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CONTENTS

*Research papers*

The effect of *Fucus vesiculosus* on the grazing of harpacticoid copepods on diatom biofilms  
M. De Troch, V.A. Chapurnov, M. Vinck and E. Orlanson ..... 139

Population structure of the small Buccinorhynchus gibbulosum (Prosobranchia, Nassariidae) in San Matias Gulf, Patagonia Argentina: Isolated enclaves?  
M. Narvarte, V. Willers, M.S. Avaca and M.E. Echave ..... 144

Influence of environment factors on bacterial ingestion rate of the deposit-feeder Hydrobia ulvae and comparison with meiobenthos  
P.-Y. Pascal, C. Dupuy, F. Richard, A. G. Haubois and N. Niquil ..... 151

Larviparity in native bivalves and an introduced oyster  
K. Troost, P. Kamermans and W.J. Wolff ..... 157

Structure of a northwest Atlantic Shelf macrofaunal assemblage with respect to seasonal variation in sediment nutritional quality  
E.J. Weisberger, P.A. Jumars, L.M. Mayer and L.L. Schick ..... 164

Active and passive migration in boring isopods Limnoria spp. (Crustacea, Peracarida) from kelp holdfasts  
L. Miranda and M. Thiel ..... 176

Inter- and intra-specific competition between Paracentrotus lividus and Arthacia lixula in resource-limited barren areas  
D. Privitera, M. Chiarone, L. Mangialajo, N. Glavic, W. Kozul and R. Cattaneo-Viati ..... 184

Comparison between disturbed and undisturbed areas of the Patagonian scallop (Zygochlamys patagonica) fishing ground "Reclutas" in the Argentine Sea  
L. Schjeller, C.S. Brimec and D. Hernández ..... 193

The effects of environmental factors on daytime sandeel distribution and abundance on the Dogger Bank  
J. van der Kooij, B.E. Scott and S. Mackinson ..... 201

Retrospective quantification of estuarine feeding activity by coastally caught marine fishes  
C.D.B. Leakey, M.J. Astrill, S. Jennings and M.F. Fitzsimons ..... 210

*Short communications*

Biometrics in Laminaria digitata: A useful tool to assess biomass, carbon and nitrogen contents  
F. Gevaert, M.-A. Janquin and D. Davoult ..... 215

Mass mussel mortality in The Netherlands after a bloom of Phaeocystis globosa (pyrenoidophyceae)  
L. Papierzak and M. Poelman ..... 220

The relationship between hatching rate and number of embryos of the brood pouch in Littorina saxatilis  
P. Conde-Padin, M. Carballo, A. Caballero and E. Rolán-Alvarez ..... 223

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## Population structure of the snail *Buccinanops globulosum* (Prosobranchia, Nassariidae) in San Matías Gulf, Patagonia Argentina: Isolated enclaves?

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### ABSTRACT

In San Matías Gulf (Patagonia, Argentina), *Buccinanops globulosum* is typically distributed in two different areas: the intertidal–subtidal zone of Playa Villarino, where conch length reaches up to 60 mm, and the inner channel of San Antonio Bay, where individuals are not larger than 30 mm. It is suggested that both populations of *B. globulosum* constitute independent enclaves adapted to the local conditions and with a different population structure. This comparative study focuses on the population structure, sex ratios, growth, and size at maturity at the two sites.

The data collected reveal that the individuals in San Antonio ranged from 5 to 29 mm whereas those in Villarino ranged from 4 to 61 mm. It was also observed that in San Antonio Bay, generally males outnumbered females whereas exactly the opposite occurred in Villarino. In addition, females were larger and showed a faster growth than males in both study areas. The number of egg capsules on each female ranged from 8 to 25 in San Antonio Bay and from 5 to 66 in Villarino. Size at maturity of females in San Antonio Bay was estimated at 14.47 mm and maximum estimated length at 6 years old was 33 mm. The same parameters in the individuals from Villarino were 45 and 65 mm, respectively. The comparative analysis of the above-mentioned features poses the question of whether these two populations represent either different species or different forms of the same species.

