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AGE STRUCTURE AND GROWTH IN AN UNUSUAL POPULATION OF PURPLE CLAMS, *AMIANTIS PURPURATUS* (LAMARCK, 1818) (BIVALVIA; VENERIDAE), FROM ARGENTINE PATAGONIA

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ABSTRACT The purple clam, *Amiantis purpuratus,* is distributed in the southwest Atlantic between Vitoria (Brazil, 200 SL) and San Matías Gulf (Argentina, 410 SL). We studied the age structure and growth in its southernmost population, which sustains small artisanal and sport fisheries. Examination of individuals collected in 1995 revealed well-marked external growth bands on the shells and a puzzling pattern: most had 15 or 16 bands. Were these annual, the implication would be virtually no successful recruitment during the 14-year period 1981-1994. We recovered and processed samples collected in the same area in 1980-1983 and 1987-1990 and conducted a comprehensive survey of the population in 1995. Examination of thin shell sections showed an almost exact correspondence between internal and external bands. The time series of size-at-age data indicated a bi-univocal correspondence between years lapsed and number of bands accumulated. This confirmed that external bands are annual and that only two significant year-classes (1979 and 1980) settled in the study area over a period of at least 15 years (1979-1994). Growth was studied at one location using size-frequency distributions and size-at-age data. Comparisons were made using likelihood methods to test differences among yearclasses (1979, 1980, older) and between two sites. Differences between the 1979 and 1980 year-classes were insignificant at both sites. Growth rate estimated for a pool of pre-1979 year-classes was high when compared with the 1979-1980 year-classes. Density dependence is advanced as a hypothesis to explain the comparatively slow growth of the 1979-1980 year-classes. Longevity is above 25 years. Implications of the findings for conservation and management are discussed.

KEY WORDS: Amiantis, purple clam, growth, age, recruitment, southwest Atlantic

INTRODUCTION

The purple clam, *Amiantis purpuratus* (Lamarck, 1818), inhabits intertidal and shallow subtidal sandy bottoms along the Atlantic coast of South America, from 200S to 410S (Scarabino, 1977; Rios, 1994) (Fig. lA). The southernmost population within this broad latitudinal range, confined to the northwest of San Matías Gulf (Fig. lB), appears to be relatively isolated. This is, also, the only stock of the species subject to exploitation. What started as a recreational intertidal fishery in the area of Playa Villarino (Fig. lC) has evolved since 1996 into a small-scale commercial diving fishery. Annual catch peaked at 382 t in 1996, and since then has fluctuated around 100 1. A preliminary survey conducted in 1995 revealed that (i) there were no juveniles, (ii) clam shells had very conspicuous external bands, and (iii) most shells had 15 or 16 bands. If those bands were laid annually, these preliminary observations would imply that the purple clam is a long-lived species, that the incipient fishery was based on two year-classes, and that pulses of recruitment are very sporadic. These prospects raised concerns with regard to the conservation of this fringe population and the sustainability of the fishery that it supports. Because there were no published antecedents on purple clam biology and ecology, we initiated a study to investigate the dynamics of this population. The first step was to develop reliable aging techniques. The simplest method traditionally used to age bivalves is based on the interpretation of external growth rings on the surface of the shells, often formed during the winter in cold-temperate seas (Richardson and Walker, 1991). In many species, however, such rings are absent or are difficult to interpret (Richardson et al. 1993). An alternative method is the study of the optical pattern of internal bands in shell cross-sections, using either acetate peels or thin sections (Cerrato 2000). Internal growth bands are more clearly defined and easier to count in shell structures such as hinge plates and chondrophores (Palacios et al. 1994; Thompson et al. 1980). The external growth rings of purple clam shells are very conspicuous, with an alternation of thick dark purple and thin pink bands. Here we report results on the nature of internal growth bands, on the matching between external rings and internal bands, and on their periodicity. Based on age data and on the analysis of sizefrequency distributions, we estimated growth parameters, compared growth curves between cohorts and between sites in the study area, and advanced hypotheses on the causes of the variation observed. This is the first study of this type conducted for this potentially significant shellfish resource. Implications of our results for the dynamics of the population and the management of the fishery are discussed.

MATERIALS AND METHODS

Study Area

Playa Villarino (Fig. lC) is a 9-km long dissipative sandy beach located in the proximity of San Antonio Bay (NW of San Matías Gulf). Average tidal amplitude is 7.62 m (maximum 9.2 m); in low tide the beach is 450-600 m wide. Sediment is predominantly fine sand, with patches of shell hash. Water temperature ranges, on average, from 6°C in August (winter) to 22.5°C in January (summer) (Kroeck and Morsán 1995). Water circulation in the NW of San Matías Gulf was described by Lanfredi and Pousa (1988) as a clockwise coastal eddy predominantly influenced by tidal currents, with limited interaction with the general circulation in the gulf. The population under study is distributed in the intertidal and subtidal zones, down to 10 m depth in low tide. The macrofauna is dominated by the purple clam (average biomass: 3235 g m-2 in a survey conducted in 1995; Morsán, 2000), followed by two scavenging/carnivore gastropods: *Buccinanops gobulosum* (NASSARIIDAE) and *Olivancillaria urceus* (OLIVIDAE).

