

Morphometry, growth and reproduction of an Atlantic population of the razor clam *Ensis macha* (Molina, 1782)*

PEDRO J. BARÓN^{1,2}, LUCIANO E. REAL², NÉSTOR F. CIOCCO^{1,2} and MARÍA E. RÉ¹

¹ Centro Nacional Patagónico, CONICET, Boulevard Brown s/n, Puerto Madryn (9120), Chubut, Argentina.
E-mail: baron@cenpat.edu.ar

² Universidad Nacional de la Patagonia San Juan Bosco, Boulevard Brown 3700, Puerto Madryn (9120), Chubut, Argentina.

SUMMARY: *Ensis macha* is a razor clam distributed throughout the coasts of southern Argentina and Chile. Even though it represents a valuable fishery resource, the exploitation of its Atlantic populations has begun only in recent years. This study provides the first estimates of growth rate, an interpretation of the reproductive cycle on the coast of the northern Argentine Patagonia and an analysis of the species morphometry. Growth was estimated by direct observation of growth rings on the valves by two observers. The reproductive cycle was interpreted by the analysis of temporal change of oocyte size frequency distributions. Parameter estimations for the von Bertalanffy equations respectively obtained by observers 1 and 2 were 154 and 153.7 mm for L_{∞} , 0.25 and 0.20 yr⁻¹ for k , and -0.08 and -0.72 yr for t_0 . Two spawning peaks were detected: September-November 1999 and May-June 2000. However, mature females were found all year round. An abrupt change in the relationship between shell length and height was detected at 11.2 mm length.

Key words: razor clam, morphometric relationships, growth, reproduction, *Ensis macha*, allometric growth.

RESUMEN: MORFOMETRÍA, CRECIMIENTO Y REPRODUCCIÓN DE UNA POBLACIÓN ATLÁNTICA DE LA ALMEJA NAVAJA *ENSIS MACHA* (MOLINA, 1782). – *Ensis macha* es una almeja navaja distribuida a lo largo de las costas del sur de Argentina y Chile. A pesar de que esta representa un valioso recurso pesquero, la explotación de sus poblaciones Atlánticas sólo ha comenzado en años recientes. El presente estudio provee las primeras estimaciones de las tasas de crecimiento, una interpretación del ciclo reproductivo en la costa norte de la Patagonia Argentina, y un análisis de la morfometría de la especie. El crecimiento fue estimado a través de observaciones directas de los anillos de crecimiento sobre las valvas por parte de dos observadores independientes. El ciclo reproductivo fue interpretado mediante el análisis de los cambios temporales en las distribuciones de frecuencias de tallas ovocitarias. Las estimaciones de los parámetros de las ecuaciones de von Bertalanffy, obtenidas respectivamente por los observadores 1 y 2, fueron: 154 y 153,7 mm para L_{∞} , 0,25 y 0,20 años⁻¹ para k , y -0,08 y -0,72 años para t_0 . Se hallaron hembras maduras durante todo el año, y se detectaron dos picos de desove: septiembre-noviembre de 1999 y mayo-junio de 2000. Se detectó un cambio abrupto en la relación morfométrica entre el largo y el ancho de las valvas a los 11,2 mm de largo.

Palabras clave: almeja navaja, relaciones morfométricas, crecimiento, reproducción, *Ensis macha*, crecimiento relativo.

INTRODUCTION

Razor clams are bivalve molluscs with low world landings, but they fetch high prices in international

markets. Although not reported in fisheries statistics (FAO, 2000), *Ensis macha* is one of the most important razor clam species in volume of captures, reaching landings of approximately 6,000 t in 1999 in Chile (Sernapesca, 2000), where beds have begun to show clear signs of overexploitation (Bustos *et al.*,

*Received July 11, 2002. Accepted September 30, 2003.