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### 1. Introduction

*Buccinanops globulosum* (Kiener, 1834) is an endemic nassariid gastropod from the Southwestern Atlantic Ocean. It is typically found in coastal waters at depths of up to 10 m (Scarabino, 1977; Pastorino, 1993) in an area extending from Uruguay (34°S) to Santa Cruz Province (48°S), in Patagonia, Argentina (Castellanos, 1967; Scarabino, 1977). In very shallow waters, the species occurs mainly on either sandy mud or seagrass bottoms. *B. globulosum* is necrophagous and it feeds mainly on crabs and molluscs. The life history of *B. globulosum* goes by larval stages (trochophore and veliger) inside the egg capsule (Penchaszadeh, 1971) restricting larval dispersal. Due to this developmental strategy, snail populations show limited spatial distribution and they may therefore form isolated enclaves (Berryman, 2003).

In San Matías Gulf, *B. globulosum* is typically found at a depth ranging between 4 and 10 m in two different areas: the intertidal–low subtidal zone of Playa Villarino on the northern coast, and the inner channel of San Antonio Bay in the NW of the gulf. In Villarino, individual conch

length reaches up to 60 mm (Narvarte, 2006) whereas in San Antonio Bay conch length is not larger than 30 mm (Narvarte et al., unpub. data). No connectivity has been observed between these enclaves (pers obs). *B. globulosum* forms dense populations constituting an important link in the estuarine food web and ecosystem dynamics (Scarabino, 1977; Daleo et al., 2006). Since 2000, it was incorporated as an incipient fishery resource (Narvarte, 2006). However, and in spite of the role recognized for *B. globulosum* in the scarce literature available, little is known about their essential life history features, population dynamics and inter and intraspecific variability along its entire distribution.

The purpose of this study is to describe the population structure of *B. globulosum*, as well as to compare the growth parameters, morphometric relationships, size at maturity, and sex ratio of this species in San Antonio Bay and Villarino.

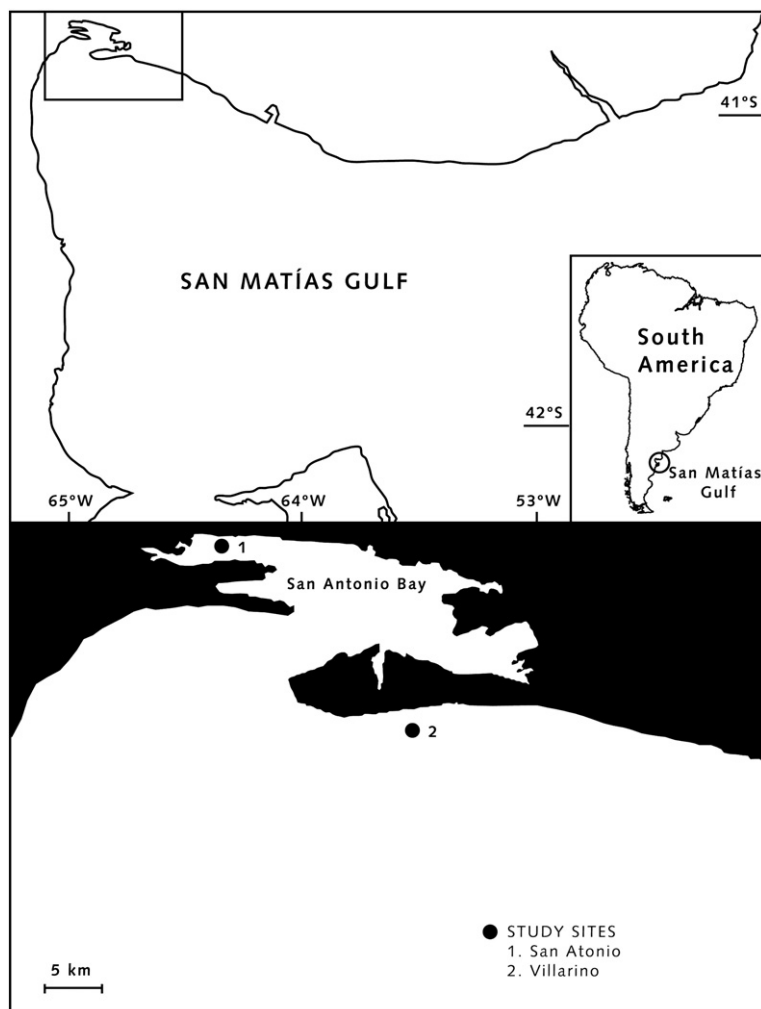
We hypothesize that due to the absence of larval dispersal, and the sedentary behaviour of the species, populations from San Antonio Bay and Villarino constitute independent enclaves characterized by a different population structure.

