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Reproductive cycle of the Patagonian scallop *Zygochlamys patagonica* in the south-western Atlantic

SILVANA CAMPODÓNICO[1], GUSTAVO MACCHI[1,2], BETINA LOMOVASKY[2,3] AND MARIO LASTA[1]

[1]Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), Paseo V. Ocampo No.1, (B7602HSA) Mar del Plata, Argentina, [2]Consejo Nacional de Investigaciones Científicas y Técnicas, Argentina (CONICET), [3]Laboratorio de Ecología, Departamento Biología (FCEyN), Universidad Nacional de Mar del Plata. CC 573 Correo Central (B7600WAG) Mar del Plata, Argentina

The reproductive cycle of Zygochlamys patagonica *was studied from October 1999 to February 2001 in a bed located in the south-western Atlantic (Reclutas bed 39°24′ S–55°56′W). Scallops were collected monthly and the sexual maturity stages were determined histologically ($N = 508$). Sex-ratio was 1:1 (*t-test $P > 0.05$*). The size of first sexual maturity was estimated from males of an average of 36.63 mm and females of 36.31 mm of shell height. The relative gonadal condition index (RGCI) showed an annual cycle, with higher values during winter–spring and lower values during summer–autumn; an inverse relationship for the relative muscle condition index (RMCI) was observed with maximum values in early summer. Thus, a reallocation of energy from soma to gonad appears to be inevitable to meet energy demand of gonad development. Seven histological stages of sexual maturity were established for both sexes: (1) immature; (2) early maturity; (3) advanced maturity,;(4) ripe; (5) spawning; (6) spent; and (7) recovery. Individuals in early and advanced maturity were found throughout the year; however, they were found more frequently between June and September. Spawning began in October (early spring) and extended through March (late summer–early autumn) coexisting with early and advanced maturity stages supported by the annual variation of the RGCI and the food availability into the system.*

Keywords: reproductive cycle; gametogenesis; size of first maturity; *Zygochlamys patagonica*; scallops

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INTRODUCTION

The life cycle of target species and knowledge of reproductive cycle of a fishery resource are a necessary step in determining when the recruitment might occur. As annual variations of recruitment in part depend on the reproductive potential (Barber & Blake, 2006), one of the basic goals of fisheries management is to conserve sufficient reproductive potential of a stock to allow a sustainable exploitation (Marshall *et al.*, 2003). This is in part supported by the knowledge of reproductive variables such as size at first maturity and extension of spawning period (Gosling, 2003). Particularly for scallop species, commercial interest is based on the adductor muscle, in which their mass varies seasonally in relation to gametogenesis and spawning (Bricelj *et al.*, 1987 a, b; Barber & Blake, 2006).

Various exogenous and endogenous factors determine the timing and extent of reproductive events for a particular species at a particular location and time (Sastry, 1979; Barber & Blake, 2006). Regarding bivalves, temperature and food supply are considered the most important environmental factors in the regulation of gamete maturation and spawning (MacDonald & Thompson, 1986; Pearse *et al.*, 1991; Brey & Hain, 1992). Life history knowledge and the relationship with the environmental parameters are the baseline to establish regulations to help preserve a target resource from the fishing effect.

Geographical distribution of the Patagonian scallop *Zygochlamys patagonica* in the south-eastern Pacific extends from Chiloé Island (42°00′S; Valladares & Stotz, 1996) to Cape Horn (55°56′S), and in the south-eastern Atlantic northwards to off the Río de la Plata estuary (35°50′S) (Lasta & Zampatti, 1981; Waloszek & Waloszek, 1986; Defeo & Brazeiro, 1994; Gutiérrez & Defeo, 2003, 2005). Location of the main aggregations of Patagonian scallop overlaps with the Shelf-break Frontal System at the 100 m isobath (Bogazzi *et al.*, 2005). This area is characterized by the development of seasonal thermocline–pycnocline and meso-scale processes influencing the circulation and exchange that would generate nutrient enrichment and hence high productivity over the front (Bogazzi *et al.*, 2005).

The Patagonian scallop fishery has been conducted since 1996 on the south-western Atlantic coast (Lasta & Bremec, 1998), with an annual catch of 39.522 tons of commercial size scallops that produce 5.535 tons of adductor muscle landing (estimated for 2005; Lasta & Campodónico, 2006). Considering the commercial importance of this species and the importance of the knowledge on reproductive biology for developing a proper management, little information concerning its reproduction is available. According to the results of Waloszek & Waloszek (1986), analysing a pool of

Corresponding author:
S. Campodónico
Email: scampodo@inidep.edu.ar

individuals from different locations across their latitudinal gradient (39°47′S to 54°30′S), first sexual maturity is reached at 45 mm shell height (SH, ≅ 2 years old) and the emission of gametes occurs in two pulses: one during spring and the other during late summer–early autumn. Although hermaphroditism is the general rule in pectinid (Beninger & Le Penec, 2006), *Zygochlamys patagonica* is a gonochoric species (Campodónico *et al.*, 2004).

In scallops with a broad geographical distribution such as *Z. patagonica*, many authors have mentioned the important role that latitudinal variations play in their reproductive cycles (Sastry, 1979; Barber & Blake, 1983), thus, it is important to consider the spatial scale of analysis. Due to the commercial importance of *Z. patagonica*, and in view of the importance of improving the knowledge about reproductive characteristics of this species, the main objectives of this study were: (1) to analyse the variations of the gonadal condition index and muscle condition index of *Z. patagonica* through the year; (2) to determine a macroscopic scale of gonadal stages; (3) to describe the gonadal development stages using histological techniques and determine the reproductive cycle; and (4) to estimate the sex-ratio and size at first maturity of this scallop at Reclutas bed.

MATERIALS AND METHODS

Monthly sub-samples of *Z. patagonica* were collected in Reclutas bed (39°20′S–56°W and 39°30′S–55°52′W, 1085 km², south-western Atlantic Ocean), in a closed fishing area of 216 km² at depths of~104 m (Figure 1). Samples were obtained on board of the RV 'Capitan Cánepa' using a non-selective 2.5 m wide dredge (Lasta & Bremec, 1997) between October 1999 and March 2001. Bottom temperature and salinity were obtained by conductivity–temperature–depth SeaBird Model 19-02.