1999). This species inhabits subtidal sandy-muddy bottoms along coastal waters of the Atlantic (40-55°S, depths of 0 to 55 m; Lasta *et al.*, 1998) and Pacific (27-55°S, depths of 0 to 13 m; Osorio *et al.*, 1979) coasts of South America (Fig. 1). Previous studies on the growth (Urban, 1996) and reproduction (Avellanal *et al.*, 2002) were conducted on Chilean populations, and no information is available on Atlantic populations. Recent work has demonstrated that the beds from the northern-Patagonian Gulfs (Argentina, 42-43°S) have a potential for exploitation (average density in beds = 51.6 clams/m², average biomass = 1-1.5 kg/m²; mean length of individuals = 124.9-134.2 mm) (Ciocco, unpublished). The artisanal shellfishery of northern Argentine Patagonia (San José Gulf and South of San Matías Gulf) is operated by hookah divers. In the last few years, 19-22 vessels 8-10 m in length, equipped with outboard engines up to 110 hp, have operated in the area landing 500-1000 tons of bivalves per year. Traditional target species include the tehuelche scallop (*Aequipecten tehuelchus*), the ribbed mussel (*Aulacomya ater*), the common mussel (*Mytilus edulis*) and the striped clam (*Protothaca antiqua*). Recently, the razor clam and another clam species, the southern geoduck (*Panopea abbreviata*), have been added. The interest in the exploitation of the former has increased after samples sent to Chile, Asia and domestic markets were found acceptable for marketing (Lasta *et al.*, 1998). The methods used to capture *E. macha* so far include grabbing it with long pincers (also employed in Chilean fisheries), seizing it directly with the hand when the sediment is soft and inserting a small metal sphere, welded to the end of an iron rod, into the clam's inhalant siphon and pulling it back when the siphon retracts. Given the lack of regulation, there is a need to establish a management plan for this incipient fishery. In support of this need, the present work reports the first data on the morphometry, growth and reproductive patterns of *E. macha* from northern Argentine Patagonia.

MATERIALS AND METHODS

Sampling

A survey was conducted from September 1999 to August 2000 on *E. macha* beds from Puerto Lobos (San Matías Gulf, Argentina; 42°00'S-65°04'W) (Fig. 1). Razor clam samples (N ≥ 30 individuals)

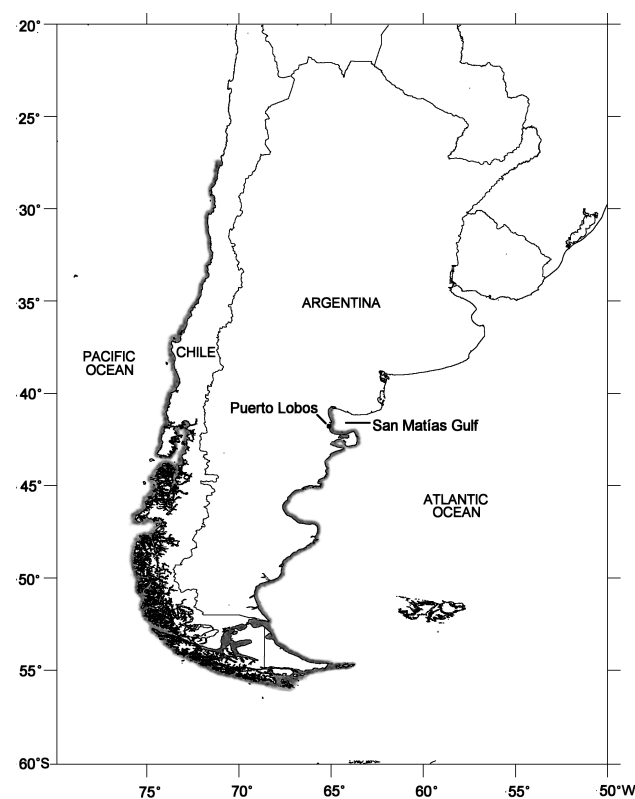


FIG. 1. – Geographical distribution of *Ensis macha* and location of the study area.

were collected monthly by SCUBA divers by water jet pumping and were fixed in 5% formaldehyde in seawater immediately after capture. In November and December 1999 and February, May, June and July 2000, sediment samples (one sample of 2000 cm³ each month without replicates) containing *E. macha* spat were taken from the seabed, frozzen, defrosted a few months later and subsequently examined under a dissecting microscope.

