

Variability in size and age at maturity in the marine scavenger *Buccinanops globulosus* (Gastropoda: Nassariidae) from Patagonia

MARÍA SOLEDAD AVACA^{1,2}, PABLO MARTÍN^{1,3} AND MAITE NARVARTE^{1,2}

¹Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina, ²Instituto de Biología Marina y Pesquera Almirante Storni, Escuela Superior de Ciencias Marinas, Universidad Nacional del Comahue, Güemes 1030, 8520 San Antonio Oeste, Río Negro, Argentina, ³Departamento de Biología, Bioquímica y Farmacia, Universidad Nacional del Sur, San Juan 670, 8000 Bahía Blanca, Buenos Aires, Argentina

Growth rates and size-age at maturity are life history traits that combine in different ways to achieve maximal fitness. The marine scavenger Buccinanops globulosus was used as a model to explore the variation on female size-age at maturity and reproductive effort among three populations characterized by different growth rates (slow, moderate and rapid). This species constitutes the target of an artisanal fishery in North Patagonia. Here, a suite of different estimators of size-age at maturity derived from gonad histological analysis and the study of females carrying egg capsules were obtained. Data were modelled using a logistic function and the maturity patterns were compared among populations. We found that female size and age at maturity were variable and site-specific. The fastest-growing population showed the lowest reproductive effort. Slow and rapid-growing females mature at different sizes but at the same age whereas moderate-growing females mature both at a different size and age (intermediate size and at earlier age). Thus, results obtained here are difficult to reconcile with a single reaction norm for a single genotype in the studied populations. Growth rate variation is not enough to explain the patterns described here. The information provided could be used for the establishment of fishery management actions, such as minimum landing size.

Keywords: life history, maturity, reproduction, whelk fishery

Submitted 3 February 2015; accepted 22 March 2015

INTRODUCTION

Size and age at maturity are key life history traits for any species, and their optimal values are attained through a complex balance of the costs and benefits of maturation at different ages and sizes (Stearns, 1992). Most species do not mature at a fixed size or age; instead, maturity could be described along a size-age reaction norm (i.e. the different combinations of age and size at maturity displayed by the same genotype in different environments; Schlichting & Pigliucci, 1998). In the context of the evolution of life history theory, early maturation entails a fitness advantage since early maturing organisms have a higher probability of surviving to maturity (Stearns, 1992). On the other hand, if delaying maturity permits further growth and fecundity increases with size, then delayed maturity leads to higher initial fecundity outweighing the advantages of early maturation.

Growth rates and juvenile mortality are primary determinants of maturation evolution (Stearns, 1992). Growth rates define the relationship between size and age and are closely linked to ecological conditions, e.g. resource availability and predation risk, thus variation among populations of a given

species is common (reviewed by Dmitriew, 2011). Regarding maturity across a range of growth rates, Stearns (1992) proposed three basic rules or reaction norms: rule one is to mature always at the same size, even at the risk of dying before reproduction; rule two is to mature always at the same age at the cost of a diminished size and fecundity; rule three is a compromise between age and size at maturity that results from the evolutionary trade-offs between these risks and costs. Early life stages of marine invertebrates are usually more susceptible than adults to environmental conditions, as shown by the relatively high mortality rates, c. 90% (Gosselin & Qian, 1997). However, the effect of juvenile mortality on age at maturity varies according to the reproductive strategy of the species. For example, in a review of 92 marine benthic invertebrates, Gosselin & Qian (1997) noted that juvenile mortality is an important determinant only in species showing an early maturity, i.e. species maturing within 4 months after beginning juvenile life, but not in late-maturing ones.

The intertidal whelk *Buccinanops globulosus* provides a good model for exploring the relationships between growth rates and maturity patterns. This species shows great variation in individual growth patterns among populations (Narvarte *et al.*, 2008; Avaca *et al.*, 2013) which is most likely related to food availability as in other nassariid species (e.g. McKillup & McKillup, 1997; Morton & Chan, 2004). Like other nassariid species, *B. globulosus* lies quiescent in the sediment but rapidly emerges when detecting carrion (Daleo *et al.*,

Corresponding author:

M.S. Avaca

Email: msavaca@yahoo.com.ar

2005, 2012). Fishermen take advantage of this behaviour to collect individuals of this species in North Patagonia where an artisanal diving fishery has been developed (e.g. in Golfo San Matías; Narvarte, 2006). The patterns of variation in size-age at maturity among populations are particularly interesting in exploited species, given its potential effects on population dynamics, catches and fishery management strategy (e.g. Shelmerdine *et al.*, 2007; Stoner *et al.*, 2012; McIntyre *et al.*, 2015).

The main goal of our study was to document the variation on female size-age at maturity, and the reproductive effort for three populations of *B. globulosus* characterized by different growth rates (slow, moderate and rapid). To meet this goal, we assessed female maturity over a wide range of shell sizes and ages. Two approaches were used: (1) histological evaluation of gonad tissues, and the input of these data into logistic models to estimate the female size (TL_{50}) and age (A_{50}) at maturity at each population, and (2) study of size and age of females carrying egg capsules. The different estimators of maturity obtained and the published female growth model for each population were used to propose a set of size-age at maturity reaction norms for this species. Determining whether intra-specific variation in size-age at maturity occurs across the populations studied is important to understand the evolution of this life history trait. A supplementary benefit of this study is to contribute with the management of this whelk fishery, since accurate estimates of female size-age maturity could be used in size-structured models to examine the population dynamics of stocks.

MATERIALS AND METHODS

Study species and study sites

Buccinanops globulosus is a small-sized species (up 62 mm total shell length) with a short lifespan (8 years; Narvarte, 2006; Narvarte *et al.*, 2008; Avaca *et al.*, 2013), commonly

found as an endemic component of soft bottom communities of the Southwestern Atlantic Ocean (Pastorino, 1993). Like other *Buccinanops*, this species is gonochoristic, with internal fertilization and direct development (Averbuj *et al.*, 2010). Egg capsules are deposited by each female on its own shell and, at oviposition, they are filled with nurse eggs that provide nutritional support to a single developing embryo (Avaca *et al.*, 2012; Averbuj *et al.*, 2014). Crawling juveniles emerge from the egg capsules and settle soon in the maternal environment. This species is sensitive to tributyltin (TBT) contamination along the Patagonia shoreline because females may be imposex-affected, i.e. characteristics of males superimposed onto females (Bigatti *et al.*, 2009). All the events of female gametogenic activity and the deposition of egg capsules have been observed in imposex-affected females of *B. globulosus* thus imposex does not appear to compromise the reproductive activity of this species (Narvarte *et al.*, 2008; Avaca *et al.*, 2012, 2015).