### 2. Materials and methods

San Antonio Bay (40°45'S/64°56'W) (Fig. 1) is about 80 km<sup>2</sup> area. It has a semidiurnal tidal regime, with a range variable from 6 to 9 m and a

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**Fig. 1.** Map of San Matías Gulf showing the study area and the sampling locations in San Antonio Bay and Villarino. The 50 km distance mentioned in the text does not consider physical barriers.

maximum depth of 4 m at low tide. It is a dry area, with no freshwater input, except for the drainage resulting from scarce rainfall and with winds which are predominantly from the northwest. In addition, atmospheric conditions play an important role in this site (Rivas, 1990, 1994). Air temperature generally varies from 6 (in July) to 30 °C (in January–February) and, due to the high evaporation mechanisms, salinity is usually higher than in the neighboring areas (34–39 ppt) (Piola and Scasso, 1988). Small pebbles alternating with sand flats and large mussel beds of *Brachydontes rodriguezii* constitute the bottom in this area. In response to the nutrient release into the bay, massive macroalgal blooms of *Ulva lactuca* have been regularly observed in the inner channel throughout the last decade (Piriz et al., 2004). Both San Antonio Bay and the surrounding areas constitute an important bird conservation site, and they form part of the Western Hemisphere Shorebird Reserve Network International (WHSRNI; González et al., 1996). *B. globulosum*, the burrowing crab *Neohelice* (= *Chasmagnathus*) *granulata*, and the mud crab *Cyrtograpsus angulatus* are the main scavengers of this marine ecosystem in San Antonio Bay (Bas et al., 2005). This area has an active fishery port and nautical activities.

Villarino is a subtidal area with a depth ranging from 4 to 10 m and a semidiurnal tidal regime ranging between 7 and 9.2 m. It is located in the northern coast of the gulf (40° 45'S/64° 30'W; Fig. 1), at 50 km from the inner channel of San Antonio Bay. The bottom in this area is mainly composed of fine sand (Morsan, 2003). Water temperature varies seasonally from 7 °C in July to 20 °C in January. At this subtidal

site, *B. globulosum* lives together with the clam *Amiantis purpurata* (Morsan, 2003; Morsan and Orensanz, 2004; Narvarte, 2006), the dominant species in Villarino.

### 2.1. Sampling methods

A monthly sampling program was carried out during low tide from December 2001 to February 2003. Biological bait (injured crabs, discarded fish and newly opened clams) was used to attract snails on the seabed. This method allowed catching individuals of both sexes and all size classes present in the neighbor area (SCUBA diving personal observations). Once in the laboratory, total shell length (TL, mm) and maximum shell width (TW, mm) were measured with Vernier calipers ( $\pm 0.01$  mm), and total wet body weight (BW, g) was recorded with an Ohaus® electric balance ( $\pm 0.01$  g). The presence of a penis was a determining factor to distinguish males from females. Due to organotin pollution (TBT) and the existence of imposex in the snails from San Antonio Bay (Willers, 2004), it was also necessary to identify the albumen-capsule gland in females. When present, the numbers of egg capsules on the shell callus of the female were counted.

### 2.2. Morphometric relationships and sex ratios

A total of 4272 snails from the San Antonio Bay subpopulation and 6405 from Villarino were measured. At least 300 individuals from

each site per season (Summer: Dec–Feb; Autumn: Mar–May; Winter: Jun–Aug; Spring: Sep–Nov; Summer: Dec–Feb) were taken into account for the construction of the TL frequency data distributions. The resulting frequencies were subsequently compared by site and sex using Kolmogorov–Smirnov tests. Morphometric relationships between TL and TW, and TL versus BW were studied using correlation analysis on log-transformed data.

The opercula in good condition were kept for growth studies (described below).