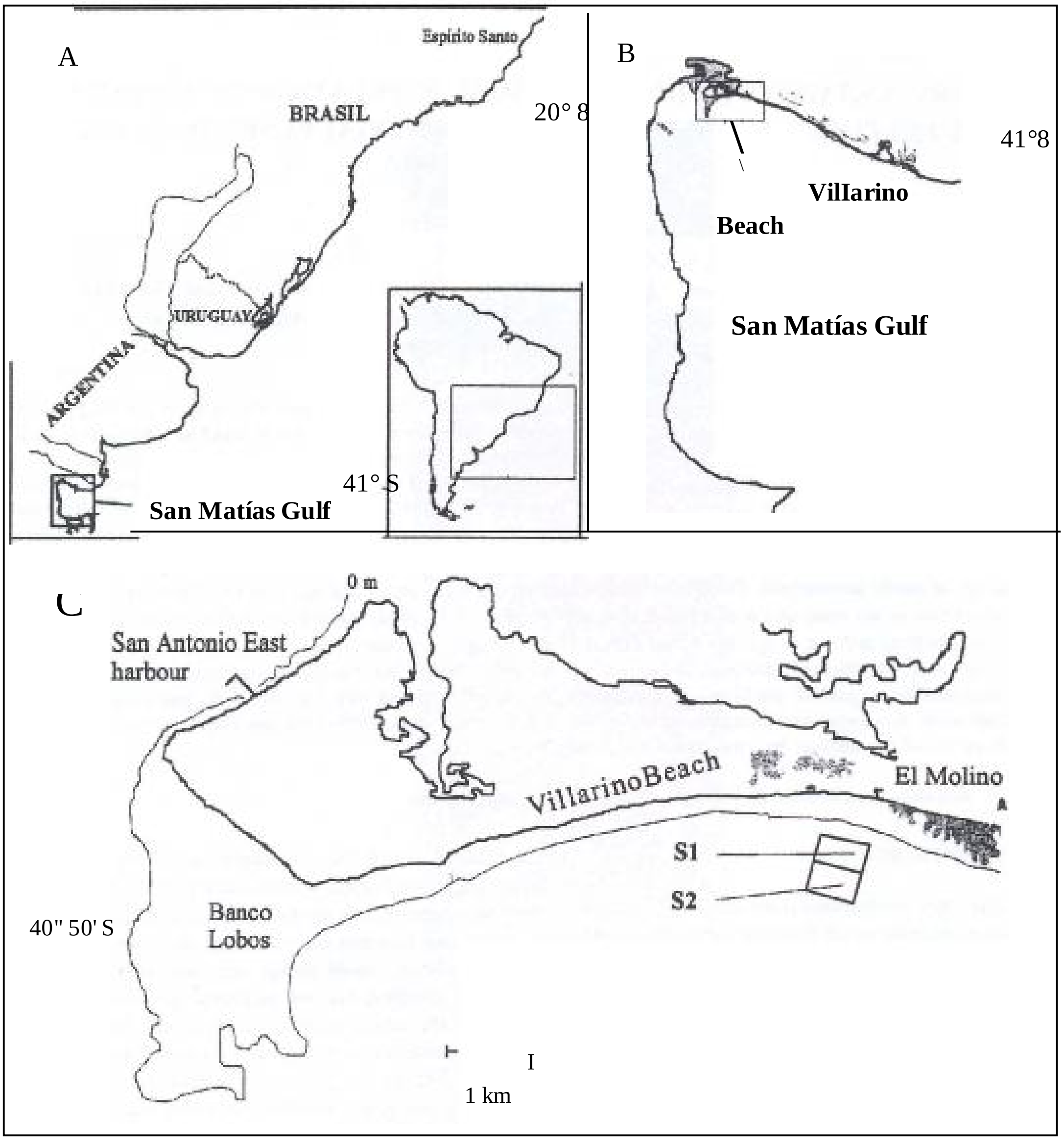

Figure 1. (A) Geographic distribution range of the purple clam, *Amiantis purpuratus.* (B) San Matías Gulf and Villarino Beach. (C) Location of sampling sites at El Molino (SI and S2)'