The present study was conducted in soft bottoms from northern Patagonia, Argentina. Two sampling sites were located in Golfo San Matías (GSM; Bahía San Antonio, [BSA]: 40°29'S 63°01'W and Playa Villarino [PV]: 40°45'S 64°40'W) and one in Golfo Nuevo (Bahía Nueva; [BN]: 42°46'S 65°02'W) (Figure 1). These sites are separated from each other along the South Atlantic Ocean coast by at least 50 km, and the two most distant sites, PV and BN, are 300 km apart potentially allowing divergence of traits such as size-age at maturity. At these sites other studies on *B. globulosus* growth, morphometrics and gonad cycle have been carried out previously (Narvarte *et al.*, 2008; Avaca *et al.*, 2013, 2015).

Buccinanops globulosus were collected monthly between September 2006 and August 2008 in the intertidal-shallow subtidal area of the three sites studied. Specimens were attracted with biological baits (mainly discarded fish) and collected by scuba diving or handpicking, at high and low tides, respectively. This method showed to be efficient to catch individuals of all sizes at each sampling site, including females

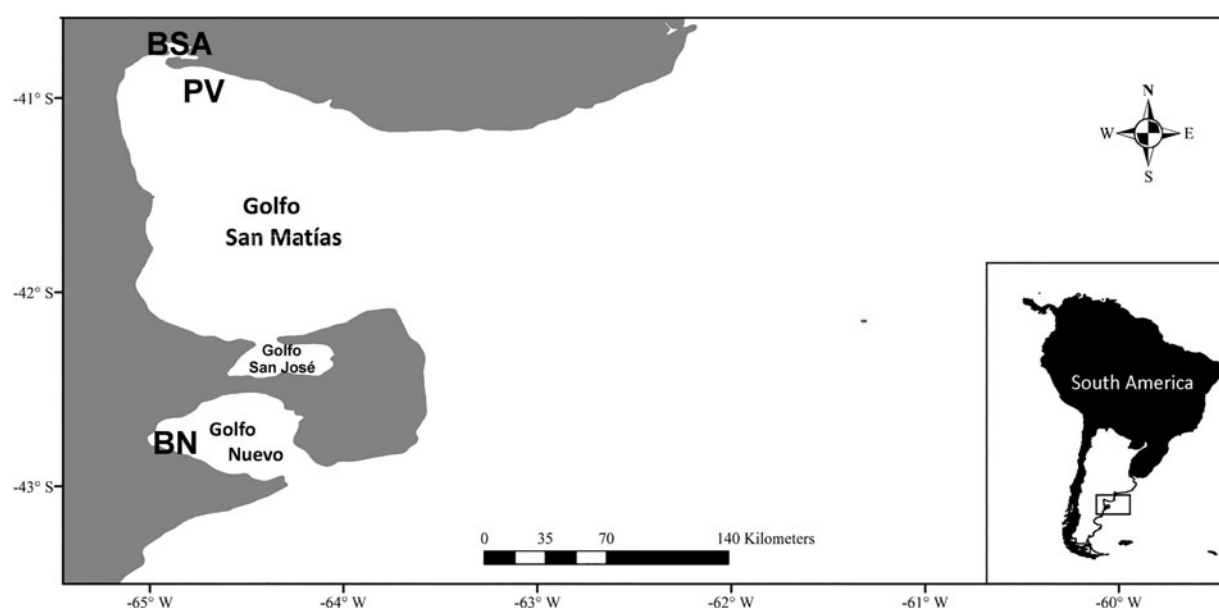


Fig. 1. North Patagonia: location of the three *Buccinanops globulosus* populations examined in this study. The two most distant sites, PV and BN, are 300 km apart; the two closest sites, BSA and PV, are 50 km apart. BSA, Bahía San Antonio; BN, Bahía Nueva; PV, Playa Villarino.

carrying egg capsules (Narvarte *et al.*, 2008). Attracted whelks were carried to the laboratory in containers filled with seawater. A subsample was maintained alive for histological analysis of the gonad and the remaining was frozen at -18°C for further studies.

Laboratory techniques

At the laboratory, total shell length (TL, mm) was measured from the apex to the tip of the siphonal canal with a digital caliper (± 0.01 mm), and the total body weight (TW, g) was recorded with an analytical scale (± 0.01 g). When present, egg masses were carefully detached from the female's shell and the weight of the egg mass (EW, g) was also recorded. In this study, only female whelks were used. After removing the shell, females were identified on the basis of the presence of accessory glands (capsule and albumen) because of the presence of imposex-affected females in two of the populations studied (BSA and BN; Bigatti *et al.*, 2009; Avaca *et al.*, 2015).

For histological analyses, a total of 7–25 individuals per month covering the whole range of size distribution of each population were studied. The total shell length of these individuals ranged from 10.6 to 31.8 mm for BSA ($N = 223$), 13.5 to 67.2 mm ($N = 224$) for PV and 12.5 to 46.3 mm for BN ($N = 248$). According to the individual size at each site, the whole body, the entire gonad or only a section was fixed in Davidson's fluid for 24 h at 4°C and subsequently stored in 70% ethanol. Tissues were dehydrated using an ascending series of ethanol concentrations and then embedded in paraffin. Sections were cut at $5\ \mu\text{m}$ with a microtome, stained with hematoxylin-eosin and observed under a light microscope. These sections were also used in the description of the gametogenic cycle of this species (Avaca *et al.*, 2015).

For age determination, the operculum was detached from the foot of each individual. Opercula were then rinsed and stored in dry conditions for later analyses. The number of rings of each operculum occurring on the ventral face was counted under a stereomicroscope (Narvarte, 2006). Only those opercula without damage and clear rings were taken into account. The annual pattern of deposition in operculum was validated for this species by Narvarte (2006) and Avaca *et al.* (2013).