Morphometry

The morphometric variables recorded include length (L), height (H), length along the diagonal axis (D) (Fig. 2), dry weight of both valves (VW), wet weight of the whole specimens (TW) and wet weight of the soft parts (SPW). Since individuals captured by SCUBA divers were fixed in formaldehyde before weighing, measurements of TW and SPW may have been biased. Individuals collected in the sediment samples were not included in the analysis of weight variables because they were subjected to a different method of preservation. Given that logarithmic transformation linearises relationships and stabilises variances (Voight, 1991, 1994),

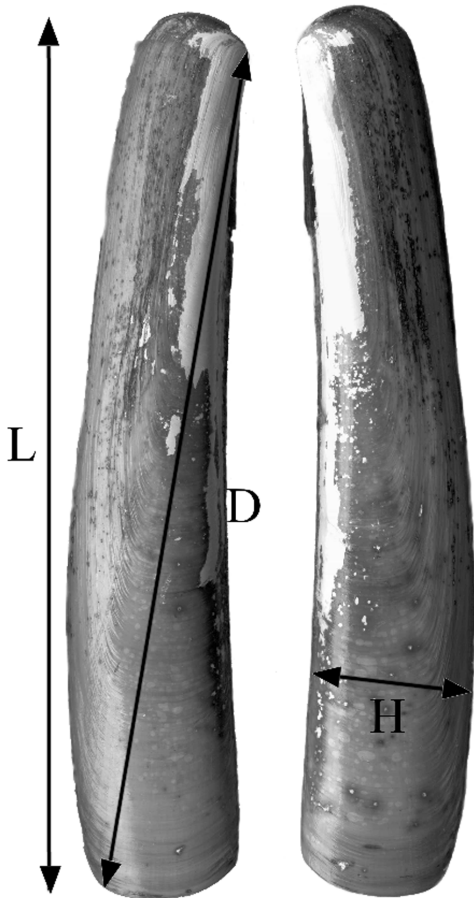


FIG. 2. – Shell dimensions measured on *Ensis macha*. L: length, H: height, D: diagonal (axis of greater growth from the hinge to the ventral margin).

all variables were ln-transformed. Regression lines were fitted in order to establish relationships between ln(L) and other ln-transformed variables and between ln(SPW) and ln(TW). The Student's *t* test was performed to establish allometry/isometry in the relationships. For one of the relationships showing a morphometric discontinuity, a piecewise regression analysis was performed running the Simplex algorithm included in Statistica (Statsoft Inc., 1996).

Growth

Growth checks were recognised by topographic discontinuities and change of colour on the valves' surface. Growth was characterised by measuring the distances from each check to the hinge along the line of maximum shell growth (D, Fig. 2). Since this method is rather subjective, growth check measurements were performed independently by two observers on the left valves of 98 and 99 individuals

respectively from a sample of 147 clams. All measurements were done with Vernier calipers to the nearest 0.1 mm. Taking into account that the measure of size for razor clams in other studies is L (Henderson and Richardson, 1994; Urban, 1996), growth in D was transformed to L using the regression equation that relates the two variables. The von Bertalanffy (1938) equation

$$L_t = L_{\infty} (1 - \exp^{-k(t-t_0)}),$$

was fitted to size-at-growth check data by means of a non-linear regression using the Simplex algorithm (Statsoft Inc., 1996) and considering that "t" is the number of growth checks marked by the animal since the beginning of shell formation, "L_t" is the valve's length (L) at growth check "t", L_∞ is the asymptotic length, k is a constant and t₀ is the number of growth checks marked at size 0. Growth parameters were estimated with maximum likelihood methods independently for the data registered by each observer. Comparisons between curves were conducted by contrasting the likelihood ratios with chi-squared tests (Cerrato, 1990). To obtain a validation for the periodicity of growth check deposition, 100 individuals were collected from the bed in November 1999, marked with a razor on the surface of their valves perpendicularly to the anterior margins and returned to the bed. Since the animals were lost at the time of recapture (November 2000), probably owing to fishing by the artisanal fishermen operating in the area, a second sample of 100 individuals were marked and left in the bed for one year until recapture (November 2001).