Study Site

Studies on age and growth were conducted at El Molino (Fig. 1C), a site located near the eastern end of the beach where periodic samples were obtained within a rectangular plot (500 m x 1000 m) perpendicular to the shoreline. Depth varies from 3 m to 9 m; strata were defined as the shallow (average depth 3.2 m) and deep (average depth 7.7 m) halves of the plot, respectively designated as sites SI and S2' Maximum density during the 1995 survey was 368 clams m-2 in SI and 216 clams m-2 in 82,

Sampling Protocol

Samples were obtained by divers between 1980 and 1995 (Table 1). Sampling units consisted of 0.25-m-2 quadrats dug to a depth of 20 cm. On a few occasions, samples were qualitative although obtained in a nonselective way. Between 1980 and 1983 clams were dug manually; an airlift was used starting in 1987. Total height (maximum distance from umbo to ventral margin) was recorded for all clams. The samples were obtained during three time intervals, under different arrangements (Table 1):

(1) 1980-1983: These samples, obtained before the beginning of our project, were belit~ved to be lost. We reconstructed their fate, tracked their location, and finally recovered them through a sequence of serendipitous circumstances.. They proved extremely valuable. The data include date, position, number of individuals, and individual sizes for 15 samples, and two sets of valves collected in 1982. The shells of individuals collected in October 8, 1982, that had presumably settled before 1979 (based on external bands, *n* = 104) were selected for aging.

(2) 1987-1990: Periodic sampling, One sample was used for age determination *(n* = 55).

TABLE 1.

Samples collected between 1980 and 1995. SI and S2 are sample sites, respectively shallow and deep strata of the El Molino plot. N/A: nonquantitative, nonselective samples.

Sampling Period	Date (month/day/year)	Site	Quadrats	Number of Individuals in Sample	Number of Individuals Aged
1980-1983	11/12/1980	SI	N/A	107	
	1/3/1981	SI	N/A	98	
	12/7/1981	SI	N/A	404	
	1/19/1982	SI	2	275	
	2/1/1982	SI	2	233	1631
	3/19/1982	SI	3	1370	
	8/27/1982	S2	3	601	
	10/8/1982	S2	2	650	1042
	4/22/1983	S,	1	199	
	7/8/1983	S2	1	343	
	9/15/1983	S2	1	368	
	10/26/1983	SI	2	737	
	11/11/1983	S2	2	333	
	12/2/1983	S2	1	442	
	12/22/1983	S2	3	676	
1987-1990 (periodic samples)	4/3/1987	SI	N/A	413	
	10/5/1987	SI' S2	2	316	
	1/9/1988	SI' S2	2	167	
	2/29/1988	S2	N/A	372	
	9/8/1988	S2	N/A	352	
	2/16/1989	S,	N/A	261	
	1/9/1990	S'' S2	1	261	
	1/22/1990	S2	N/A	248	
	2/1/1990	SI	N/A	320	553
	3/23/1990	S2	1	247	
	9/29/1990	S,	N/A	164	
	11/28/1990	S,	N/A	191	
1995 (survey)	3/10/1995	S2	8	280	1804
	3/24/1995	S,	4	208	1603
	5/27/1995	SI' S2	8	247	

I External bands counted but not measured.

2 External bands counted and measured.

3 External bands counted but not measured.

4 External bands counted and measured; internal bands counted.

(3) 1995: Quantitative survey of the entire population, conducted in March 1995. Individuals from two samples were used for age determination.

Analysis of SFDs

Size data were grouped at 1-mm intervals. Mean size, standard deviation, and proportion of each annual separable modal group were estimated for each sample unit. In some cases the groups could be identified visually. When modal groups overlapped, the decomposition was done by means of maximum likelihood methods, assuming that the components were normally distributed (MacDonald & Pitcher 1979).

Age Determination

Subsamples from five samples were used for aging (Table 1). Of these, two subsamples from the 1995 survey were used to study external and internal bands. External bands were counted and measured in a third subsample (sample collected on October 8, 1982), and only counted in two subsamples (samples collected on February 1, 1982, and February 1, 1990).

The external banding pattern of purple clam shells is very conspicuous, with an alternation of thick dark purple and thin pink bands. We counted the number of pink narrow bands; the beginning of the well-defined pink band was defined as the boundary between two consecutive bands. Bands were measured (distance from the umbo to the distal border of the band) along the same axis used to measure total height and to cut the shells for the observation of internal bands (see below).

To count internal bands, thin sections were obtained, cutting each valve with a low-speed diamond saw along the same axis used to count and measure external bands, running from the umbo to the ventral margin through the hinge plate. The surface left by the cut of one of the two valve halves was ground and polished using sandpaper of very fine grain (4000 grit) on a rotating platform at variable speed. The polished surface was glued with epoxy resin to a microscope slide. A 0.5-mm thick slice was obtained by means of a second cut along a plane parallel to the slide's surface. The exposed face of the thin section was ground and polished with sandpaper of medium grain (1000 grit) and very fine grain (4000 grit) until adequate thickness and texture were reached. Mounted thin sections were examined under a dissecting scope with trans mitted light to identify internal growth bands and to establish their correspondence with external bands.