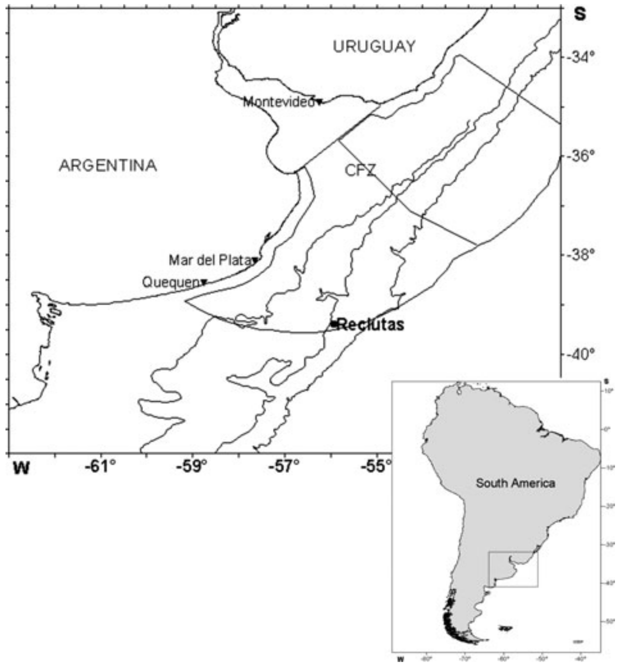

Fig. 1. Sampling area: location of Reclutas bed, in the south-western Atlantic. CFZ, Common Fishery Zone. Isobaths of 100, 200 and 1000 m.

Shell height (umbo to ventral axis, SH) was measured for each individual ($N = 1368$) to the nearest 1 mm and gonadal mass and muscle mass (GM, MM; ± 0.01 g) were recorded. Sex-ratio was analysed for the total sub-sample by examining gonadal smears and was tested against a 1:1 ratio by performing a χ^2-test (Zar, 1999).

Relative condition indices

Gonadal (RGCI) and muscle (RMCI) condition values were estimated using a condition index (with adult individuals > 45 mm SH). For size–mass relationships, $\text{Mass} = a * \text{SH}^b$, linear regression analysis was carried out on the log-transformed data by: $\log(\text{Mass}) = a + b * (\log(\text{SH}))$.

Monthly gonadal condition values were analysed using the condition index: $\text{CI} = \text{Mass}/\text{SH}^b$, where b is the slope from the linear regression, and was normalized using the relative condition index (see Lasta *et al.*, 2001 for details):

$$\text{RCI} = (\text{CI} - \text{mean CI})/(\text{SD of CI}). \quad \text{SD, standard deviation.}$$

A two-way analysis of variance (ANOVA) was used to examine differences in the RGCI and RMCI among seasons and sexes. Given the RGCI data heteroscedasticity (Cochran's C, $P < 0.01$), ANOVA was still performed since this test is robust to heterogeneity of variance; however, the level of significance was set at $\alpha = 0.01$ to reduce the risk of Type I error (Underwood, 1997). Multiple comparisons were made using Scheffé's F-test when differences were found (Zar, 1999).

Macroscopic and microscopic observations

Gonadal maturity was analysed from specimens collected in early March 2001 ($N = 247$) in order to define a macroscopic sexual maturity scale. The scallops were shucked and gonads were examined macroscopically for determination of sexual maturity mainly based on colour, external appearance and size of testes and ovaries and posterior, validated by histological analysis.

For histological analysis, a total of 508 scallops (about 30 individuals per month) between 55 and 65 mm SH were sampled. Gonads were removed and preserved in 7% formalin for 24 h. After fixation, a tissue portion was dehydrated in ethanol, cleared in xylol and embedded in paraffin. Sections were cut of 5-μm thickness and stained with Harris's haematoxylin followed by eosin counterstain. Histological staging of gonads was based on the development stage of germinal cells, following the description of Beninger & Le Pennec (2006) and Eckelbarger & Davis (1996 a, b).

Regarding gonadal stages there have been some discrepancies in terms used in the literature such as follicle, acini and alveolar; thus to avoid possible confusions we followed the meanings proposed by Beninger & Le Pennec (2006).

Size at first maturity

Shell height at first maturity was based on 864 specimens between 16 and 55 mm SH collected from November 2000 to February 2001. Individuals were grouped in 1 mm size-classes and classified histologically as mature (with oocytes or sperm present in the acini) or immature (with scantly and small acini containing few sexual cells). To estimate size at L50% a logistic model was fitted to the proportion of mature individuals by SH class using the maximum likelihood method (Kendal & Stuart, 1967). Also, it registered the size of the smallest male and female with active gonads such as individuals capable of spawning at the time of capture or in the near future (according with Hunter *et al.*, 1992).

RESULTS

Zygochlamys patagonica is a gonochoric species. The sex-ratio was no different to 1:1 (238 males; 237 female, χ^2-test, $P > 0.05$) for the complete studied period. Maximum and minimum values of sea bottom temperature occur in early winter (June, 6.64°C) and early spring (October, 5.53°C) respectively.

Relative condition indices

RELATIVE GONADAL CONDITION INDEX

The RGCI varied among seasons (two-way ANOVA, $P < 0.01$) showing the higher value in winter 2000 with respect to the rest of the seasons, spring 1999 with an intermediate value between winter 2000 and all the other seasons, and the lower values in summer 2000 and 2001 (Figure 2 A, Scheffé's F-test, $P < 0.05$). No differences were observed between sexes (two-way ANOVA, $P > 0.05$).

RELATIVE MUSCLE CONDITION INDEX

The RMCI varied among seasons (two-way ANOVA, $P < 0.01$) showing the lower value in winter 2000 with the higher value in summer 2001 and intermediate values in the rest of the seasons (Scheffé's F-test, Figure 2 B). No differences were observed between sexes (two-way ANOVA, $P > 0.05$).