Sex ratios were estimated for each sampling trip of the year and were compared by a goodness of fit test. The null hypothesis of no differences between sexes was tested. A 0.05 significance level was taken into account in all the statistical tests applied in this study.

Size at maturity for both populations was identified as the size of the smaller females carrying egg capsules.

### 2.3. Estimation of growth

The number of operculum rings of the individuals at each site was counted under a binocular stereoscopic microscope (according to

Kideys, 1996; Narvarte, 2006). Most of the opercula were found damaged and therefore only those in very good condition were taken into account. The dark and clear rings of each operculum on the ventral face were counted from the nucleus (the operculum of the crawling juvenile) to the posterior border. In order to validate the periodicity of rings deposition, the final portion of each operculum was observed and classified as either “dark” (newly-formed ring) or “clear” (irregular edge). The frequencies corresponding to both types were recorded on a sample of at least 30 individuals per month over a year. Age determination data were used to fit the von Bertalanffy growth function:

$$TL_t = TL_\infty (1 - e^{-k(t-t_0)})$$

where  $TL_t$  is the shell length at age  $t$ ,  $TL_\infty$  is the asymptotic total length (mm),  $k$  is the curvature parameter, and  $t_0$  is the estimated age at length zero. The model was fitted using the generalized least square method and parameters ( $TL_\infty$ ,  $k$ , and  $t_0$ ) were estimated following the maximum likelihood method (Kimura, 1980; Cerrato, 1990). Comparisons of parameters of the growth curves between sites and sexes