Growth Modeling

Growth was modeled using (i) size-frequency distributions (SFDs) obtained between 1980 and 1995 and (ii) size-at-age back-calculated using external band measurements *(H*$_i$*,* where i indicates the boundary sequential number counting from the umbo) in samples collected in 1982 and 1995 (Table 1). Likelihood methods were used to fit the von Bertalanffy growth model,

H, = Hoo (1 - e-k(HO) + 8,

where Hoo is asymptotic shell height (expressed in mm), *k* is a constant (expressed in yr-I), *t* is age (in years), *to* is the age at size zero and 8 is an error term distributed normally (8 ~ *N* (O, *a). In* doing so, we assumed that external bands are laid down annually (see Results for validation of this assumption). The likelihood ratio test was used to compare growth curves between cohorts and/or locations (Kimura 1980; Cerrato 1990). Null hypotheses are of the form

Ho : *H=,I = Hoo,2'"; k, = k2...; tO.1 = tO.2*

and combinations of them, where 1 and 2 denote the two statistical populations being compared. Under the null hypothesis, the test statistic -210g(A) converges asymptotically to a X2 (g) distribution with *g* degrees of freedom (equal to the number of fixed parameters) .

RESULTS

Age Determination

Matching between external and internal growth bands (Fig. 2) was almost perfect. Internal growth lines are more evident in the hinge plate when the cut is perpendicular to the valve and runs across one of the cardinal teeth. Clams sampled during the late summer of 1982 *(n* = 163, Table 1) had two or three pink bands. Eight years later, in late summer 1990, individuals *(n* = 58) collected in the same location showed 10 or 11 bands. Finally, most individuals (97%) in two samples collected during late summer in 1995 *(n* = 180 and 160, Table 1) had 15 or 16 bands (Fig. 3). This indicates that between 1982 and 1995 the population was dominated by two year-classes and confirms that internal and external bands are laid annually. A dark purple band was visible along the border of the valves in all specimens collected in late summer. Summer is the spawning season of the purple clam in Villarino. Although the length of the larval stage is unknown, settlement is assumed to occur in late summer. Purple clams would mark their first clear growth band during the following winter. If this interpretation is correct, then the two cohorts must have settled during late summer in 1979 and 1980. The number of bands in shells from

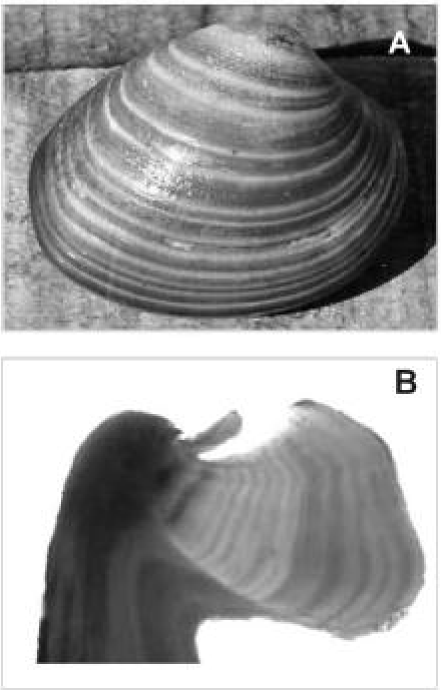

Figure 2. Growth pattern in the shell. (A) External view of a shell showing the external growth bands; (B) cross-section through the hinge region of a 13+ year-old individual.

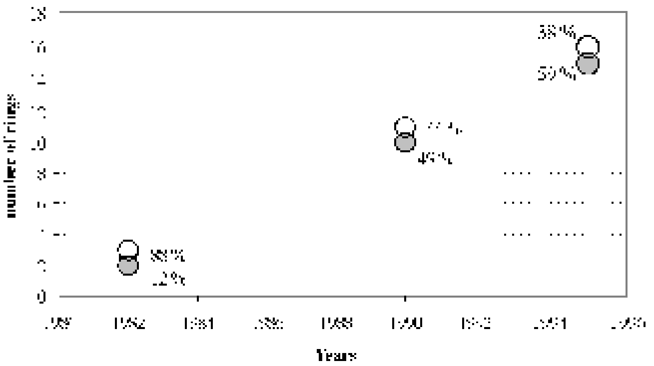

Figure 3. Correspondence between time elapsed between sampling dates and bands accumulated. Empty circles, 1979 cohort; solid circles, 1980 cohort. Percentages refer to number of individuals aged per sample.

old clams collected on 10/8/1982 (Table 1) varied from 9 to 18, indicating that they settled during the period 1965-1974. These cohorts had vanished from the population in 1995. The maximum number of bands recorded (i.e., maximum inferred longevity) was 42 years.