Reproductive patterns

Three hundred and forty-nine individuals ranging from 50 to 165 mm in L were dissected and tissue samples were taken from the gonads. Sex was determined by observation of gonadal smears under binocular microscope. Once all females had been identified, ovary pieces were stained with Methylene Blue, smeared on glass slides and photographed with a digital camera. The areas of the projections of 100 oocytes on the photo images were measured by pixel counting (Aldus Photo Styler, v2) and the area of the rectangles containing each oocyte were calculated by multiplying the length of the largest axis of the oocyte by that of its largest perpendicular axis (measured with Scion image 4). In view of the high correlation between the two measures of area (R =

TABLE 1. – Morphometry of *Ensis macha*. (L: length, H: height, D: diagonal axis, TW: wet weight of the whole specimens, SPW: wet weight of the soft parts, VW: dry weight of both valves, a: intercept, b: slope, SE_b: standard error of b, 0: isometry, -: negative allometry, +: positive allometry)

	N	L range (mm)	Slopes test P-level	Intercepts test P-level	Isometry/ Allometry	Isometry test t	Isometry test P-level	r ²	a	b	SE _b
ln D on ln L	520	1.6-165	0.21	> 0.05	0	0.13	0.89	0.99	-0.11	1.01	< 0.01
ln H on ln L	108	1.6-11.2			-	28.09	< 0.001	0.94	-0.61	0.55	0.01
	412	11.2-165			+	3.31	< 0.001	0.99	-1.74	1.02	< 0.01
ln TW on ln L	270	55-165			0	0.42	0.67	0.86	-11.47	3.03	0.07
ln VW on ln L	270	55-165	0.92	> 0.05	+	7.59	< 0.001	0.92	-15.73	3.56	0.07
ln SPW on ln L	270	55-165			-	3.01	< 0.001	0.68	-10.18	2.66	0.11
ln SPW on ln TW	270	55-165			-	2.99	< 0.001	0.92	-0.34	0.95	0.02

0.97), their relationship was estimated by regression. Then, the rectangular areas of at least 50 vitellogenic oocytes per female were calculated and transformed into the projection areas using the regression equation. To obtain an estimation of oocyte size, it was considered that oocytes were perfectly circular, their diameters (d) being related to the projection areas by the equation:

$$d = 2 \sqrt{(\text{projection area}/\pi)}$$

From these calculations, monthly size frequency distributions of vitellogenic oocytes were drawn.

RESULTS

Morphometry

The morphometric relationships established in this study, along with some sample descriptive statistics are given in Table 1. The left and right valves of *E. macha* are symmetrical and have a similar weight. Growth of D relative to L is isometric. In contrast, growth of H relative to L is negatively allometric for individuals with L < 11.23 mm and slightly positively allometric for larger ones. Growth of TW relative to L is isometric. On the other hand, growth of SPW relative to L is negatively allometric and that of VW relative to L is positively allometric. Accordingly, SPW relative to TW is negatively allo-

metric, SPW varying between approximately 50 and 70% (mean 60%) of TW.

Growth

Observer 1 noted alternating light concavities and dark convexities on the surfaces of the valves of *E. macha* along their axes of maximum growth, each concavity being separated from the following convexity by a conspicuous step. For this observer, only these steps represented seasonal growth checks. On the other hand, observer 2 considered that a growth check was any conspicuous topographic discontinuity on the valves' surface. Maximum likelihood growth curves obtained by the two independent observers were significantly different from each other, the one obtained by observer 2 showing greater dispersion (Table 2). Between-observer differences were related to parameters k and t₀ (Table 2). The maximum numbers of growth checks were 14 and 16 for observers 1 and 2 respectively, the modal number of checks being seven for both. Even though validation experiments on the periodicity of deposition of the check marks were conducted by marking 200 individuals, only one of them was recaptured alive after one year. This individual grew from L = 125.7 mm (November 2000) to 130.1 mm (November 2001) and deposited only one check mark (its 7th one) during this period. The other 199 clams were lost due to unknown reasons, probably including fishing, depredation, self-dispersion and scattering due to stormy weather conditions.

TABLE 2. – Growth parameters of *Ensis macha* from a northern Patagonian population and results of the comparisons between growth curve likelihood ratio with Chi-squared test (df = 3, α = 0.05). L_∞, k and t₀: parameters of the von Bertalanffy equation, n: total number of growth checks, S²: estimator of error variance, LR: likelihood ratio, P: level of probability.