Maturity assessment

Gonad sections were classified into immature and mature. Immature individuals were characterized by either no differentiation of gonadal tissue or a small gonadal bulk, which in females was composed of oogonia and primary oocytes but without vitellogenic or degenerating oocytes. The criteria used for maturity were the presence of vitellogenic oocytes in abundance or, when there were few mature oocytes, the presence of degenerating ones and other gametogenic remains (at: Growth II, Pre-evacuation, Evacuation and Post-evacuation; Avaca *et al.*, 2015). Additionally, females carrying egg capsules on their shells were considered mature.

Size and age at maturity

Size-age at first gonadal maturity was defined at the individual level as the minimum female size (TL) or age at which gonad matures at each population, and at the population level as the

total shell length or age at which 50% of the population is mature (TL_{50} and A_{50}). To estimate TL_{50} and A_{50} , the percentage of mature individuals were combined by 4 mm TL size classes and 1 year classes, respectively, and were modelled using the logistic equation,

$$P(x) = \frac{1}{(1 + e^{(-C(x-X_{50}))})}$$

where P is the proportion of mature females at size or age class x , C is a parameter defining the shape of the curve and X_{50} is the total shell length (TL_{50}) or age (A_{50}) at which 50% of the females in the population are mature. The parameters (X_{50} and C) were estimated following the maximum likelihood method (Aubone & Wöhler, 2000). Logistic models obtained were compared between populations by likelihood ratio tests (Cerrato, 1990), under different null hypotheses, H_{01} : $X_{50(1)} = X_{50(2)}$; H_{02} : $C_{(1)} = C_{(2)}$ and H_{03} : $\Theta_{(1)} = \Theta_{(2)}$, where 1 and 2 indicate different populations, and Θ is the vector of model parameters (X_{50} and C).

The median TL and the minimum age of females carrying egg capsules were also considered as alternative estimators of female maturity for each population. Numbers of females carrying egg capsules studied were 41 in BSA, 26 in PV and 190 in BN for size and 13, 5 and 34 for age, respectively. Since the data did not meet ANOVA assumptions, even after data transformation, a non-parametric Kruskal–Wallis test was used to compare the size of females carrying egg capsules among populations. In contrast, the mean age of females carrying egg capsules among populations was compared by one-way ANOVA. No transformations of the data were necessary since the assumptions of the ANOVA model were met. All statistical analyses were conducted using *Statistica* 7.0 software.

Reproductive effort

To seek for biological significance of the different maturity patterns, we estimated an index of reproductive effort using the equation of the weight-specific reproductive effort (WRE) proposed by Perron (1982) with some modifications. This measure is a proxy of reproductive effort, which should be determined as the proportion of assimilated energy which is allocated to reproduction (e.g. Hughes & Roberts, 1980). The equation used was,

$$\text{WRE} = R \times \text{TW}^{(-1)}$$

where R is the reproductive output measured as the mean weight of egg masses and TW is mean female's body weight. Only females with egg masses in early and mature stages of development (Avaca *et al.*, 2012) were included in these calculations (BSA: 10, PV: 11 and BN: 112). Results were expressed as means of females at each population. The mean RE was compared among populations by one-way ANOVA; data were arcsine-transformed to meet the assumptions of the ANOVA model.

Reaction norm models

The different estimators of maturity obtained and the female growth model for each population were used to graphically represent the variability in size and age at maturity in this

Table 1. *Buccinanops globulosus*. Growth parameters of von Bertalanffy curves (VBG) and growth performance (P) for female whelks from populations studied. VBGF, $TL(t) = TL_{\infty}(1 - e^{-k(t-t_0)})$, and $P = \log(KTL_{\infty}^3)$.

Population	TL_{∞} (mm)	K (year ⁻¹)	t_0 (year)	P	Source
Bahía San Antonio	33.1	0.21	-1.03	3.88	Narvarte <i>et al.</i> (2008)
Playa Villarino	65.4	0.28	-0.30	4.89	Narvarte <i>et al.</i> (2008)
Bahía Nueva	38.0	0.38	-0.43	4.32	Avaca <i>et al.</i> (2013)

species; i.e. reaction norm. Female growth models were taken from Narvarte *et al.* (2008) for Golfo San Matías populations and from Avaca *et al.* (2013) for Golfo Nuevo. In all these studies, growth curves were obtained by fitting von Bertalanffy equations to data obtained from the opercula reading (Table 1).

RESULTS

A total of 695 histological sections were studied. Histological examination showed immature and mature gonads in the three populations studied (Figure 2). Despite the presence of imposex-affected females in two of the studied populations, the maturity status could be easily attributed to all individuals. The number of mature females observed was similar between populations (BSA: 147, PV: 128 and BN: 179). Based on these

observations, the size of the smallest mature female was 15.6 mm in BSA, 38.7 mm in PV and 19.8 mm in BN. The largest immature individual was 25.0 mm in BSA, 44.07 mm in PV and 30.1 mm in BN. The minimum age of a female with a mature gonad was 4 years in BSA and PV and 2 years in BN. The oldest immature females were 6, 5 and 4 years in PV, BSA and BN, respectively.

The percentage of mature females as a function of size (TL) and age (A) for each population shows good fit to the logistic curve (Figure 3). Comparisons of pairs of maturity models for the three populations (Table 2) indicated that in most cases there were statistically significant differences between the maturity parameters (Table 3). Playa Villarino and Bahía San Antonio females had the smallest and largest TL_{50} , respectively (mean \pm SE, 44.0 ± 8.91 and 19.4 ± 2.75 mm, respectively), whereas Bahía Nueva females had intermediate TL_{50} (26.5 ± 3.7 mm). No significant differences were apparent between BSA and PV in the parameter C of the size at maturity model. Regarding age, Bahía Nueva and Bahía San Antonio females had the youngest and oldest A_{50} , respectively (2.6 ± 0.74 years and 4.6 ± 1.21 years, respectively) whereas PV females had intermediate A_{50} (4.3 ± 1.28 years). However, no significant differences were found between PV and BSA females in the vector of age model parameters.