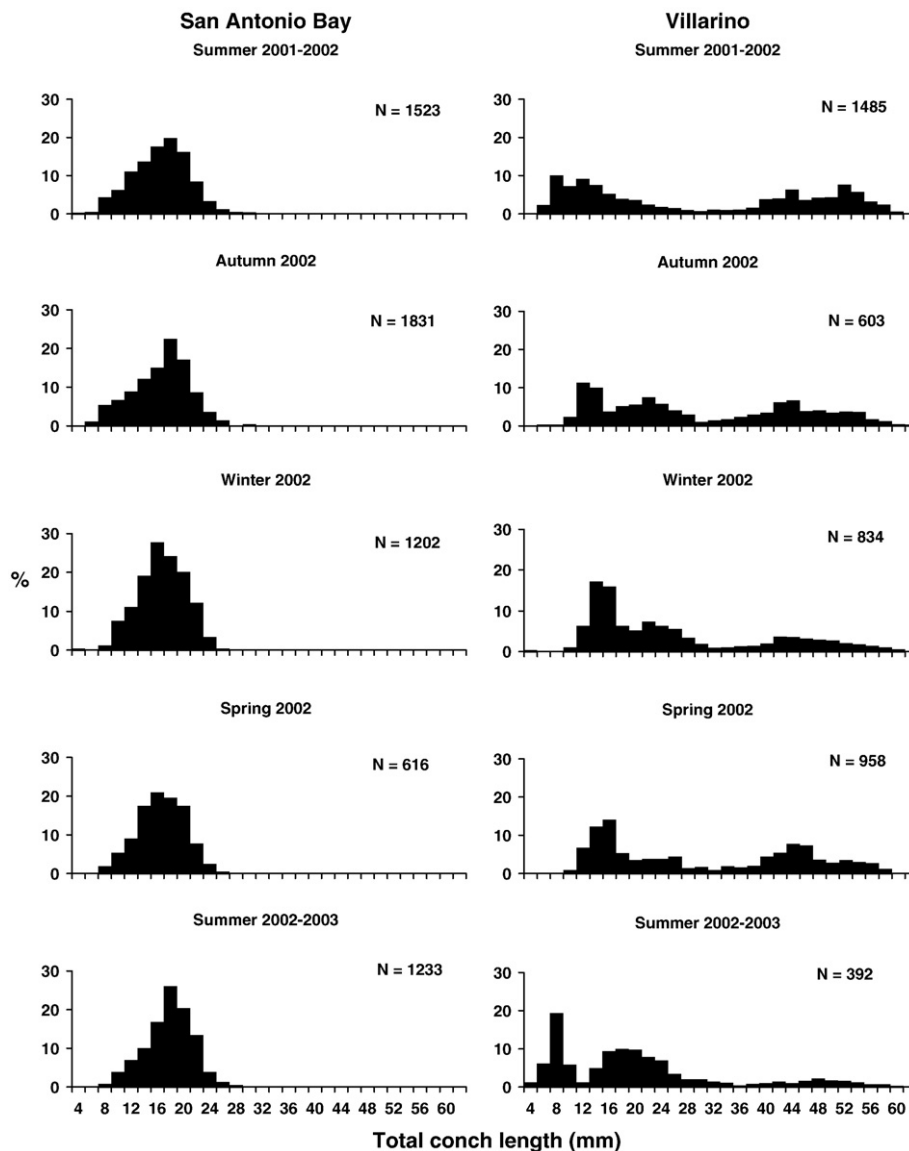


Fig. 2. Seasonal distributions of shell length frequencies for males and females of *B. globulosum* from 2001 to 2003. (Summer: December–February; Autumn: March–May; Winter: June–August; Spring: September–November).

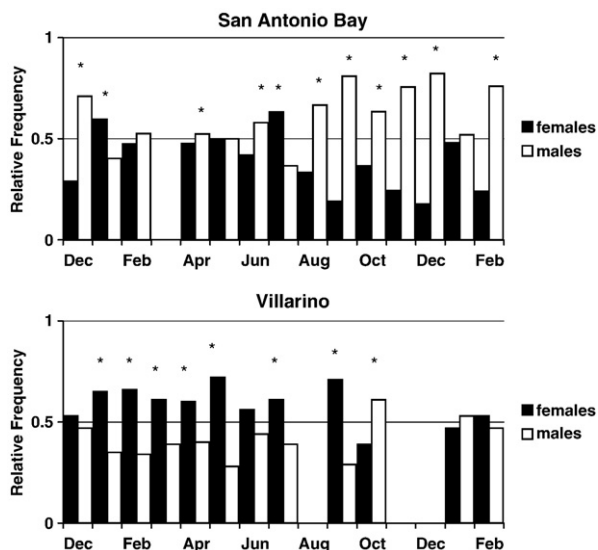


Fig. 3. Sex ratio of *B. globulosum* in San Antonio Bay and Villarino (\* indicate statistical differences performing  $\chi^2$  tests; San Antonio Bay (SAB) df: 29–257; Villarino df: 198–296).

were made by means of a likelihood ratio test (Cerrato, 1990; Narvarte, 2006). An algorithm created in a common worksheet using the Excel Program (Microsoft®) was used to process the data collected.

$TL_{\infty}$  and  $k$  (the annual growth constant) are not independent from each other. Several combinations of both parameters could be obtained in order to compare adaptations to local conditions for different populations of the same species. Pauly and Munro (1984) have developed the index  $\Phi$  ( $\log(k) + 2 \log(TL_{\infty})$ ) as a new parameter, which integrates  $TL_{\infty}$  and  $k$  and which can be used as a unique indicator of the overall growth performance by sex and population.

### 3. Results

#### 3.1. Population structure

Based on the length frequency distribution obtained, two modes could be clearly observed in Villarino whereas only one mode was observed in San Antonio Bay (Fig. 2). The null hypothesis of no differences in the length frequency distribution between sites was rejected for all the pair comparisons ( $P < 0.05$ ; Summer 2001–2002:  $D = 0.48$ ; Autumn:  $D = 0.51$ ; Winter:  $D = 0.40$ ; Spring:  $D = 0.53$ ; Summer 2002–2003:  $D = 0.27$ ). In Villarino, TL of individuals ranged from 4.2 to 60.9 mm whereas TW ranged between 0.58 and 58.73 g. Only individuals larger than 20 mm could be sexed. In San Antonio Bay, TL ranged from 5.24 to 28.97 mm and TW ranged between 0.55 and 4.74 g (Fig. 2). The individuals whose TL was smaller than 13 mm could not be sexed. Length frequency distributions had a narrow range of lengths and animals larger than 30 mm were absent.