Observer	L _∞	k	t ₀	n	S ²	LR	P
1	154	0.25	-0.08	550	59.5	131.4	<0.001
2	153.7	0.2	-0.72	749	133.2		

TABLE 3. – Sex ratio of *Ensis macha* divided into three length (L) classes

L range (mm)	Male	Female	Expected
90-115	20	22	21
115-140	128	119	123.5
140-165	35	25	30
Total	183	166	174.5

Overall sex ratio = 1.10
Chi-squared = 1.05 (P = 0.59)

Reproductive patterns

Out of a total of 349 clams analysed, 183 were males, 166 were females and none was hermaphrodite. The sex ratios of individuals divided into three size classes were not significantly different to 1:1 (Table 3). Vitellogenic oocytes were found in all female clams and in all months sampled, suggesting that in northern Patagonia there is no resting period. Size of the vitellogenic oocytes was in the range 16-110 μm . Monthly frequency distributions of vitellogenic oocyte diameter are shown in Figure 3. In September of 1999, oocyte size classes between 36-80 μm were evenly represented. In November of the same year, the largest size classes were much less frequent than in September, indicating that partial spawning had occurred. In December, there was a recovery of the largest size classes, two modal components being clearly distinguishable until May 2000; by then the largest size classes had become less abundant. From May to June, there was an abrupt disappearance of the largest modal component, indicating that massive spawning took place in this period. Finally, from July to August the largest classes of oocyte size gradually recovered, the maximum average oocyte size being observed during the last month. Seventy one *E. macha* individuals of 1.6-23.5 mm L were found in the sediment samples. From these, spat smaller than 4 mm L were only present in November, July and August, suggesting that spawning may have taken place during spring and late fall, as was shown by the vitellogenic oocyte frequency distributions.

DISCUSSION

An abrupt change in growth pattern of $\ln(H)$ relative to $\ln(L)$, from negatively allometric to isometric, reveals that the valves of individuals smaller than 11 mm in L modify their shapes from more