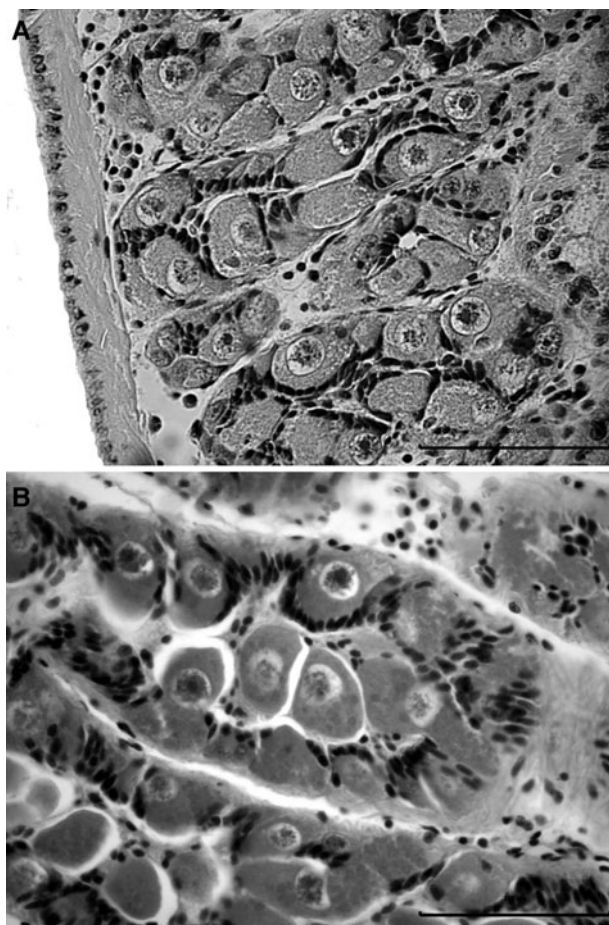


Fig. 2. *Buccinanops globulosus*. (A) Immature ovary of a 25.8 mm total shell length female from Bahía Nueva; (B) mature ovary of a 50 mm total shell length female from Playa Villarino. Scale bar: 100 μ m.

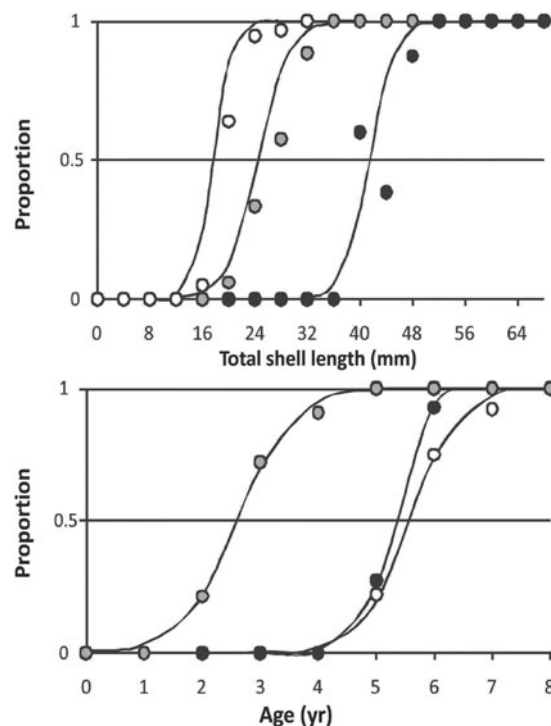


Fig. 3. Logistic curves fitted to the proportion of mature females by size (total shell length, top) and age (bottom) to estimate sexual maturity (TL_{50} and A_{50}) at each population studied. Bahía San Antonio (white circles); Playa Villarino (black circles); Bahía Nueva (grey circles).

Table 2. *Buccinanops globulosus*. Mean (\pm SE) maturity parameters (X_{50} , C) of logistic curves for female whelks from the studied populations. X_{50} , represents total shell length or age at which the 50% of the females in the population is mature; C, curve shape; N, sample size.

Population	X_{50}	C	N
Bahía San Antonio			
Size (mm)	19.4 (\pm 2.75)	0.6 (\pm 0.09)	223
Age (years)	4.6 (\pm 1.21)	2.0 (\pm 0.49)	81
Playa Villarino			
Size (mm)	44.0 (\pm 8.91)	0.5 (\pm 0.09)	224
Age (years)	4.3 (\pm 1.28)	3.8 (\pm 1.13)	64
Bahía Nueva			
Size (mm)	26.5 (\pm 3.7)	0.4 (\pm 0.05)	248
Age (years)	2.6 (\pm 0.74)	2.1 (\pm 0.56)	68

The size of females carrying egg capsules varied among populations (Kruskal–Wallis, $H_2 = 142.3$, $P = 0.000$) (Figure 4). The median shell length of females carrying egg capsules was 22.3 in BSA (range: 17.0–26.1 mm), 56.4 mm in PV (47.9–59.8 mm) and 31.4 mm in BN (21.2–43.0 mm). The age of the youngest female carrying egg capsules was 4 years in BSA, 5 years in PV and 2 years in BN. However, no significant differences were found in the mean age of females carrying egg capsules between populations (ANOVA, $F_{2,54} = 1.6$, $P = 0.22$ untransformed data).

The mean RE was significantly different among populations (ANOVA, $F_{2,130} = 5.8$, $P = 0.004$ arcsine-transformed data), PV females had the lowest RE (mean \pm SD, 0.08 ± 0.04) whereas BSA and BN females had a similar RE (0.20 ± 0.10 , 0.14 ± 0.08 , respectively).

Based on the growth model of females for each population previously published and the different estimates of maturity obtained in this study, a set of possible reaction norms are presented in Figure 5. Our results do not seem to support a single and parsimonious reaction norm for size and age at maturity in the three populations of *B. globulosus*. Even though females from BSA and PV showed different growth models, and have different mean sizes, they mature at the same age. The overall growth rate of BN is intermediate between PV and BSA but BN females attain maturity 2 years earlier than the other two populations.