SFD Analysis

The progression of SFDs from 1980 to 1995 is shown in Figure 4 (seasonal pools, only six periods represented). Individuals smaller than 25 mm prevailed between 1980 and 1983, with the exception of a few larger than 40 mm. Between 1987 and 1990, most of the clams ranged between 25 and 35 mm. Finally, in 1995, most clams were larger than 35 mm. No juveniles were found after 1982. Two modal components were clearly distinguishable in the SFDs through 1987; afterward they overlap, making their recognition difficult. The presence of two consecutive cohorts in each of the subsamples used for aging (Table 2) is consistent with the two modal components observed in the SFDs, presumably corresponding to the year-classes settled in 1979 and 1980. The mean size of modal components estimated for all sampling units clearly shows the growth of these two cohorts between November 1980 and May 1995 (Fig. 5).

Growth

Growth rate was very similar between the 1979 and 1980 cohorts (Fig. 6). Although the complete parameter vectors were significantly different (Ho4, Table 2), pairs of analogous parameters do not show significant differences ($P > 0.05$, Ho1-Ho3, Table 3). Parameters $H=$ and k were analyzed together in a single test (Ho5). The null hypothesis was rejected only for estimates based on growth-band data. Differences between the 1979 and 1980 cohorts were not significant within each stratum, although differences between strata were significant for both cohorts (Ho5, Table 3). Parameter k did not differ significantly between groups in any case. Difference between sites was driven by parameter $H=$, which was higher in the deepest stratum where density was lower. Growth parameters estimated on the basis of size-at-age backcalculation for the multicohort group sampled in 1982 were higher than those of the 1979-1980 cohorts (Fig. 6). The null hypothesis of equal growth coefficients *(k)* could not be rejected, but all others were ($P < 0.01$).

DISCUSSION

When a preliminary survey of purple clams was conducted in Playa Villarino (San Matías Gulf, northern Argentine Patagonia) during the summer of 1995, some aspects of this population proved intriguing. First, there were no juveniles; second, most shells had 15 or 16 conspicuous external bands. If interpreted as annual, these preliminary observations would imply that the purple clam is a long-lived species, that the incipient fishery was based on two year-classes, and that pulses of recruitment are very sporadic. Collating information obtained during three intervals over a period of 15 years (Table 1) confirmed that, indeed, the population had been dominated all along by two year-classes, presumably settled during the summers of 1979 and 1980. Three pieces of information are remarkably consistent with each other, substantiating that hypothesis: (i) the number of external bands increased bi-univocally with time over the years (Fig. 3), (ii) there was an almost perfect correspondence between external and internal bands (Fig. 2), and (iii) the progression of SFDs through time show a modal structure that matches the age structure inferred from the analysis of growth rings (Fig. 4).

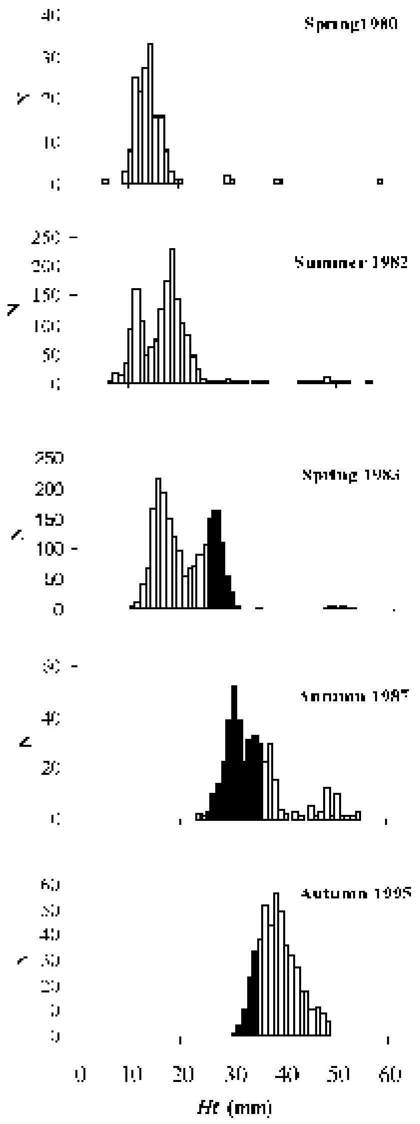

Figure 4. Size-frequency distributions (SFDs) during the period 19801995. Samples were pooled into several seasons. Solid bars indicate the range 25-35 mm for visual reference.

The recovery of data and samples collected in 1980-1983 (presumed lost) was most significant for the interpretation of the data. Shells collected at that early time in the life history of the two cohorts facilitated tracking the latter through time and validation of growth marks. External annual bands in this purple clam stock are among the clearest reported for bivalves, to the extent that we first thought of them as an endogenous sculpture pattern. This may be

TABLE 2.