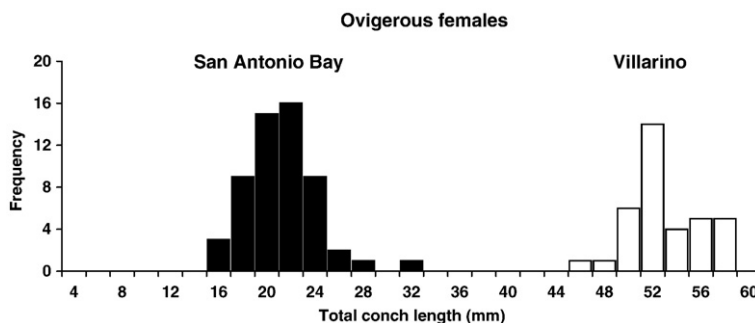


Fig. 4. Sizes of females carrying egg capsules at San Antonio Bay and Villarino.

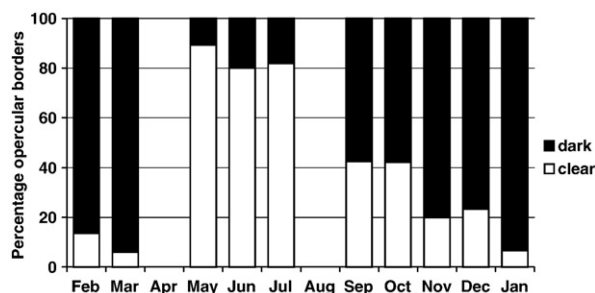


Fig. 5. Frequencies of dark ring and clear edge of the opercula analyzed for age determination.

Correlations between TL, TW and BW for both sexes and sites were significant ( $r^2 > 0.88$ ). TL frequency data distributions were significantly different between sexes ( $P < 0.05$ ; San Antonio Bay:  $D = 0.17$ ; Villarino:  $D = 0.34$ ). At both study sites, females were found to be larger than males.

#### 3.2. Sex ratios

In San Antonio Bay, the sex ratio was significantly different from 1:1 and in almost all months surveyed males significantly outnumbered females ( $P < 0.05$ ; Fig. 3). Exceptions were observed in February, May and January 2003. In Villarino, the opposite pattern was detected, i.e. the number of females was higher than the number of males ( $P < 0.05$ ) (Fig. 3); no differences were found in December 2001, June 2002 and January–February 2003.

#### 3.3. Size at maturity

In San Antonio Bay, the smallest females carrying egg capsules were 14.47 mm TL ( $n = 56$ ) (Fig. 4). The number of egg capsules per female ranged from 1 to 25. From October 2002 to January 2003, females were found carrying egg capsules. The smallest females carrying egg capsules in Villarino were 45 mm TL and the number of capsules per female varied between 2 and 66. Significant differences in the number of capsules per female were found between sites ( $t_{75} = 4.5$ ;  $P < 0.001$ ).

#### 3.4. Growth

Correlations between TL and operculum length (OL) for both sexes and sites were significant ( $r^2 > 0.93$ ;  $n$  San Antonio Bay = 329;  $n$  Villarino = 450). The plot of frequencies corresponding to the opercula with dark rings in San Antonio Bay (Fig. 5) revealed that a dark ring forms annually, i.e. the presence of each pair of borders (clear+dark) represents 1 year of growth. The highest number of rings was six in San Antonio Bay and seven in Villarino.

A total of 329 measurements (174 from females and 155 from males) were taken into account for the estimation of the growth



**Table 1**  
Growth parameters (von Bertalanffy model) estimated for both sites and sexes of *B. globulosum* based on operculum striae

	<i>k</i>	$TL_{\infty}$	$t_0$	<i>N</i>	$\Phi$
<i>San Antonio Bay</i>					
Females	0.21	33.1	-1.03	174	2.365
Males	0.31	24.8	-1.03	155	2.277
Overall	0.22	30.8	-1.03	329	2.320
<i>Villarino*</i>					
Females	0.28	65.4	-0.30	263	3.128
Males	0.46	48.6	-0.30	187	3.112
Overall	0.49	51.6	-0.30	450	3.115

\* *k*,  $TL_{\infty}$  and  $t_0$  taken from Narvarte (2006).  $\Phi$  is the index developed by Pauly and Munro (1984) which integrates  $TL_{\infty}$  and *k* to allow comparisons of the overall growth pattern using  $\Phi = \log(k) + 2 \log(TL_{\infty})$ .

parameters in individuals from San Antonio Bay whereas a total of 450 individuals (263 females and 187 males) were considered for the Villarino population (Table 1; Fig. 6). Overall growth (defined by parameter  $\Phi$ ) was higher in Villarino ( $\Phi=3.115$ ) than in San Antonio Bay ( $\Phi=2.320$ ). Significant differences of parameters *k*,  $TL_{\infty}$  and  $t_0$  were found between sites ( $\chi^2=888$ ;  $df=3$ ;  $P<0.0001$ ).