DISCUSSION

We found that female size and age at maturity were variable and site-specific in *Buccinanops globulosus*; each population

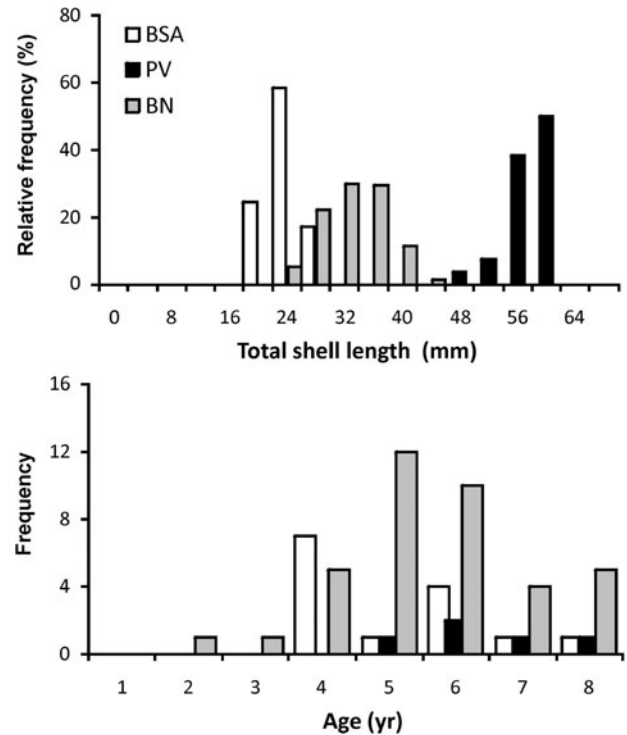


Fig. 4. Size (top) and age (bottom) distributions of *Buccinanops globulosus* females carrying egg capsules. BSA, Bahía San Antonio; PV, Playa Villarino; BN, Bahía Nueva.

has its own maturity pattern. Size at maturity estimates varied among populations, ranging from 19.4 mm (females at Bahía San Antonio) to 44.0 mm (females at Playa Villarino). Differences in age at maturity were also detected, females in the population with moderate growth mature at a younger age (2 years) than females in the rapid- and the slow-growing populations (4.3 and 4.6 years, respectively). The different estimators used in this study were useful to support these findings. The reproductive effort also varied between populations; it was lower in the population with relatively faster growth. The results obtained here are difficult to reconcile with a single reaction norm for a single genotype in the populations studied. The alternative explanations seem to be that two different genotypes or gene pools are present (probably Golfo San Matías (BSA + PV) vs Golfo Nuevo) or that there is a single genotype and we are observing its reactions norms to different environmental cues (e.g. food availability, exposure and water temperature).

Table 3. *Buccinanops globulosus*. Likelihood ratio tests for comparison of pairs of logistic parameters between populations. X_{50} , represent total shell length or age at which the 50% of the females in the population is mature; C, curve shape; Θ , vector of model parameters. **Highly significant differences.

Pairs of populations compared	$H_{01}: X_{50(1)} = X_{50(2)}$	$H_{02}: C_{(1)} = C_{(2)}$	$H_{03}: \Theta_{(1)} = \Theta_{(2)}$
Bahía San Antonio-Playa Villarino			
Size	222.23 (**)	0.68 (ns)	346.11 (**)
Age	51.76 (**)	51.76 (**)	1.91 (ns)
Bahía San Antonio-Bahía Nueva			
Size	25.21 (**)	24.46 (**)	36.19 (**)
Age	8.83 (**)	0.00 (ns)	12.26 (**)
Playa Villarino-Bahía Nueva			
Size	1082.70 (**)	187.86 (**)	89.71 (**)
Age	47.45 (**)	0.93 (ns)	16.71 (**)

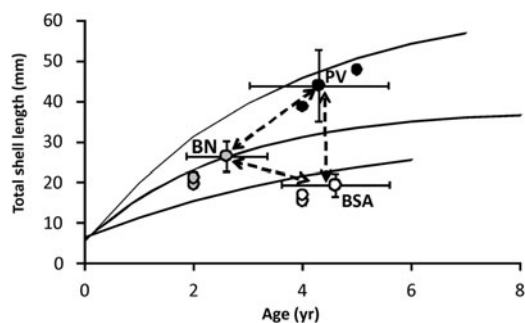


Fig. 5. Mean growth curves (solid lines) and three hypothetical reaction norms for size and age at female maturity (arrows) of *B. globulosus*. Symbols: different estimates of female maturity, including the minimum measures for which maturity was observed on gonadal samples, for which the 50% of the population sampled was sexually mature (TL_{50} , A_{50}) and the minimum size and age for females carrying egg capsules (see text). Bars indicate one SE. Females' von Bertalanffy growth models are presented in Table 1.

For the two neighbouring populations from Golfo San Matías, it seems clear that the reaction norm fits Stearn's rule 2, since they mature at the same age and in the slow-growing population (BSA), females sacrifice size at maturity and show a higher reproductive effort, probably due to the risk of never attaining maturity; in fact females of BSA never reach the PV size at maturity (44.0 mm) since their asymptotic size is 33.1 after c. 4 years of post-maturity growth. On the other hand, comparing BN and BSA, the females mature at almost the same size in both populations but in the faster-growing one (BN) they mature earlier than in BSA (2 years of age vs 4). This reaction norm seems to conform to Stearns' rule 1 in which slow-growing females prioritize fecundity at the cost of delayed maturity and of dying before reproduction. For the populations of PV and BN, females from BN mature earlier and at a lower size than those of PV. The earlier maturation of BN in terms of age and size only seems explainable in terms of a higher mortality risk in this location, which resulted in the evolution to a different optimum for these parameters (e.g. high predation). The earlier maturation entails a higher reproductive effort in this population, in which the weight of the egg capsules represents c. 14% of the female weight whereas it is around 8% in PV. This probably results in the stunted post-maturity growth observed in BN compared with the PV females. The onset of sexual maturity is accompanied by a cessation or decrease in growth in many species, for example *Nassarius reticulatus* (Tallmark, 1980; Barroso et al., 2005). In the context of life history theory, an increased reproductive effort and an earlier maturation are favoured when adult survival is low in relation to juvenile survival (Stearns, 1992; Hutchings, 1993).