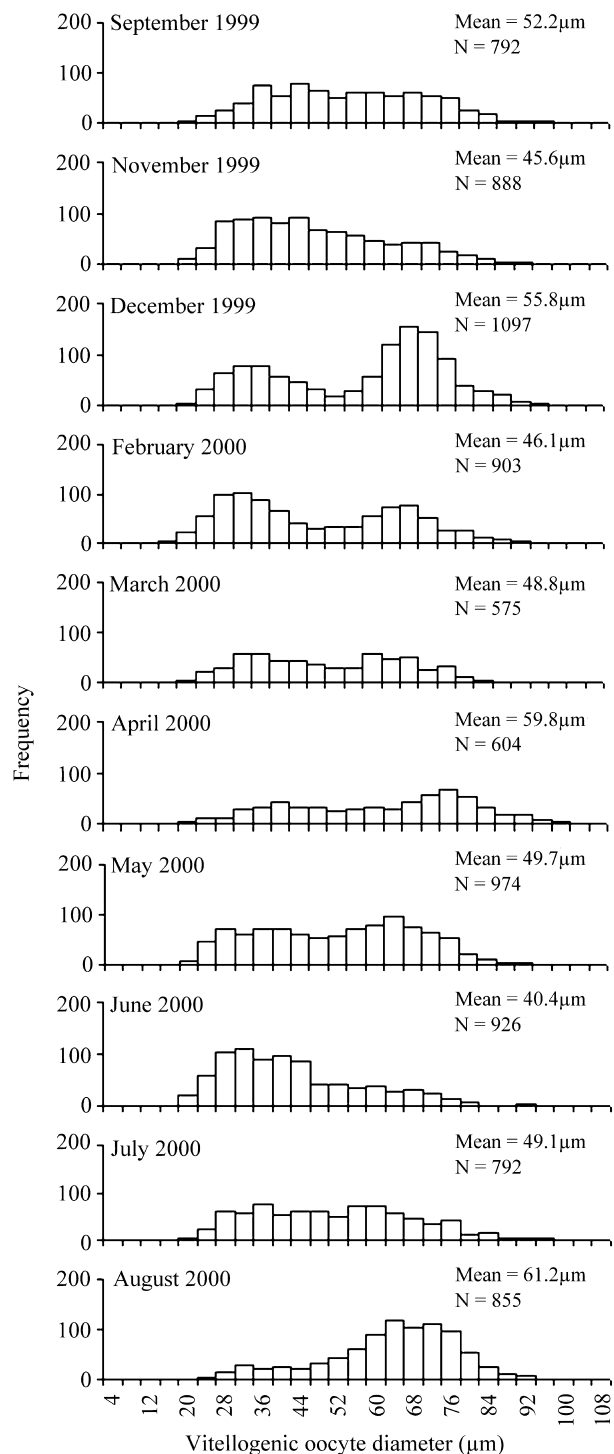


FIG. 3. – Monthly frequency distributions of *Ensis macha* vitellogenic oocyte diameters.

square to more elongated as they grow and that for larger individuals the shape does not vary with size. The elongated form of some infaunal species like razor clams enables them to burrow deep with low energy requirements to escape from predators (Trueman, 1967; Urban, 1994). For recently settled clam

spat, which are light and unable to burrow deep, stability against bottom currents may also be important for survival (Stanley, 1970). Since the form of *E. macha* spat has a lower surface-to-volume ratio than that of adults, it is probably more stable against the drag forces of bottom currents. As individuals grow, shell elongation might give them an adaptive advantage to become effective burrowers. Therefore, the change in the growth of H relative to L can be thought of as the result of a shift in the mode of life of individuals, from subsurface dwelling spat to active digging juveniles. The growth rates of TW and SPW relative to L found in *E. macha* in the present study are lower than those found for *Ensis ensis* and *Ensis siliqua* by Henderson and Richardson (1994). However, since the protocol used to weigh the last two species was different from that used for by us for *E. macha*, this comparison must be considered cautiously. The slightly negatively allometric growth of SPW relative to TW reveals that there is a slight loss in meat yield at the expense of shell weight as the clams grow.

Growth estimates obtained in the present study by observer 1 resulted in a von Bertalanffy's k value of 0.25 yr^{-1} , which is similar to that estimated by Carmona *et al.* (1999) by tracing modal components of size of an *E. macha* Chilean population. On the other hand, the parameter k obtained by Observer 2 was similar to that obtained by Urban (1996) by mark and recapture ($k = 0.21 \text{ yr}^{-1}$). L_{∞} values obtained by both observers were lower than those estimated by Carmona *et al.* (1999) (216 mm) and Urban (1996) (189.9 mm). Differences in the estimates of k by both observers might be due to the interpretation of growth checks. Gaspar *et al.* (1994) analysed the growth checks of *E. siliqua* both by direct observation and using acetate peel replicas of shell sections, reaching the conclusion that growth check counting with the first method underestimated the growth rate (k) in that species. These authors noted that the clams that are disturbed form clefts on the surface of their valves that are frequently confused with seasonal growth checks under direct observation. On the other hand, there is another razor clam species (*Ensis directus*) in which seasonal growth checks are more conspicuous than disturb marks, allowing a reliable estimation of the growth parameters using direct observations (Swennen *et al.*, 1985). The length of an individual at its 7th growth check was 127.8 mm in the growth model of observer 1 and 120.9 mm in that of observer 2. Since the only marked individual recovered formed its 7th

growth check between 125.7 mm and 130.1 mm, its growth seems to be better explained by the first model. However, since there is a degree of variability in the length-at-growth check data (Table 2), no definitive conclusion can be derived on this aspect. Even though the validation of the periodicity of growth check deposition in *E. macha* was based on the observations conducted in one individual, the maximum number of growth checks found (observer 1: 14; observer 2: 16) is similar to the maximum age (13.5 y) estimated by Urban (1996) for the same species, giving additional support to the consideration of an annual deposition pattern for growth checks.