Growth parameters estimated for different cohorts at El Molino, using size-at-age and size-frequency distribution (SFD) data.

		Size-at-age Data			SFD Data		
Cohorts	Site	k	Hoo	lo	k	Hoo	lo
1965-74		0.154	57.2347	-0.246	-	-	
1979	El Molino	0.1329	43.545	-1.412	0.149	44.125	-0.424
1980		0.1333	42.025	-1.199	0.095	48.971	-0.863
1979	SI	0.1340	40.533	-1.402	0.1758	40.925	-0.375
	S2	0.1233	45.631	-1.820	,"0.1390	47.553	-0.030
1980	SI	0.1385	40.947	-1.038	0.1185	43.649	-0.679
	S2	0.1159	45.208	-1. 820	0.1028	48.906	-0.399

due in part to the strong seasonal variation in temperature and in part to the fact that the porcelain-textured and color banding of the outer surface of the shells, which are rarely deteriorated, greatly facilitate observation.

The virtual absence of new settlers during the 15-year period 1981-1995 indicates that the population is sustained by very sporadic pulses of settlementlrecruitment. This could be explained by two hypotheses. The first, and most obvious, is dependence of reproductive success on suitable combinations of environmental conditions (environmental windows) that occur only sporadically. This is to be expected: this being the southernmost population of the species,[3] those windows may open up only occasionally. The dynamics of the purple clam may be representative of that of other species in the same region. Biogeographically, the northwestern corner of San Matías Gulf is an enclave where populations of several warm-temperate species live in apparent isolation, southward from their normal range of distribution. There is evidence of the recent local extinction of some of those, for example, the common drumfish *(Pogonias chromis,* Sciaenidae), whose otoliths are found in shell middens but which has not been recorded in the region during historical times. Sporadic pulses of recruitment may be indicative of the dynamics of extinction, perhaps the fate of this population unless there were a significant change in the environment (e.g., global warming) that reverses the trend.

A second plausible hypothesis that could explain sporadic settlementlrecruitment is density dependence. Density and biomass observed during the 1995 survey (15 years after the settlement of 1979-1980 cohorts) were very high (Morsán, 2003), and rough back-calculations indicate that they must have been so over the preceding years. Compensatory density-dependent settlement in dense populations of suspension-feeding bivalves has been documented 01' hypothesized for other populations (Wilson 1991; Bachelet et al. 1992). If the density of residents were inhibiting the settlementlrecruitment of new year-classes, the effects of density dependence should likely be observed in growth as well. Interestingly, individuals of the 1979-1980 year-classes reached comparatively small sizes-at-age. Asymptotic height estimated with different methods was in the range of 40-49 mm. By comparison, Carcelles (1944) reported much larger specimens (maximum height 72 mm) collected at the same location (Playa Villarino) during the period 1923-1933, close to maximum height reported for the species (73 mm, in subfossil deposits; Camacho 1966).

Size-at-age (Figs. 5 and 6) and estimated growth rate (overall sizes, Fig. 7) were much higher when estimated with data from a subsample of shells settled before 1979 (1965'-1974), collected in October 1982. As compared with the 1979-1980 cohorts, asymptotic size was much higher in this multicohort group (57.2 mm) although differences in parameter *k* of the von Bertalanffy model were not significant (Table 3, Fig. 7). According to general theory (Sebens 1987) and empirical evidence (Guillou and Sauríau 1985; Harrington 1987), differences in *k* (which reflects catabolic activity) should be influenced by temperature, whereas variation in asymptotic size should reflect food availability. The latter should

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[3] A few isolated individuals have been found further south, in San José Gulf (El Fracaso and El Riacho Beaches, JO, personal observation), but they do not seem to belong to a self-sustaining population. These are considered here as extralimital records.

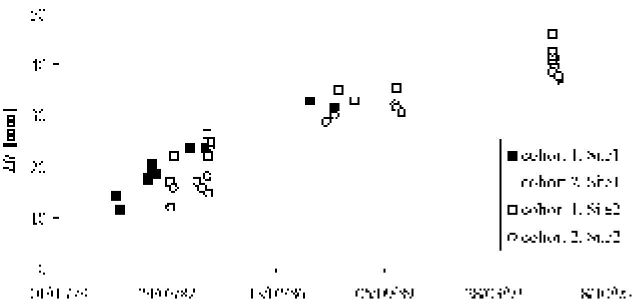

Figure 5. Temporal trend of mean size by cohorts and sites.