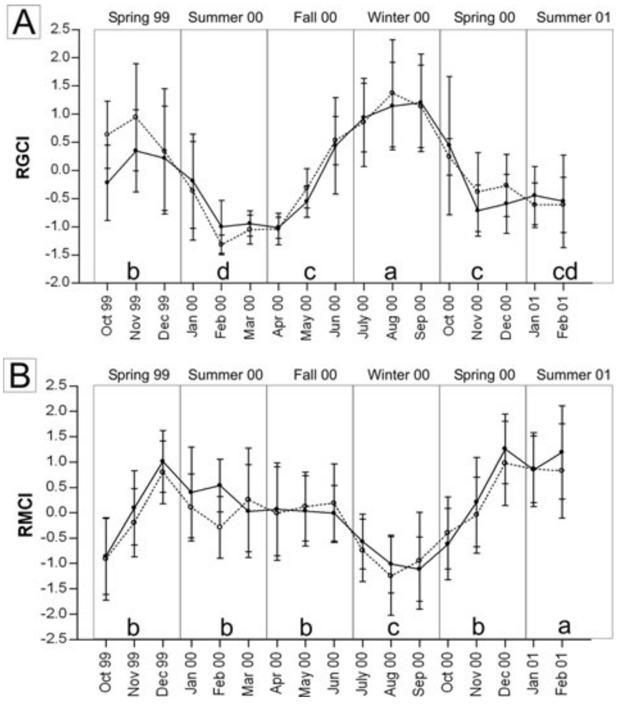

Fig. 2. Variation of relative gonadal condition index (RGCI) and relative muscle condition index (RMCI) from October 1999 to February 2001 in males and females of *Zygochlamys patagonica*. Male, solid line; female, dotted line. Equal letters indicate no significant differences at $\alpha = 0.05$. The average ratio of dependent variable decreases in alphabetical sequence.

Male and female gonadal stages

MACROSCOPIC OBSERVATION

No sexual external dimorphism was found, although during periods of middle and maximum gonadal development, it was possible to differentiate both sexes by the coloration of the gonads: female gonad was orange whereas the male gonad was cream.

A macroscopic gonadal scale of five stages (I–V) for both sexes was defined as follows:

I. Juvenile–early maturation

Small gonads, transparent or colourless, with an angular and flattened appearance.

II. Advanced maturation

Gonads near to maximum size, testis is white or cream (Figure 3 A) and the ovary is orange or bright orange (Figure 4 A).

III. Ripe

Gonads larger than other body organs (the most conspicuous structure in the scallop), rounded, and the surface smooth and glossy. Intense coloration: testis are white or cream (Figure 3 B); the ovary is bright orange (Figure 4 B).

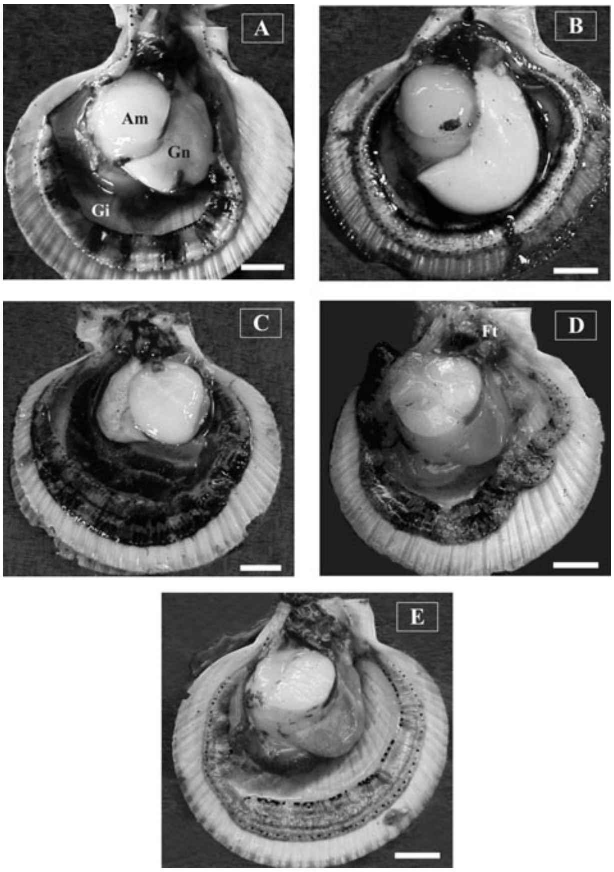

Fig. 3. Macroscopic observation of gonadal stages of male of *Zygochlamys patagonica*. (A) Stage II; (B) Stage III; (C) Stage IV (partially spawned); and (D–E) Stage V. Am, adductor muscle; Gn, gonad; Ft, foot; Gi; gill. Scale bar = 1 cm.

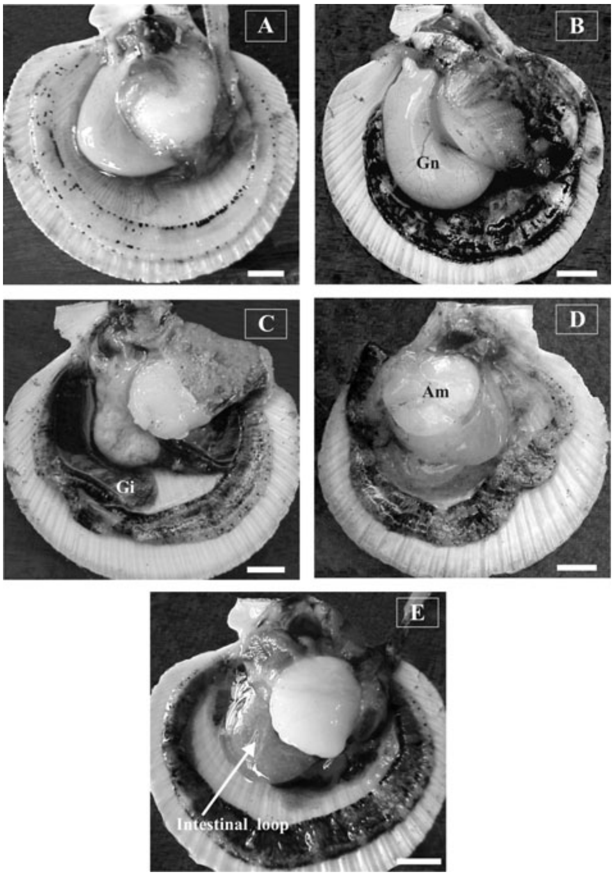

Fig. 4. Macroscopic observation of gonadal stages of female of *Zygochlamys patagonica*. (A) Stage II; (B) Stage III; (C) Stage IV (partially spawned); and (D–E) Stage V. Am, adductor muscle; Gn, gonad; Gi, gill. Scale bar = 1 cm.