The present work shows that in northern Argentine Patagonia, the male to female ratio of *E. macha* is not significantly different from 1:1 for the three size classes analysed. This indicates that mortality throughout the size range of 90-165 mm is not sex dependent. In this population females do not have a resting period and they show two spawning peaks, one in spring (September to November) and the other in late autumn (May to June). Studies conducted by Avellanal *et al.* (2002) in the same species show that the Chilean populations within 37-42°S also remain in advanced stages of maturity (late active, ripe and partially spawned) most of the year. Furthermore, two peaks of maturation were observed by these authors in two out of three beds studied (Avellanal *et al.*, 2002). Other razor clam species, such as *E. siliqua* from the coasts of Portugal (Gaspar and Monteiro, 1998), *Solen strictus* from Korea (Hong and Lee, 1990) and *Siliqua patula* from the Pacific coast of Canada (Bourne, 1979) spawn only once a year, generally from spring to summer. The samples of *E. macha* considered in this study came from populations located at the northernmost (warmest) limit of the species distribution. Specimens of this species and other clams with similar geographic distributions (e.g. *Protothaca antiqua* and *Eurhomalea exalbida*; Schuldt, 1975; Verdinelli and Schuldt, 1976; Borzone, 1989), are found in mature condition all year round. Also, they spawn more than once a year, either in the cold or the warm seasons. In contrast, other clam species whose southern (coldest) limit of distributions is the northern Patagonia (e.g. *Tellina petitiana*, Barón and Ciocco, 2001; *Amiantis purpurata*, Morsán, 2000) show clearly defined spawning peaks and mature individuals only during the late spring-summer period.

This study documents the general patterns of growth and reproduction for the northern Patagon-

ian populations of *E. macha*. Although this information is relevant to regulate the imminent fishing activity, more detailed studies are still necessary to allow the design of a long-term management plan. However, preliminary exploitation strategies could be considered based on the present information. For example, brief reproductive closures could be implemented to avoid disturbance of the beds during spawning peaks. If this measure is to be taken, the annual schedule of male evacuation should be also analysed. Size limits could also be evaluated taking into account the biomass yield of a cohort under a reasonable range of natural mortality coefficients.

ACKNOWLEDGEMENTS

We appreciate the help given by Norberto De Garín and Alejandra Monsalve during the field and laboratory tasks. Miguel A. Díaz and Ricardo B. Vera made sampling possible. Two anonymous reviewers gave valuable comments to improve the original version of the manuscript. This research was funded by PID CONICET (Argentina) 656/98.