The gonad maturity shows differences in the size range over which females mature among populations. Sizes at first maturity were about 16, 20 and 39 mm total shell length in BSA, BN and PV, respectively. The sizes at which 50% of the females are mature, are obviously larger (mentioned above). The lower size at maturity in *B. globulosus* from Bahía San Antonio may be the result of energy being allocated to other components of fitness (i.e. growth or survivorship) at the expense of reproduction. The reduction in reproductive allocation in favour of somatic allocation has been postulated to be adaptive for scavengers since they face periods of

starvation or low-food availability (Cheung & Lam, 1999). However, the females from the three populations do not mature before reaching 50% of maximum individual growth, thus suggesting the existence of a body size constraint to achieve successful reproduction (female asymptotic sizes; BSA: 33 PV: 65, BN: 38 mm; Narvarte et al., 2008; Avaca et al., 2013). In a review of abundant experimental data, Roff (2000) found that, typically, maturity is initiated when an individual exceeds a critical size during development, as seems to occur in this nassariid species. Positive relationships between body size and fitness, e.g. fecundity and mating success, occur across a variety of taxa (see Andersson, 1994). Our model species shows a positive correlation between the number of egg capsules as a proxy of fecundity and the typical body size (Narvarte et al., 2008; Avaca et al., 2012) of each population in line with these findings.

Females of *B. globulosus* attained sexual maturity at different ages, c. 2–5 years. Thus, it seems that each female is able to pass through a different number of reproductive seasons in its lifetime (8 years) depending on the population it belongs to. Among other neogastropods, reports on age at maturity are diverse: females of the red whelk *Neptunea antiqua* mature at 6–9 years and live up to 12 years, whereas *N. arthritica* mature at 4.6–6 years and live up to 10 years (Power & Keegan, 2001; Miranda et al., 2008). Several Volutid species with longer potential lifespan than *B. globulosus* were also studied in the Argentine Sea: *Adelomelon beckii* lives for 29 years and attains maturity at 14 years whereas *Adelomelon brasiliana*, *Zidona dufresnei* and *Odontocymbiola magellanica*, although having lifespans varying from 12 to 20 years, mature at about the same age, 7 to 8 years (Giménez & Penchaszadeh, 2003; Bigatti et al., 2008; Arrighetti & Penchaszadeh, 2010). For other species there are reports on size but not on age at maturity, for example females of *Buccinanops cochlidium* reach maturity at 80 mm and their maximum shell length is 108 mm (Averbuj et al., 2010).

Differences in size-age at maturity among marine gastropod populations are most likely related to local ecological conditions and not to latitudinal trends or the mode of development, e.g. direct or indirect development. For example, the direct-developer *Buccinum undatum* in the northern Gulf of St Lawrence reaches sexual maturity at 7–8 cm in shell length whereas in England at 5 cm and in Quebec at 6.0–6.5 cm (Martel et al., 1986; Gendron, 1992; Kideys et al., 1993). Moreover, differences in size at maturity may occur even at smaller scales such as among close populations of *B. undatum* located in the English coast (McIntyre et al., 2015). Regarding the age at maturity, *B. undatum* also showed marked differences among the Magdalen Islands and sites located in the northern part of the Gulf of St Lawrence (Gendron, 1992). Among indirect-developers species, abalone species (*Haliotis* spp.) exhibit different sizes at maturity both at small (1–1000 m) and large geographical scales (several km) (Prince, 2003 and references therein). On the other hand, despite differences among populations of the netted whelk *Nassarius reticulatus* (indirect-developer) in their maximum age and sizes, females reach maturity at about 4–5 years through Europe (Tallmark, 1980; Barroso et al., 2005).

Exposed sandy beaches and tidal flats represent a large proportion of open shores; the most noticeable feature of soft-sediment invertebrate communities is that individual abundances, biomass and species composition vary greatly with

both time and space (Lenihan & Micheli, 2001). Also, growth conditions for organisms may change along their distribution giving rise to different growth patterns. Empirical evidence suggests that low-stress environments may promote the rapid growth of individuals whereas in high-stress environments or when resources become limiting, individuals may benefit from growing more slowly (Monro & Marshall, 2014). Studies performed on other intertidal nassariids have related variation in different life history traits, including growth rates and size at maturity, with food availability, water temperature, exposure and predation pressure (e.g. McKillup & McKillup, 1997; Morton & Chan, 2004; Chatzinikolaou & Richardson, 2008). Our study system encompasses exposed sandy beaches (PV and BN) and a tidal flat (BSA). The whelks living in the tidal flat (slow growth) fed mainly on carcasses of crab species, *Cyrtograpsus angulatus* and *Neohelice granulata*, and the small mussel *Brachidontes rodriguezi* (Daleo *et al.*, 2005) which probably had a low nutritional value. Also at this site, the tidal amplitude (maximum tidal amplitude: 9.7 m) and the semidiurnal tidal regimes cause a prolonged exposure period for the individuals, about 4–5 h twice a day. These characteristics allow us to classify this site as high-stress for this whelk species. In contrast, whelks living in PV fed mainly on the venerid clam, *Amiantis purpurata* (personal observation) which may have high nutritional or energy value which supports the faster growth of this population, such as occurs with other venerid species (Cheung *et al.*, 2006). Also, at this beach, individuals are distributed from the intertidal to the low-subtidal zone, thus the exposure period for the individuals during the low tides is low or null. Thus, we can think of PV as a low-stress habitat for this whelk species that here shows a larger body size and size at maturity. Finally, the other beach (BN, moderate growth) probably represents a more stable environment than BSA with less exposure (maximum tidal amplitude: 6.1 m) but with a different thermal regime than the Golfo San Matías population (Avaca *et al.*, 2013). Although the causal mechanisms that determine patterns can only be detected by experimentation, our observational study based on abundant data may serve to propose those hypotheses that could be experimentally tested.

