2) \Delta \hat{L}_i = (L_\infty - L_{c_i})(1 - e^{-k\Delta t_a}) + \varepsilon$$

Gompertz (Gz). This model predict a humped growth rate curve, with increasing growth rate for juveniles until a maximum and a decreasing growth rate for adult stage

$$(3) \Delta \hat{L}_i = L_\infty \left(\frac{L_{c_i}}{L_\infty} \right)^{e^{-gM_a}} - L_i + \varepsilon$$

Exponential (Exp). This model assumes a growth rate proportional to the initial length. An empiric function for individual growth increment data was used

$$(4) \Delta \hat{L}_i = Max\Delta L_{c_i} e^{-cL_{c_i}} + \varepsilon$$

Inverse Logistic (iLog). This model implies constant growth increments in small individuals, and decreasing growth rate for intermediated sizes, until the growth increments are close to zero at larger sizes

$$(5) \Delta \hat{L}_i = \frac{Max\Delta L_i}{1 + e^{\frac{\ln(19)}{L_{95} - L_{50}}(L_{c_i} - L_{50})}} + \varepsilon$$

where $\Delta \hat{L}_i$ represent the expected length increment for individual i , L_∞ the asymptotic length (vB and Gz), L_{c_i} the length at tagging (initial length) for individual i , k is the growth parameter (vB), g and c is the rate of change in length increment (Gz and Exp, respectively), Δt_a is the time at liberty as annual fraction (vB and Gz), $Max\Delta L_i$ is the maximum length increment, L_{50} is the initial length at 0.5 times $Max\Delta L_i$ and L_{95} is the initial length at 0.05 times $Max\Delta L_i$.

The term ε represents process stochasticity, and is an independent additive normal random error term.

Selection complementary criteria

Selection among tested growth functions was based on two complementary criterions:

(i) log-Likelihood. The model which presents the greatest estimate for the log-Likelihood will best represent the data. For this criterion, as more parameters are incorporated into the model, uncertainty will be lower and higher the degree of explanation (Burnham & Anderson, 2002).

Through this function the negative log-Likelihood (LL) was minimized for each fitted growth function,

$$(6) -LL = -\frac{1}{2} n \log \left[\frac{\sum_{i=1}^n (\Delta L_i - \Delta \hat{L}_i)^2}{n} \right]$$

where ΔL_i is the observed length increment for each of the $i=1$ to n observations and $\Delta \hat{L}_i$ is the expected length increment for observations i for one of the four candidate growth models; $(\Delta L_i - \Delta \hat{L}_i)$ differences is the produced error among predicted and observed growth increment due to the fit of each growth function to data.

(ii) Akaike Information Criterion corrected for small sample size (AIC_c). This version of AIC is recommended for cases in which the ratio between sample size and number of estimated parameters is less than 40 (Burnham & Anderson, 2002); This technique is frequently used for models selection in mark-recaptured studies (Johnson & Omland, 2004). According to AIC , the model with the smallest value will present the best fit to the data among the candidate models considered (Quinn & Deriso, 1999). Finally, AIC_c :

$$(7) AIC_c = -2\log(L) + 2k \left(\frac{n}{n-k-1} \right)$$

were L is the Likelihood, k is the number of parameters to estimate and n is the sample size. We used AIC because it allows selection among models based on adequate fit and

parsimony (e.i., simple models are preferred to complex).

To deal with heterocedasticity, the selected growth function was refitted using weighted least squares

$$(8) \quad w_i = \frac{1}{(\hat{y}_i)^2}$$

where w_i represented the weight given to each \hat{y}_i predicted values from the original selected

growth function. The improvement was evaluated by values of residual standard errors, where minor values represent better model performance.

To confirm starting values for iLog model fitting, several ($n = 60$) fits were generated using different sets of starting values (combinations), and collected the final estimates (see Complementary data section), then the mean and sd for this distribution of generated estimates was compared with the original analysis.