REFERENCES

- Avellanal, M.H., E. Jaramillo, E. Clasing, P. Quijón and H. Contreras. – 2002. Reproductive cycle of the bivalves *Ensis macha* (Molina, 1782) (Solenidae), *Tagelus dombeii* (Lamarck, 1818) (Solecurtidae) and *Mulinia edulis* (King, 1831) (Mactridae) in Southern Chile. *Veliger*, 45: 33-44.
- Barón, P.J. and N.F. Ciocco. – 2001. Reproductive cycle of the *Tellina petitiana* d'Orbigny, 1846, in Nuevo Gulf (Argentina). *Veliger*, 44: 370-380.
- Bertalanffy, L. von - 1938. A quantitative theory of organic growth (inquiries in growth laws II). *Hum. Biol.*, 10: 181-213.
- Borzzone, C.A. – 1989. El ciclo gonadal de *Venus antiqua* King & Broderip, 1835 (Verinidae: Bivalvia) en el golfo San José. *Physis*, 47: 61-72.
- Bourne, N. 1979. Razor clam, *Siliqua patula* Dixon, breeding and recruitment at Masset, British Columbia. *Proc. Natl. Shellfish. Assoc.*, Md., 69: 21-29.
- Bustos, E., S. Olave, I. Lépéz and E. Pacheco. – 1999. Producción de semillas de *Ensis macha* en sistema controlado. Abstracts of the "IV Congreso Latinoamericano de Malacología", 6-10 September 1999, Coquimbo, Chile.
- Carmona, M.A., O. Aracena, C. Santos and I. Lopez. – 1999. Crecimiento de *Ensis macha* en la VIII Región. Abstracts of the "IV Congreso Latinoamericano de Malacología", 6-10 September 1999, Coquimbo, Chile.
- Cerrato, R.M. – 1990. Interpretable Statistical Test for Growth Comparisons using Parameters in the von Bertalanffy Equation. *Can. J. Fish. Aquat. Sci.*, 47: 1416-1426.
- FAO. – 2000. Fyshstat Plus: Universal software for fishery statistical time series, Version 2.3.
- Gaspar, M.B., C.A. Richardson and C.C. Monteiro. – 1994. The effects of dredging on shell formation in the razor clam *Ensis siliqua* from Barrinha, southern Portugal. *J. Mar. Biol. Ass. U.K.*, 74: 927-938.
- Gaspar, M.B. and C.C. Monteiro. – 1998. Reproductive cycles of the razor clam *Ensis siliqua* and clam *Venus striatula* off Vilamoura, southern Portugal. *J. Mar. Biol. Ass. U. K.* 78: 1247-1258.
- Henderson, S. and C.A. Richardson. – 1994. A comparison of the age, growth rate and burrowing behavior of the razor clams, *Ensis siliqua* and *Ensis ensis*. *J. Mar. Biol. Ass. U.K.*, 74: 934-954.
- Hong, S.S. and J.J. Lee. – 1990. Histological studies on the gametogenesis and the reproductive cycle of razor clam, *Solen stric-tus* Gould, in Cheju-do. *Bull. Mar. Res. Inst. Cheju Natl. Univ.* 14: 39-59.
- Lasta, M., N.F. Ciocco, C. Bremec and A. Roux. – 1998. Moluscos bivalvos y gasterópodos, In: "El Mar Argentino y sus recursos Pesqueros" (Boschi, Ed.), 2: 115-142, INIDEP, Mar del Plata, Argentina.
- Morsán, E. – 2000. *Dinámica poblacional y explotación de la almeja púrpura*, *Amiantis purpura* (Lamarck, 1856) (Bivalvia: Verinidae). PhD thesis, Universidad Nacional del Sur, Argentina. 119 pp.
- Osorio, C., J.A. Cifuentes and S. Mann. – 1979. Moluscos marinos de importancia económica en Chile. *Biol. Pesq.* (Chile), 11: 3-47.
- Sernapesca. – 2000. *Anuario estadístico de pesca*. Servicio Nacional de Pesca, Ministerio de Economía, Fomento y Reconstrucción. Chile. 291 pp.
- Schuldt, M. – 1975. Consideraciones sobre la reproducción de los pelecipodos chionidos en la cholguera de Punta Loma, Golfo Nuevo, *Chubut. Physis*, 34: 137-146.
- Stanley, S.M. – 1970. Relation of shell form to life habits in the Bivalvia. *Geol. Soc. Amer. Mem.* 125: 1-296.
- Swennen, C., M.F. Leopold and M. Stock – 1985. Notes on growth and behaviour of the American razor clam *Ensis directus* in the Wadden Sea and the predation on it by birds. *Helgol. Meeresunters.*, 39: 255-261.
- Statsoft Inc. – 1996. *Statistica for Windows: Computer user manual*, Tulsa, OK. Statsoft Inc.
- Trueman, E.R. – 1967. The dynamics of burrowing in *Ensis* (Bivalvia). *Proc. R. Soc. (B)* 166: 459-476.
- Urban, H.J. – 1994. Adaptations of six infaunal bivalve species of Chile: Coexistence resulting from differences in morphology, burrowing depth and substrate preference. *Arch. Fish. Mar. Res.*, 42: 183-193.
- Urban, H.J. – 1996. Population dynamics of the bivalves *Venus antiqua*, *Tagelus donbeii* and *Ensis macha* from Chile at 36°S. *J. Shellfish Res.*, 15: 719-728.
- Verdinelli, M.A. and M. Schuldt. – 1976. Consideraciones preliminares sobre aspectos de la dinámica poblacional y reproducción de la almeja rayada *Ameghinomya antiqua* (King, 1831) (Chionidae) en Punta Loma, Golfo Nuevo-Chubut. *Rev. Museo de La Plata*, 12: 183-202.
- Voight, J.R. – 1991. Morphological variation in octopod specimens: reassessing the assumption of preservation-induced deformation. *Malacologia*, 33: 241-253.
- Voight, J.R. – 1994. Morphological variation in shallow-water octopuses (Mollusca: Cephalopoda). *J. Zool.*, 232: 491-504.

Scient. ed.: C. Richardson