Taking into account the growth curve obtained in both sites and the logistic curve for the estimation of length at first maturity, it can be concluded that age at first maturity for females of *B. globulosum* is approximately 2 years in San Antonio Bay and 4 years in Villarino.

#### 4. Discussion

Findings from the present research indicate that the snails of *B. globulosum* from San Antonio Bay and Villarino form independent enclaves characterized by a different population structure:

##### 4.1. Frequency distributions

The length frequency histograms of whelks in Villarino indicate the presence of two main modes or size groups, one approximately 10–28 mm and another ranging from 40 to 62 mm, with a notorious *hiatus* between them. Almost all along the study conducted in San Antonio Bay, the length frequency histograms showed the presence of only one mode which was approximately 16–22 mm. Different processes could be responsible for the skewness observed towards the left of the frequency distributions in San Antonio Bay (Fig. 3).

Firstly, stunting, which is common in gastropod populations (Mouritsen et al., 1999; Robson et al., 2005), may result from dense nursery concentrations of animals having insufficient resources for a faster growth (Fahy et al., 1995). Even when in San Antonio Bay *B. globulosum* is subsidized by the oystercatcher *Haematopus palliatus* preying on crabs, carrion availability is ephemeral and unpredictable (Daleo et al., 2006). Dead crabs are rapidly detected and consumed by

snails. Then, small-sized individuals keep buried within the sediment for almost all the time and the possibility of finding food is restricted to the uncertain availability of dead organisms (Martel et al., 1986; Chen and Richardson, 1987).

Secondly, food quality within San Antonio Bay could be lower than in Villarino. Several studies on intertidal organisms indicate that growth rate declines in an upshore direction apparently because time available for feeding is limited (Vermeij, 1972; McCormack, 1982; McQuaid, 1982; Chapman, 1994) and this could be the case of *B. globulosum* in San Antonio Bay. The differences in the adult size in both study areas could be due to the higher availability of food in the low subtidal zone of Villarino, where there is a unique population of the clam *A. purpurata* (the dominant species in this fine sandy habitat), whose adult density is the highest along its distributional range (up to 240 clams  $m^{-2}$ ; Morsan, 2003). The maximum yield per recruit was registered more than 10 years ago. At present clams are therefore approximately 26 years old and they maintain their biomass. They stop growing as they have reached the maximum age/size relationship. Although clams show a very low mortality rate (Morsan and Orensanz, 2004) at these densities, a high number of them may die at the bottom and they could be scavenged by snails as observed by fishermen operating in this area. In fact, newly open clams are used as bait by fishermen to catch these whelks (Narvarte, 2006).

Synergistic effects related to the combination of the previous causes may also explain the observed pattern.

##### 4.2. Sex ratios

Each population had a singular pattern of sex ratios. In most months of the present study, males dominated the samples in San Antonio Bay while in Villarino they constitute the minor fraction.

The phenomena that could explain this variation is *imposex* (Bryan et al., 1987). This factor affected between 21 and 71% of the females in the population of San Antonio Bay (Willers, 2004). Areas having little or no imposex tend to have a higher female:male sex ratio (Nicholson and Evans, 1997). Interestingly, in the population of Villarino, where imposex was not recorded, the sex ratio was favourable for females.

##### 4.3. Growth rates

In Villarino, it was observed that *B. globulosum* reaches  $TL_{\infty}$  values ranging between 48 (males) and 65 mm (females) (Narvarte, 2006). Compared to these values, the growth pattern found in the population of San Antonio Bay was characterized by a lower  $TL_{\infty}$  (25 and 33 mm, for males and females, respectively).