IV. Spawning

Gonads reduced in size and collapsed, with empty areas. Testis is white or practically colourless (Figure 3 C) and the ovary is amber or dull orange (Figure 4 C).

V. Spent

Gonads flaccid. Testis containing sex cells cloudy white, rest transparent (Figure 3 D). The ovary is amber or pale orange, or transparent and colourless (Figure 4 D). It is possible to discern the intestinal loop within them. In some cases, sexes are not differentiated (Figures 3 E & 4 E).

HISTOLOGICAL DESCRIPTION OF MATURITY STAGES

A scale of seven stages for both sexes was defined by analysis of different development phases of germinal cells as follows:

I. Immature (corresponding to macroscopic Stage I)

Sexes are microscopically indistinguishable with absence of gametes. Only few acini surrounded by abundant lax connective tissue are observed (juvenile, Figure 5).

II. Early maturation (corresponding to macroscopic Stage I)

Gonads at this stage contain abundant inter-acinal connective tissue and small acini. The first gametogenesis stages are observed. In males, the acini show a row of spermatogonia and a wide band of spermatocytes and spermatids forming a germinal layer (Figure 5 B). In females, basophilic previtellogenic oocytes in first growth phase are observed covering the acini walls (Figure 6 A).

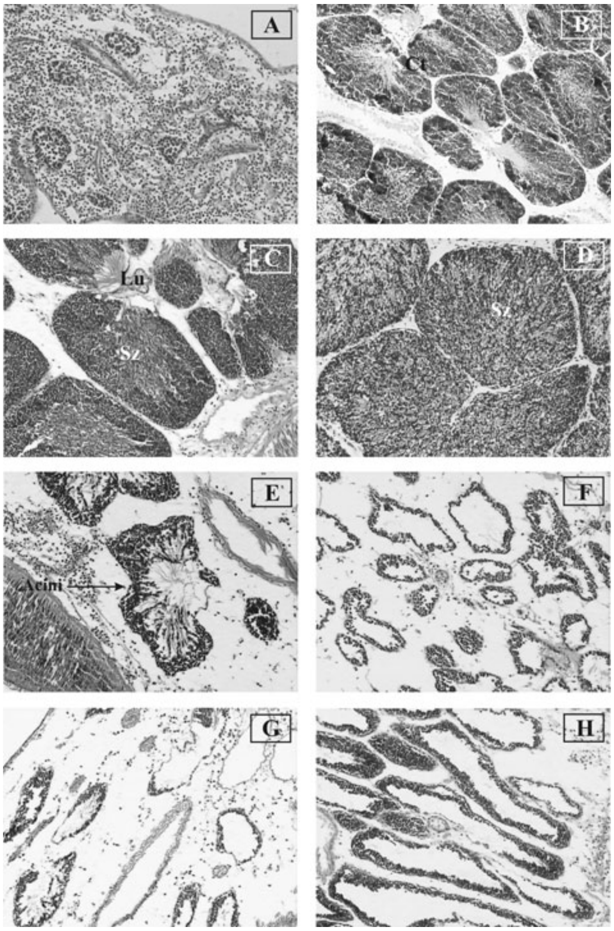

Fig. 5. Photomicrographs of gonadal stages of males of *Zygochlamys patagonica*. (A) Juvenile; (B) Stage II; (C) Stage III; (D) Stage IV; (E) Stage V (partially spawned); (F) Stage V; (G) Stage VI; and (H) Stage VII. Sz, spermatozoa; Ct, connective tissue; Lu, lumen. Magnification, 10X.

III. Advanced maturation (corresponding to macroscopic Stage II)

Inter-acinal connective tissue is scarce. The acini are very large and touching each other. In males, the layer of spermatocytes and spermatids is very reduced, and there are spermatozoa in the lumen. The spermatozoa become arranged with tails pointing toward the centre of the lumen (Figure 5 C). In females, yolked oocytes with eosinophilic cytoplasm are free in the centre of the lumen while others are fixed to the acinal wall by a thin stalk (Figure 6 B).

IV. Ripe (corresponding to macroscopic Stage III)

Gonads attain maximum size. Connective tissues are replaced by acini full of ripe gametes and acinal walls are thin. In males the lumen are packed with ripe spermatozoa (Figure 5 D). In females yolked, oocytes have the maximum size and take on oval or polygonal shapes (Figure 6 C).

V. Spawning (corresponding to macroscopic Stage IV)

Some empty alveoli can be seen. Acini are more or less empty, depending on the spawning degree, the presence of residual sperm or oocytes in restoration (atresia) can be observed. Acini with different abundance of spermatozoa or yolked

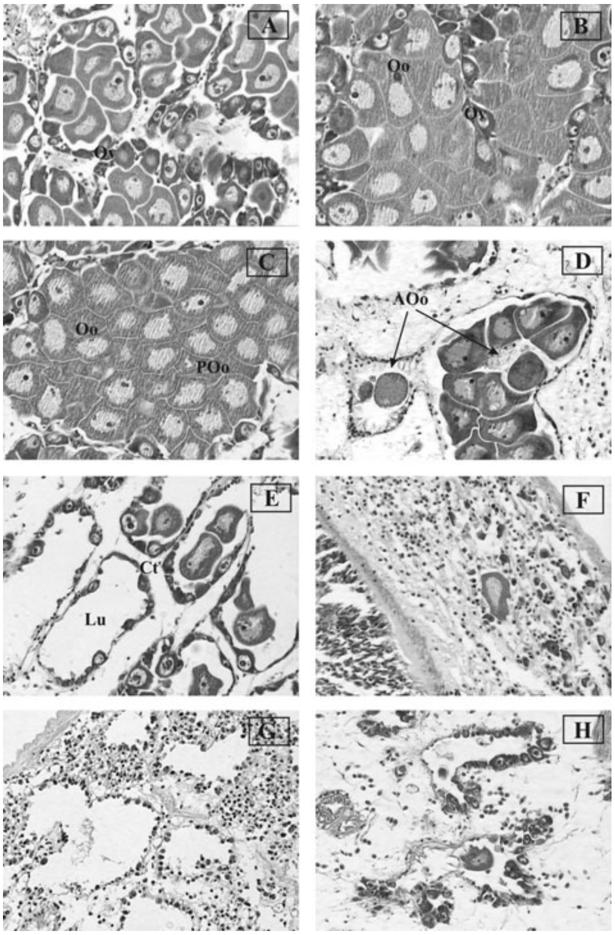

Fig. 6. Photomicrographs of gonadal stages of females of *Zygochlamys patagonica*. (A) Stage II; (B) Stage III; (C) Stage IV; (D) Stage V (partially spawned); (E) Stage V (spent); (F) Stage VI; (G) Stage VI (alveolar); and (H) Stage VII. AOo, atresic oocytes; Ov, ovocyte; Oo, oocyte; POo, polygonal oocyte; Ct, connective tissue; Lu, lumen; Magnification, 10X.