The results found in this study could be of potential interest for fishery management purposes. It has long been recognized that several life history traits of marine snails (e.g. slow growth rates, late maturity and low dispersal capability) make them prone to local extinction and overharvesting when fished (reviewed by Leiva & Castilla, 2002). To ensure that a proportion of the population could reproduce before recruitment into the fishery, the establishment of minimum legal sizes (MLS) above the size at sexual maturity has been recommended (e.g. Gendron, 1992; Shelmerdine *et al.*, 2007; Eversole *et al.*, 2008; Stoner *et al.*, 2012). Females have a major role in stock-recruitment relationships because of their higher reproductive potential compared with males (Valentinsson, 2002). Thus, management measures are mainly focused on female reproductive biology. The only commercial fishery developed on *B. globulosus* is located at Playa Villarino (Golfo San Matías), where the maximum shell sizes are reached. In light of our results, the MLS for that fishery should be 45 mm of total shell length. Preliminary results on male size-age at maturity indicated that male maturity is achieved at smaller size-age than females owing to their lower growth rates (Narvarte *et al.*, 2008; Avaca *et al.*, unpublished data). As the

maximum male shell length is 55 mm (Narvarte, 2006), the establishment of a safe MLS for the overall population (i.e. to also prevent the harvest of immature males) should be considered for management purposes. In this framework, other management actions should be proposed and further investigated to attain sustainability in the *B. globulosus* fishery (e.g. forbidding the collection of females carrying egg capsules, regulation of fishery licences, and establishment of no-take reserves in appropriate locations). Sizes at maturity of exploited resources may vary in time and space (e.g. Torroglosa & Giménez, 2010; McIntyre *et al.*, 2015), thus it is necessary to follow the performance of the established MLSs over time. Also, if new stocks of *B. globulosus* start being exploited the existence of differences among populations should be taken into account for the establishment of any management action.

Overall, our study shows that size-age at maturity patterns in this intertidal whelk with direct development are not solely explained by the variation in growth rates. Further research is needed to elucidate the underlying mechanisms (i.e. genetic or environmental) of the variation observed, and their possible consequences on the evolutionary biology of this species with direct development and under fishing pressure.

ACKNOWLEDGEMENTS

We thank 'Kelo' Camarero for technical support in the field and Roxana Soler for histological assistance.

FINANCIAL SUPPORT

This work was partially supported by the following projects financed by the Agencia Nacional de Promoción Científica y Tecnológica (ANPCyT): PID #371 and PICT CONAE-CONICET #042010. The authors are members of CONICET.

REFERENCES

- Andersson M. (1994) *Sexual selection*. Princeton, NJ: Princeton University Press.
- Arrighetti F. and Penchaszadeh P.E. (2010) Size and age at first sexual maturity of the edible giant snail *Adelomelon beckii* (Neogastropoda: Volutidae) from Mar Del Plata, Argentina. *Malacologia* 53, 193–197.
- Aubone A. and Wöhler O.C. (2000) Aplicación del método de máxima verosimilitud a la estimación de parámetros y comparación de curvas de crecimiento de von Bertalanffy. Instituto Nacional de Investigación y Desarrollo Pesquero Informe Técnico 37, Mar del Plata.
- Avaca M.S., Martín P.R., van der Molen S. and Narvarte M.A. (2015) Comparative study of the female gametogenic cycle in three populations of *Buccinanops globulosus* (Caenogastropoda: Nassariidae) from Patagonia. *Helgoland Marine Research* 69, 87–99. doi: 10.1007/s10152-014-0418.
- Avaca M.S., Narvarte M.A. and Martín P.R. (2012) Size assortative mating and effect of female size on reproductive output of the nassariid *Buccinanops globulosus*. *Journal of Sea Research* 69, 16–22.
- Avaca M.S., Narvarte M.A. and Martín P.R. (2013) Age, growth and mortality in *Buccinanops globulosus* (Gastropoda: Nassariidae) from Golfo Nuevo (Argentina). *Marine Biology Research* 9, 208–219.