Among the snails whose population dynamics has been studied, *Buccinum undatum* seems to be similar to *B. globulosum*, and both are phylogenetically related (Ponder and Lindberg, 1997). Kideys (1993) estimated growth parameters in *B. undatum* using a variety of methods and observed that  $TL_{\infty}$  ranged between 123.7 and 125.0 mm

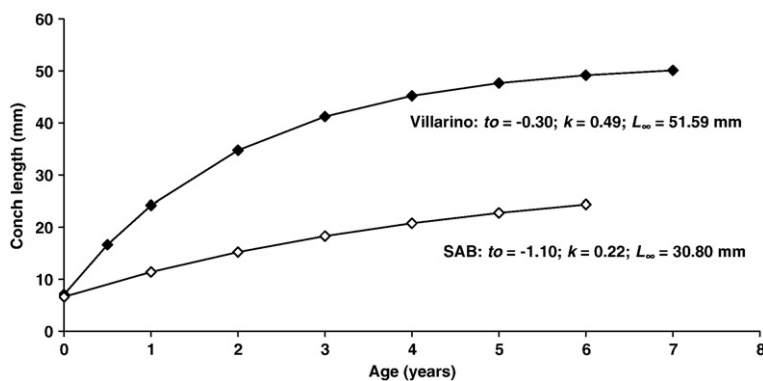


Fig. 6. Fitted growth curves constructed for the subpopulations of San Antonio Bay (SAB) and Villarino.

and that  $k$  values ranged between 0.20 and 0.22 in whelk populations close to the Isle of Man. In a study regarding the same species on the Normandy coast of France, Santarelli and Gros (1984) provided  $TL_{\infty}$  values ranging from 85.5 to 139.5 mm and  $k$  values of 0.071–0.180. Shelmerdine et al. (2007) found similar geographical variation in the size, age and estimated growth rates of *B. undatum* at a small geographic scale.

Phillips et al. (1973) carried out laboratory experiments showing that temperature and food have a significant impact on shell forms, growth rate, and sculpture in Australian thaidids. These factors have been shown to control growth rate in other gastropods (Duda and Palumbi, 1999).

#### 4.4. Sexual maturity

Sexual maturity was found to occur at a smaller size and apparently at an earlier age in the individuals from San Antonio Bay with respect to those from Villarino. These differences in size and age at maturity between the populations of *B. globulosum* in the two study areas might be linked to predation pressure and food availability in each benthic assemblage. It is known that investment in reproductive activity can reduce growth and that larger organisms usually avoid predation better than smaller organisms (Stearns, 1992). This fact was documented for a variety of marine snails (Stoner and Waite, 1990; Stoner et al., 1998; Rochette et al., 2001, 2003). Such predation/maturity pattern would be observed in Villarino, and it could be the result of a long-term selective pressure.

Even though the whelks analyzed belong to two sites separated from each other by 50 km, significant differences in their age (size) at sexual maturity were detected. This distance may be large for a species lacking larval dispersal. The life history traits of *B. globulosum* (direct development and limited adult movement) would reduce the possibility of mixing with adjacent populations, thus leading to a genetic differentiation even at small spatial scales (McQuaid, 1996; De Wolf et al., 1998). Individuals may therefore be adapted locally. Large morphological and strong genetic differentiation over short distances has been identified for a number of gastropods lacking a planktonic dispersal phase (Behrens Yamada, 1989; Rochette et al., 2003). Yet, either the high fidelity of adult snails to their native shore level or their habit of living buried most of the time (McCormack, 1982; Rochette and Dill, 2000) seem to be the main factors that minimize gene flow between San Antonio Bay and Villarino populations. In this sense, an analysis of the population genetic structure is needed.

The comparative analysis of the above-mentioned features poses the question of whether these two populations represent either different species or different forms of the same species. The present study shows that in patchy environments, such as the northern coast of San Matías Gulf, species may consist of a large number of isolated enclaves in which microevolution may occur. In this framework, local adaptations would take place and ecological speciation may occur (Sokolova and Boulding, 2004; Weetman et al., 2006; Rolán-Álvarez, 2007). Future research guidelines will be performed to acquire the molecular, behavioral and morphological data needed to address this issue.

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