oocytes can be observed for males and females, respectively (Figures 5 E, 5 F, 6 D & 6 E).

VI. Spent (corresponding to macroscopic Stage V)
After spawning. Inter-acinal connective tissue increases and acini reduce in size (Figures 5 G & 6 F, males and females respectively). In cases with advanced degradation of residual gametes, sexes can be undifferentiated (Figure 6 G).

VII. Recovery
Acini remain empty and abundant. Early gametogenetic stages apparent around periphery of acini (Figures 5 H & 6 H, males and females respectively).

Reproductive cycle

The reproductive cycles of females and males were described from the monthly percentage of microscopic gonadal development stages. Both sexes were synchronic in gametogenic development and in the spawning period.

MALE REPRODUCTIVE CYCLE

Analysis of the monthly distribution of maturity stages showed that Stage IV was predominant from November 1999 to January 2000 (75–80%, Figure 7 A). Temporal distribution of Stage III was similar, but with lower percentages. From February to April, most of individuals were in the spent stage, with low percentages of spawning. During May mostly males were in the recovery phase, while from June to September 2000 the predominant stage was advanced maturity. During October, as in February 2001, spawning stage showed a high percentage (39%). In November and December 2000, males were mainly in spent condition (59% and 45%, respectively); while in January 2001 the spawning and spent stages were the most representative.

FEMALE REPRODUCTIVE CYCLE

Spawning activity was observed in October 1999, increasing until December 1999 with the highest percentage of Stage V (85%; Figure 7 B). Between February and April 2000, females were predominantly in the spent condition while in May recovery was the most conspicuous stage. From June to September, most of females were in early or advanced maturation. From October 2000 to February 2001, some females were in spawning stage, coinciding with females in recovery (October and November) and spent stages.

Size at first maturity

The size at first maturity was 36.63 mm SH for males and 36.31 mm SH for females (Figure 8). No differences were observed between both sexes ($P > 0.05$). The smallest male and female with active gonads corresponded to 25 and 32 mm SH respectively.

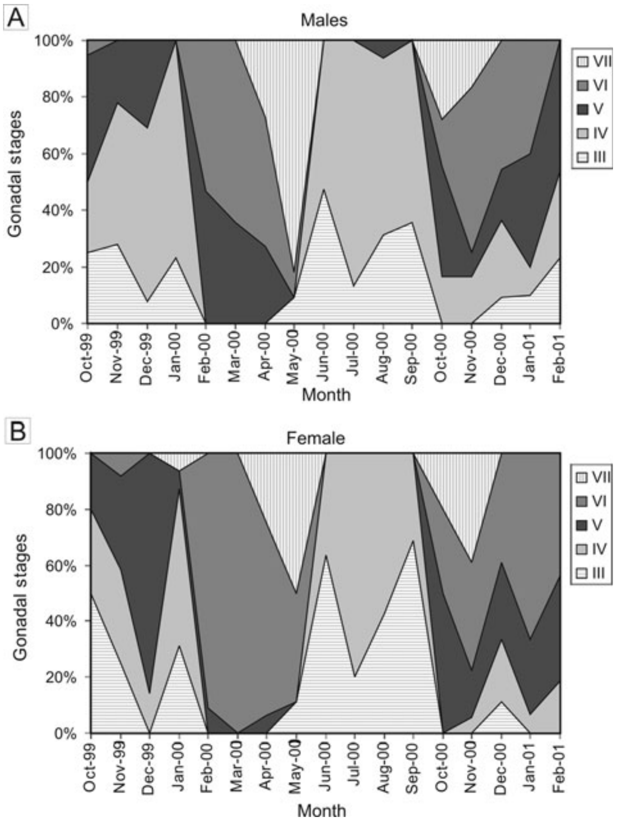

Fig. 7. Percentage of *Zygochlamys patagonica* in each gonadal stage, between October 1999 and February 2001(N = 503). (A) Male; and (B) female.

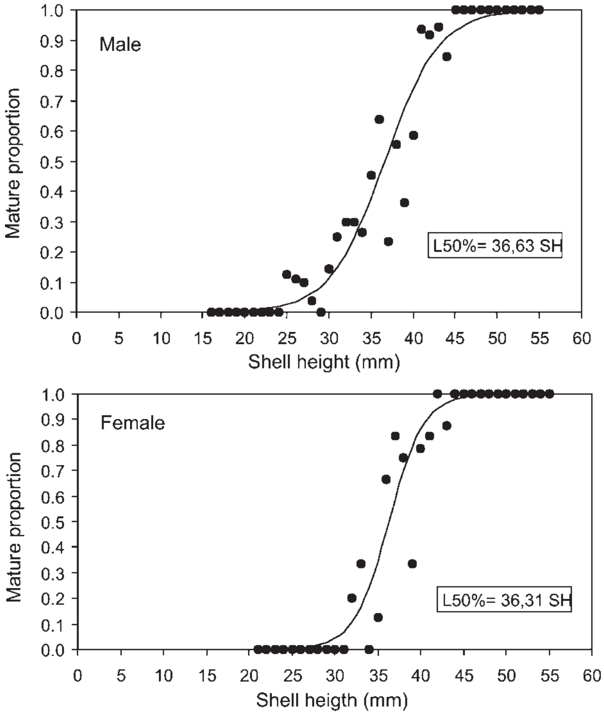

Fig. 8. Size at first maturity of *Zygochlamys patagonica* in Reclutas bed. (A) Male (N = 585); and (B) female (N = 279).