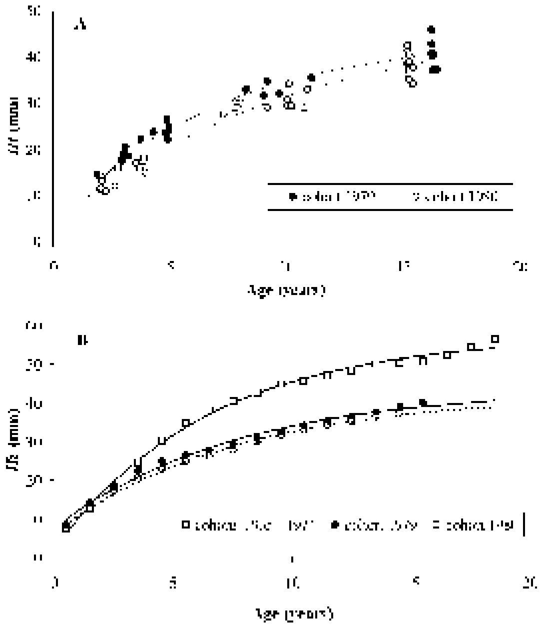

Figure 6. Estimated growth curves. (A) SFD data. (B) Back-calculated sizeoat-age data, multicohort group 1965-1974, and cohorts 1979 and 1980.

be affected by density, at least under high-density conditions such as observed during the survey when density reached 620 clam m^{-2} (corresponding to a biomass of 10 kg m^{-2}; Morsán, 2003). Density-dependent growth in clams, long hypothesized and demonstrated experimentally under field conditions (e.g. Peterson 1982; Peterson and Black 1987), is proposed here as a hypothesis to explain the comparatively low growth rate of the 1979-1980 yearclasses. It is interesting that although there was a big difference in asymptotic size, there was virtually no difference in parameter *k*, even when the pattern could have been concealed by structural correlation between the two parameters. This hypothesis will be explored in a forthcoming study.

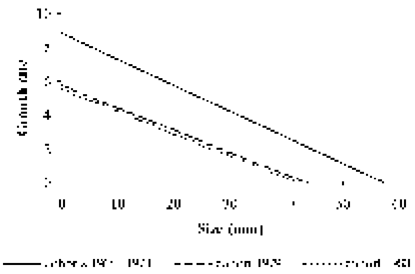

Figure 7. Estimated growth rate as a function of size. Cohorts com pared, age data.

The oldest specimens belonging to pre-1979 year-classes collected in 1982 were 17 years old. The 1979-1980 yearclasses were 16-17 years old when the 1995 survey was conducted. Recent informal observations by one of us (EM, 2003) indicate that those two strong year-classes still dominate the population about 25 years after they settled. This, thus, is a low bound to longevity. The latter was higher than we had expected for a warm-temperate, shallow-water venerid clamo Other species in the same subfamily (Pitariinae), however, are also reportedly longevous: 76 years in *Callista brevisiphonata* (Zolotarev 1980) and 40 years in *Callista chione* (Powell and Cummins 1985).

The exploitation of a population that (i) is isolated at the boundary of the species' geographic range of distribution and (ii) depends on very sporadic pulses of recruitment brings up concerns regarding management and conservation. The population may persist because significant longevity bridges long periods with no recruitment ("storage effect"; Warner and Chesson 1985), but reduced survival due to harvesting could shorten the effective length of those bridges. At the same time, however, there is the possibility that settlement of new cohorts was inhibited in a high-density scenario driven by two exceptional year-classes. If that were the case, thinning of the aging population through harvesting could alleviate overcompensatory density dependence, "creating room" for new settlers. These hypotheses could be explored through ex

TABLE 3.

Comparisons between cohorts and sites (SI and Sz) using the likelihood ratio test. Ho is the null hypothesis; numbers correspond to probability values. Values less than 0.05 are in italics. SFD: size-frequency distribution; AGR: size-at-age data from annual growth rings.

Comparison	Sitel Cobort	Estimation Metbod	HOI HI = Hz	Hoz kl = kz	H03 tOI = toz	H04 el = ez	Hos HIO kl = Hz' kz
Cohort 1979-Cohort 1980	El Molino	AGR	0.438	0.985	0.499	*0.0003*	*0.035*
		SFD	0.315	0.141	0.579	*0.00004*	0.132
	S.	AGR	0.795	0.769	0.173	0.167	0.161
		SFD	0.462	0.162	0.656	*0.0013*	0.112
	S2	AGR	0.676	0.977	0.716	*0.0301*	0.287
S,-S2		SFD	0.848	0.516	0.765	*0.0024*	0.208
	1979	AGR	*0.026*	0.491	0.246	*0.0000004*	*0.00004*
		SFD	0.D70	0.524	0.765	*0.021*	*0.014*
	1980	AGR	0.078	0.291	*0.034*	*0.00001*	*0.016*
		SFD	0.414	0.688	0.742	0.254	0.136

perimental management, opening sectors *of* the grounds to the fishery, leaving others as controls, and monitoring the dynamics *of* recruitment in both treatments.