- Averbuj A., Bigatti G. and Penchaszadeh P. (2010) Gametogenic cycle and size at first maturity of the Patagonic edible snail *Buccinanops cochlidium* from Argentina. *Marine Biology* 157, 2229–2240.
- Averbuj A., Rocha M. and Zabala S. (2014) Embryonic development and reproductive seasonality of *Buccinanops globulosus* (Nassariidae) (Kiener, 1834) in Patagonia. *Invertebrate Reproduction and Development* 58, 138–147.
- Barroso C.M., Moreira M.H. and Richardson C.A. (2005) Age and growth of *Nassarius reticulatus* in the Ria de Aveiro, north-west Portugal. *Journal of the Marine Biological Association of the United Kingdom* 85, 151–156.
- Bigatti G. and Penchaszadeh P. (2008) Seasonal reproduction and sexual maturity in *Odontocymbiola magellanica* (Neogastropoda, Volutidae). *Invertebrate Biology* 127, 314–326.
- Bigatti G., Marzinelli E.M. and Penchaszadeh P.E. (2008) Seasonal reproduction and sexual maturity in *Odontocymbiola magellanica* (Neogastropoda, Volutidae). *Invertebrate Biology* 127, 314–326.
- Bigatti G., Primost M.A., Cledón M., Averbuj A., Theobald N., Gerwinski W., Arntz W., Morriconi E. and Penchaszadeh P.E. (2009) Biomonitoring of TBT contamination and imposex incidence along 4700 km of Argentinean shoreline (SW Atlantic: From 38S to 54S). *Marine Pollution Bulletin* 58, 695–701.
- Cerrato R.M. (1990) Interpretable statistical tests for growth comparisons using parameters in the von Bertalanffy equation. *Canadian Journal of Fisheries and Aquatic Sciences* 47, 1416–1426.
- Chatzinikolaou E. and Richardson C.A. (2008) Population dynamics and growth of *Nassarius reticulatus* (Gastropoda: Nassariidae) in Rhosneigr (Anglesey, UK). *Marine Biology* 153, 605–619.
- Cheung S.G., Gao Q.F. and Shin S.P.K. (2006) Energy maximization by selective feeding on tissues of the venerid clam *Marcia hiantina* in the marine scavenger *Nassarius festivus* (Gastropoda: Nassariidae). *Marine Biology* 149, 247–255.
- Cheung S.G. and Lam S. (1999) Effect of food availability on egg production and packaging in the intertidal scavenging gastropod *Nassarius festivus*. *Marine Biology* 135, 281–287.
- Daleo P., Alberti J., Avaca M.S., Narvarte M.A., Martinetto P. and Iribarne O. (2012) Avoidance of feeding opportunities by the whelk *Buccinanops globulosum* in the presence of damaged conspecifics. *Marine Biology* 159, 2359–2365.
- Daleo P., Escapa M., Isaacch J.P., Ribeiro P. and Iribarne O. (2005) Trophic facilitation by the oystercatcher *Haematopus palliatus* Temminck on the scavenger snail *Buccinanops globulosum* Kiener in a Patagonian bay. *Journal of Experimental Marine Biology and Ecology* 325, 27–34.
- Dmitriew C.M. (2011) The evolution of growth trajectories: what limits growth rate? *Biological Reviews* 86, 97–116.
- Eversole A.G., Anderson W.D. and Isely J.J. (2008) Age and growth of the knobbed whelk *Busycon carica* (Gmelin 1791) in South Carolina subtidal waters. *Journal of Shellfish Research* 27, 423–426.
- Gendron L. (1992) Determination of the size at sexual maturity of the waved whelk *Buccinum undatum* Linnaeus, 1758, in the Gulf of St. Lawrence, as a basis for the establishment of a minimum catchable size. *Journal of Shellfish Research* 11, 1–7.
- Giménez J. and Penchaszadeh P.E. (2003) Size at first sexual maturity in *Zidona dufresnei* (Caenogastropoda: Volutidae) of the Southwestern Atlantic Ocean (Mar del Plata, Argentina). *Journal of the Marine Biological Association of the United Kingdom* 83, 293–296.
- Gosselin L.A. and Qian P.Y. (1997) Juvenile mortality in benthic marine invertebrates. *Marine Ecology Progress Series* 146, 265–282.
- Hughes R.N. and Roberts D.J. (1980) Reproductive effort of winkles (*Littorina* spp.) with contrasted methods of reproduction. *Oecologia* 47, 130–136.
- Hutchings J.A. (1993) Adaptive life histories effected by age-specific survival and growth rate. *Ecology* 74, 676–684.
- Kideys A.E., Nash R.D.M. and Hartnoll R.G. (1993) Reproductive cycle and energetic cost of reproduction of the neogastropod *Buccinum undatum* in the Irish Sea. *Journal of the Marine Biological Association of the United Kingdom* 73, 391–403.
- Leiva G. and Castilla J.C. (2002) A review of the world marine gastropod fishery: evolution of catches, management and the Chilean experience. *Reviews in Fish Biology and Fisheries* 11, 283–300.
- Lenihan H.S. and Micheli F. (2001) Soft-sediment communities. In Bertness M.D., Gaines S.D. and Hay M.E. (eds) *Marine community ecology*. Sunderland, MA: Sinauer Associates, pp. 253–287.
- Martel A., Larriveé D.H. and Himmelman J.H. (1986) Reproductive cycle and seasonal feeding activity of the neogastropod *Buccinum undatum*. *Marine Biology* 92, 211–221.
- McIntyre R., Lawler A. and Masefield R. (2015) Size of maturity of the common whelk, *Buccinum undatum*: is the minimum landing size in England too low? *Fisheries Research* 162, 53–57.
- McKillup S.C. and McKillup R.V. (1997) Effect of food supplementation on the growth of an intertidal scavenger. *Marine Ecology Progress Series* 148, 109–114.
- Miranda R.M., Fujinaga K. and Nakao S. (2008) Age and growth of *Neptunea arthritica* estimated from growth marks in the operculum. *Marine Biology Research* 4, 224–235.
- Monro K. and Marshall D.J. (2014) Faster is not always better: selection on growth rate fluctuates across life history. *American Naturalist* 183, 798–809.
- Morton B. and Chan K. (2004) The population dynamics of *Nassarius festivus* (Gastropoda: Nassariidae) on three environmentally different beaches in Hong Kong. *Journal of Molluscan Studies* 70, 329–339.
- 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.
- Narvarte M.A., Willers V., Avaca M.S. and Echave M.E. (2008) Population structure of the snail *Buccinanops globulosum* (Prosobranchia, Nassariidae) in San Matías Gulf, Patagonia Argentina: isolated enclaves? *Journal of Sea Research* 60, 144–150.
- Pastorino G. (1993) The taxonomic status of *Buccinanops* d'Orbigny, 1841 (Gastropoda: Nassariidae). *The Veliger* 36, 160–165.
- Perron F.E. (1982) Inter- and intraspecific patterns of reproductive effort in four species of cone shells (*Conus* spp.). *Marine Biology* 68, 161–167.
- Power A.J. and Keegan B.F. (2001) Seasonal patterns in the reproductive activity of the red whelk, *Neptunea antiqua* (Mollusca: Prosobranchia) in the Irish Sea. *Journal of the Marine Biological Association of the United Kingdom* 81, 243–250.
- Prince J. (2003) The barefoot ecologist goes fishing. *Fish and Fisheries* 4, 359–371.
- Roff D.A. (2000) Trade-offs between growth and reproduction: an analysis of the quantitative genetic evidence. *Journal of Evolutionary Biology* 13, 434–445.
- Schlichting C.D. and Pigliucci M. (1998) *Phenotypic evolution: a reaction norm perspective*. Sunderland, MA: Sinauer Associates.
- Shelmerdine R.L., Adamson J., Laurenson C.H. and Leslie B. (2007) Size variation of the common whelk, *Buccinum undatum*, over large and

small spatial scales: potential implications for micro-management within the fishery. *Fisheries Research* 86, 201–206.

Stearns S.C. (1992) *The evolution of life histories*. New York, NY: Oxford University Press.

Stoner A.W., Mueller K.W., Brown-Peterson N.J., Davise M.H. and Booker C.J. (2012) Maturation and age in queen conch (*Strombus gigas*): urgent need for changes in harvest criteria. *Fisheries Research* 131, 76–84.

Tallmark B. (1980) Population dynamics of *Nassarius reticulatus* (Gastropoda, Prosobranchia) in Gullmar Fjord, Sweden. *Marine Ecology Progress Series* 3, 51–62.

Torroglosa E.M. & Giménez J. (2010) Temporal variation in size at maturity of the snail *Zidona dufresnei* from the southwestern

Atlantic Ocean after ten years of fishery exploitation. *Aquatic Biology* 11, 163–167.

and

Valentinsson D. (2002) Reproductive cycle and maternal effects on offspring size and number in the neogastropod *Buccinum undatum* (L.). *Marine Biology* 140, 1139–1147.

Correspondence should be addressed to:

M.S. Avaca
Instituto de Biología Marina y Pesquera Almirante Storni,
Escuela Superior de Ciencias Marinas, Universidad Nacional
del Comahue, Güemes 1030, 8520 San Antonio Oeste, Río
Negro, Argentina
email: msavaca@yahoo.com.ar