DISCUSSION

The annual reproductive cycle of *Zygochlamys patagonica* at Reclutas bed showed a sharp seasonality that involves a period of gametogenesis during autumn and winter followed by a protracted spawning event with partial emissions that takes place during spring and summer, supported by the annual variation of the RGCI and the food availability into the system.

Based on a sex–size frequency analysis distribution, it was suggested that *Z. patagonica* presents sequential protandric hermaphroditism (Orensanz *et al.*, 1991) or a possible sexual inversion (Calvo *et al.*, 1998). However, as was previously observed (Campodónico *et al.*, 2004), we found that in the Reclutas bed, *Z. patagonica* is a gonochoric species presenting a sex-ratio of 1:1.

The RGCI showed an annual cycle, with higher values during winter–spring, matching with the gametogenesis process and lower values during summer–autumn coinciding with the spawning and postspawning period. This pattern of monthly variation in RGCI was similar to that previously observed for individuals from the same bed where an inverse relationship for the muscle condition index was found (Lomovasky *et al.*, 2007 a; this study). A similar pattern of variation between the gonadal mass and adductor muscle mass through the year occurs in other pectinids such as *Argopecten irradians irradians* (Bricelj *et al.*, 1987a, b), *Chlamys opercularis* (Taylor & Venn, 1979), *C. septemradiata* (Ansell, 1974), *Patinopecten caurinus* (MacDonald & Bourne, 1987), *Placopecten magellanicus* (Robinson *et al.*, 1981; MacDonald & Thompson, 1988) and *Pecten maximus* (Comely, 1974), where there is an energetic investment in gonadal production at the expense of adductor muscles mass (see Bricelj *et al.*, 1987 a, b). This phenomenon was associated with the use of muscular glycogen reserves for gamete production (Bayne, 1976; Zaba, 1981). In *Aequipecten (Chlamys) tehuelcha*, the muscle weight showed also seasonal fluctuation, associated with the primary production cycle and spawning season (Orensanz, 1986), in which muscle rapidly grows during the autumn (matching the autumn phytoplankton bloom); this tissue does not change during winter, and later it lost weight during spring–summer coinciding with spawning. The interannual differences observed in the RGCI and RMCI from *Z. patagonica* could be due to interannual fluctuations in the nutrient storage cycle caused by variations in food availability (e.g. Robinson *et al.*, 1981; Navarro *et al.*, 1989).

Both spawning periods detected in our study were followed by very strong and successful recruitments (1999–2000 and 2000–2001) (Lasta & Campodónico, personal observation). The extended spawning period with partial emissions observed for *Z. patagonica*, and the different gonadal stages coexisting during long periods throughout the year, could be a strategy which provides multiple opportunities for larval development in unpredictable environments and thus, leads to high larval survival becoming an important factor in determining recruitment success, such as was observed for *Pecten maximus* (Paulet *et al.*, 1988). A similar annual reproductive cycle was found for this species from individuals of a wide range of distribution (39°47′S to 54°30′S, Waloszek & Waloszek, 1986).

The size at first maturity was approximately 36 mm SH for both males and females, which correspond to an age between 2–3 years old (following Lomovasky *et al.*, 2007 b). A previous study analysing samples obtained from a wide latitudinal range (between 40° and 54° S) showed a value of 45 mm SH (Waloszek & Waloszek, 1986); these differences could be attributable to the different scales of analysis. It is known that the reproductive cycle in marine bivalves shows high intraspecific variations (Sastry, 1970), moreover, in scallops with a broad geographical distribution, many authors have mentioned the important role that latitudinal variations play in their reproductive cycles (Sastry, 1979; Barber & Blake, 1983), therefore it is important to consider the spatial scale. Our work is restricted to micro or small scale (place or patch) where population processes (trophic or reproductive) correspond to the neighbourhoods of individuals (Orensanz & Jamieson, 1998).

What factors are the main triggers in the regulation of the reproductive cycle in Z. patagonica*?*

Temperature and food supply are the most important parameters as regulators of reproductive cycle in bivalves (e.g. Broom & Mason, 1978; Luna Gonzalez *et al.*, 2000; Darriba *et al.*, 2004; Delgado & Perez Camacho, 2005). However, the reproductive cycle of *Z. patagonica* was not clearly related to the water temperature according to the lack of differences found in metabolic rate measured between temperatures existing in the study area (Heilmayer, 2004) and to the seasonal variation of 2°C of sea bottom temperature on Reclutas bed (Baldoni & Guerrero, 2000; Lomovasky *et al.*, 2007 a) which is not expected to affect the reproductive cycle (Lomovasky *et al.*, 2007 a). Thus, we focused on the food supply as a regulator.

The main concentration of chlorophyll-*a* of the annual phytoplankton growth cycle in the study area occurs during austral spring (Carreto *et al.*, 1995); at the same time, the water column vertical stratification begins (2–3°C, thermocline development) between October and November (Baldoni & Guerrero, 2000; Romero *et al.*, 2006), coinciding with the spawning period and a decrease of RGCI values (this study). The phytoplankton growth continues during summer coupled with maximum somatic growth of scallops, as indicated by the rapid increase in adductor RMCI since September onwards. Phytoplankton biomass remains high in autumn, when the secondary peak and the vertical mixture of the water column occur (by connective circulation pattern) and the stratification is broken off (Baldoni & Guerrero, 2000; Rivas & Piola, 2002). This process coincides with the beginning of gonadal development. *Zygochlamys patagonica* switches from somatic to gonad production around May–June (Lomovasky *et al.*, 2007 a), at the same time when primary production and thus food supply cease. Thus, a reallocation of energy from soma to gonad, as observed in other pectinid species (Bricelj *et al.*, 1987a, b; Bricelj & Shumway, 1991) appears to be inevitable to meet energy demand of gonad development. Subsequently, gonads grow until August–September, when they must be ready for spawning in order to match larval development with the spring bloom enhancing the prospects for larval survival (Bogazzi *et al.*, 2005; Lomovasky *et al.*, 2007 a).

As was previously mentioned, it is important to consider the latitudinal range because it is closely linked to environmental conditions and with gonad development. The present study evaluated the reproductive cycle of *Z. patagonica* for a small area compared with the species distribution. We think it creates a basis of forthcoming studies dealing with latitudinal trends, linking gonad development with environmental conditions.