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LITERA TURE CITED

Bachelet, G., M. Desprez, J-P. Ducrotoy, J. Guillou, P-J. Labourg, H. Rybarczyk, P-G. Sauriau, B. Elkaim & M. Glémarec. 1992. R61e de la compétition intraspécifique dans la régulation du recrutement chez la coque, *Cerastoderma edule* (L.). Ann. Inst. océanogr. (Paris) 68:75-87.

Camacho, H. H. 1966. Paleontología bonaerense, Fascículo 3, Invertebrados. *In:* Borrello, A.V. (ed.). Paleontografía Bonaerense. Como Invest. Ciento Prov. Buenos Aires (La Plata, Argentina), 159 pp.

Carcelles, A. 1944. Catálogo de moluscos marinos de Puerto Quequén (R.Argentina) Rev. Museo La Plata (NS, *200/.* (La Plata, Argentina) 3:233-309.

. Cerrato, R. M. 1990. Interpretable statistical test for growth comparison using parameters in the von Bertalanffy equation. *Can. J. Fish. Aquat. Sei.* 47:1416-1426.

Cerrato, R. M. 2000. What fish biologists should know about bivalve shells. *Fish. Res.* 46:39-49

Guillou, J. & P. G. Sauriau. 1985. Some observations on the biology and the ecology of a *Venus striatula* population in the Bay of Douamenez, Brittany. *J. Mar. Bio/.* Ass. *U.K.* 65:889-900.

Harrington, R. J. 1987. Skeletal growth histories of *Prothaea staminea* (Conrad) and *Protothaea grata* (Say) throughout their geographic ranges, northeastem Pacifico *The Veliger* 30:148-158.

Kimura, D. K. 1980. Likelihood methods for the estimation the von Ber talanffy growth curve. *Fish. Bull.* 77:765-776.

Kroeck, M. & E. Morsán. 1995. Biología reproductiva de la almeja púrpura. *In: Estudio biologieo pesquero de la almeja púrpura* Amiantis purpurata. Project Final Report, National University of the Comahue (San Antonio Oeste, Argentina), unpublished.

Lanfredi, N. W. & J. L. Pousa. 1988. Mediciones de corrientes, San Antonio Oeste, Provincia de Río Negro. Instituto de Biología Marina y Pesquera Alte. Stomi, \3 pp., unpublished reporto

MacDonald, P. D. M. & T. J. Pitcher. 1979. Age-groups from size frequency data: a versatile and efficient method of analyzing distributions mixtures. *J. Fish. Res. Board Can.* 36:987-1001.

Morsán, E.M. 2000. Dinámica poblacional y explotación de la almeja púrpura, *Amiantis purpurata* (Lamarck, 1818) (Bivalvia: Veneridae). Ph.D. Dissertation., Universidad Nacional del Sur (Bahía Blanca, Argentina), 182 pp.

Morsán, E. M. 2003.. Spatial analysis and abundance estimation of the southemmost population of purple clam, *Amiantis purpurata* in Patagonia (Argentina). *J. Mar. Biol.* Ass. *U.K.* 83:1073-1082.

Palacios, R., J. M. Orensanz & D. Armstrong. 1994. Seasonal and life-Iong variation of Sr/Ca ratio in shells of *Mya arenaria* from Grays Harbor (Washington)-An ancillary criterion in demographic studies. *Estuar. Coast. Shelf Sci.* 39:313-327.

Peterson, C. H. 1982. The importance of predation and intra- and interspecific competition in the population biology of two infaunal suspension-feeding bivalves, *Protothaea staminea* and *Chione undatella. Ecol. Monogr.* 52:437-475.

Peterson, C. H. & R. Black. 1987. Resource depletion by active suspension-feeders on tidal flats: influence of local density and tidal elevation. *Limno/. Oeeanogr.* 32:143-166.

Powell, E. N. & H. Cummins. 1985. Are molluscan maximum life spans determined by long-term cycles in benthic communities? *Oeeologia* 67:177-182.

Richardson, C. A. & P. Walker. 1991. The age structure of a population of the hard-shell clam, *Mercenaria mercenaria* from Southampton Water, England, derived from acetate peel replicas of shell sections. *ICES J. Mar. Sci.* 48:229-236.

Richardson, C. A., S. A. Collis, K. Ekaratne, P. Dare & D. Key. 1993. The age determination and growth of the European flat oyster, *Ostrea edu*lis, in British waters determined from acetate peels of umbo growth lines. *ICES J. Mar. Sci.* 50:493-500.

Rios, E. 1994. Seashells of Brazil. Rio Grande, Brazil: Editora da FURG, 368 pp., 113 plates.