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REFERENCES

Ansell A.D. (1974) Seasonal changes in biochemical composition of the bivalve *Chlamys septemradiata* from the Clyde Sea area. *Marine Biology* 25, 85–99.

Baldoni A. and Guerrero R. (2000) Seasonal pattern of temperature over the outer shelf of the Argentinean Basin. In *IV Jornadas Nacionales de Ciencias del Mar, Puerto Madryn, Argentina*, pp. 36.

Barber B.J. and Blake N.J. (1983) Growth and reproduction of the bay scallop, *Argopecten irradians* (Lamark) at its southern distributional limit. *Journal of Experimental Marine Biology and Ecology* 66, 247–258.

Barber B.J. and Blake N.J. (2006) Reproductive physiology. In Shumway S. and Parsons G.J. (eds) *Scallops: biology, ecology and aquaculture*. 2nd edn. Amsterdam: Elsevier, pp. 357–416.

Bayne B.L. (1976) *Marine mussels: their ecology and physiology*. Cambridge: Cambridge University Press.

Beninger P.G. and Le Penec M. (2006) Functional anatomy of scallops. In Shumway S. and Parsons G.J. (eds) *Scallops: biology, ecology and aquaculture*. 2nd edn. Amsterdam: Elsevier, pp. 123–227.

Bogazzi E., Baldoni A., Rivas A., Martos P., Reta R., Orensanz J.M., Lasta M., Dell'Arciprete P. and Werner F. (2005) Spatial correspondence between areas of concentration of Patagonian scallop (*Zygochlamys patagonica*) and frontal systems in the southwestern Atlantic. *Fisheries Oceanography* 14, 359–376.

Brey T. and Hain S. (1992) Growth, reproduction and production of *Lissarca notorcadensis* (Bivalvia: Philobryidae) in the Weddell Sea, Antarctica. *Marine Ecology Progress Series* 82, 219–226.

Bricelj V.M. and Shumway S.E. (1991) Physiology: energy acquisition and utilization. In Shumway S. (ed.) *Scallops: biology, ecology and aquaculture*. New York: Elsevier, pp. 305–346.

Bricelj V.M., Epp J. and Malouf R.E. (1987a) Intraspecific variation in reproductive and somatic growth cycles of bay scallops *Argopecten irradians. Marine Ecology Progress Series* 36, 123–137.

Bricelj V.M., Epp J. and Malouf R.E. (1987b) Comparative physiology of young and old cohorts of bay scallops *Argopecten irradians irradians* (Lamarck): mortality, growth and oxygen consumption. *Journal of Experimental Marine Biology and Ecology* 112, 73–91.

Broon M.J. and Mason J. (1978) Growth and spawning in the pectinid *Chlamys opercularis* in relation to temperature and phytoplankton concentration. *Marine Biology* 47, 277–285.

Calvo J., Morriconi E. and Orler P.M. (1998) Estrategias reproductivas de moluscos bivalves y equinoideos. In Boschi E. (ed.) *El mar Argentino y sus recursos pesqueros*. INIDEP (Mar del Plata, Argentina) 2, 195–231.

Campodónico S., Macchi G. and Lasta M. (2004) Gonocorismo en la vieira patagónica *Zygochlamys patagonica* (King y Broderip, 1832) en el Banco Reclutas, Argentina. *Revista de Investigación y Desarrollo Pesquero* 16, 91–95.

Carreto J.I., Lutz V., Carignan M.O., Cucchi Colleoni A.D. and De Marco S.G. (1995) Hydrography and chlorophyll a in a transect from the coast to the shelf-break in the Argentinean Sea. *Continental Shelf Research* 15, 315–336.

Comely C.A. (1974) Seasonal variations in the flash weights and biochemical content of the scallop *Pecten maximus* L. in the Clyde Sea area. *Journal of the International Council for the Exploration of the Sea* 35, 281–295.

Darriba S., San Juan F. and Guerra A. (2004) Reproductive cycle of the razor clam *Ensis arcuatus* (Jeffreys, 1865) in northwest Spain and its relation to environmental conditions. *Journal of Experimental Marine Biology and Ecology* 311, 101–115.

Defeo O. and Brazeiro A. (1994) Distribución, estructura poblacional y relaciones biométricas de la vieira *Zygochlamys patagonica* en aguas Uruguayas. *Comunicaciones de la Sociedad Malacologica del Uruguay* 7, 362–367.

Delgado M. and Perez Camacho A. (2005) Histological study of the gonadal development of *Ruditapes decussatus* (L.) (Mollusca:

Bivalvia) and its relationship with available food. *Scientia Marina* 69, 87–97.

Eckelberger K.J. and Davis C.V. (1996a) Ultrastructure of the ovary and gametogenesis in the eastern oyster, *Crassostrea virginica*. I Ovary and oogenesis. *Marine Biology* 127, 79–87.

Eckelberger K.J. and Davis C.V. (1996b) Ultrastructure of the gonad and gametogenesis in the eastern oyster, *Crassostrea virginica*. II testes and spermatogenesis. *Marine Biology* 127, 89–96.

Gosling E. (2003) Fisheries and management of natural populations. In *Fishing new book. Bivalve mollusks: biology, ecology and culture*. Oxford: Blackwell Science, pp. 225–283.

Gutiérrez N. and Defeo O. (2003) Development of new scallop *Zygochlamys patagonica* fishery in Uruguay: latitudinal and bathymetric patterns in biomass and population structure. *Fisheries Research* 62, 21–36.

Gutiérrez N. and Defeo O. (2005) Spatial patterns in population dynamics of the scallop *Zygochlamys patagonica* at the northern edge of its range. *Journal of Shellfish Research* 24, 877–882.

Heilmayer O. (2004) Environment, adaptation and evolution: scallop ecology across the latitudinal gradient. *Reports for Polar and Marine Research. 480, Universität Bremen, Bremen*, 161 pp.

Hunter J.R., Macewicz B.J., Lo N.C. and Kimbrell C.A. (1992) Fecundity, spawning and maturity of female Dover sole *Microstomus pacificus*, with an evaluation of assumptions and precision. *Fisheries Bulletin* 90, 101–128.

Kendal M. and Stuart A. (1967) *The advanced theory of statistics*. 2. 2nd edn. New York: Hafner Publishing Co.

Lasta M. and Bremec C. (1997) *Zygochlamys patagonica* (King & Broderip, 1832): development of a new scallop fishery in the southwestern Atlantic Ocean. In *Proceedings of the XI International Pectinid Workshop, La Paz, México* 1, 138–139.

Lasta M. and Bremec C. (1998) *Zygochlamys patagonica* in the Argentine Sea: a new scallop fishery. *Journal of Shellfish Research* 17, 103–111.

Lasta M. and Campodónico S. (2006) Vieira Patagónica (*Zygochlamys patagonica*): operatividad de la flota, captura y desembarco de callo durante el año 2005. *Informe Técnico INIDEP*, no. 8, 14 pp.

Lasta M. and Zampatti E. (1981) Distribución de capturas de moluscos bivalvos de importancia comercial en el mar argentino. Resultados de las campañas de los B/I "Walther Herwig" y "Shinkai Maru", años 1978 y 1979. *INIDEP (Mar del Plata, Argentina), Contribución*, 383, 128–135.

Lasta M., Valero J., Brey T. and Bremec C. (2001) *Zygochlamys patagonica* beds on the Argentinean Shelf. Part II: Population dynamics of *Z. patagonica. Archive of Fishery and Marine Research* 49, 125–137.

Lomovasky B.J., Iribarne O., Brey T., Mackensen A., Baldoni A., Lasta M. and Campodónico S. (2007a) Annual growth line formation in the deep water Patagonian scallop *Zygochlamys patagonica*. In *Proceedings of the 16th International Pectinid Workshop, Nova Scotia, Canada*, pp. 154–155.

Lomovasky B.J., Lasta M., Valiñas M., Bruschetti M., Ribeiro P., Campodónico S. and Iribarne O. (2007b) Differences in shell morphology and internal growth pattern of the Patagonian scallop *Zygochlamys patagonica* in the four main beds across their SW Atlantic distribution range. *Fisheries Research* (In press, doi:10.1016/j.fishres.2007.09.006)

Luna González A., Cáceres Martinez C., Zúñiga Pacheco C., Lopez Lopez S. and Ceballos Vazquez B.P. (2000) Reproductive cycle of *Argopecten ventricosus* (Sowerby 1842) (Bivalvia: Pectinidae) in the rada del Puerto de Pichilingue, B.C.S., Mexico and its relation to temperature, salinity and food. *Journal of Shellfish Research* 19, 107–112.

MacDonald B.A. and Bourne N.F. (1987) Growth, reproductive output, and energy partitioning in Weathervane scallops, *Patinopecten caurinus*, from British Columbia. *Canadian Journal Fisheries and Aquatic Science* 44, 152–160.

MacDonald B.A. and Thompson R.J. (1986) Influence of temperature and food availability on the ecological energetics of the giant scallop *Placopecten magellanicus. Marine Biology* 93, 37–48.

MacDonald B.A. and Thompson R.J. (1988) Intraspecific variation in growth and reproduction in latitudinally differentiated populations of the giant scallop *Placopecten magellanicus* (Gmelin). *Biological Bulletin. Marine Biological Laboratory, Woods Hole* 175, 361–371.

Marshall T., O'Brien L., Koster F.W., Morgan J., Saborido-Rey F., Secor D.H., Wright P.J., Mukhina N.V. and Björnsson H. (2003) Developing alternative indices of reproductive potential for use in fisheries management: case studies for stocks spanning an information gradient. *Journal of Northwest Atlantic Fishery Science* 33, 161–190.

Navarro E., Iglesias J.I. and Larrañaga A. (1989) Interannual variation in the reproductive cycle and biochemical composition of the cockle *Cerastoderma edule* from Mundaca estuary (Biscay, North Spain). *Marine Biology* 101, 503–511.

Orensanz J.M. (1986) Size, environment and density: the regulation of scallop stock and its management implications. *Canadian Special Publication of Fisheries and Aquatic Sciences* 92, 195–227.

Orensanz J.M. and Jamieson G.S. (1998) The assessment and management of spatially structured stocks: an overview of the North Pacific Symposium on Invertebrate Stock Assessment and Management. *Canadian Special Publication of Fisheries and Aquatic Sciences* 125, 441–459.

Orensanz J.M., Parma A.M. and Iribarne O. (1991) Population dynamics and management of natural stocks. In Shunway S. (ed.) *Scallops: biology, ecology and aquaculture*. Amsterdam: Elsevier, pp. 625–714.

Paulet Y.M., Lucas A. and Gerard A. (1988) Reproduction and larval development in two *Pecten maximus* (L.) populations from Brittany. *Journal of Experimental Marine Biology and Ecology* 119, 145–156.

Pearse J.S., McClintock J.B. and Bosch I. (1991) Reproduction of Antarctic benthic marine invertebrates: tempos, modes and timing. *American Zoologist* 31, 65–80.

Rivas A.L. and Piola A.R. (2002) Vertical stratification on the shelf off northern Patagonia. *Continental Shelf Research* 22, 1549–1558.

Robinson W.E., Wehling W.E., Morse M.P. and McLeod G.C. (1981) Seasonal changes in soft-body component indices and energy reserves in the Atlantic deep-sea scallop, *Placopecten magellanicus. Fisheries Bulletin* 79, 44–458.

Romero S.I., Piola A.R., Charo M. and García C.E. (2006) Chlorophyll *a* variability off Patagonia based on SeaWiFS data. *Journal of Geophysical Research* 111, C05021, doi:10.1029/2005JC003244.

Sastry A.N. (1970) Reproductive physiological variation in latitudinally separated populations of the bay scallop, *Aequipecten irradians* Lamarck. *Biological Bulletin. Marine Biological Laboratory, Woods Hole* 138, 56–65.

Sastry A.N. (1979) Pelecypoda (excluding Ostreidae). In Giese C. and Pearse J.S. (eds) *Reproduction of marine invertebrates*. New York: Academic Press, pp. 113–292.

Taylor A.C. and Venn T.J. (1979) Seasonal variation in weight and biochemical composition of the tissues of the queen scallop, *Chlamys opercularis*, from the Clyde Sea area. *Journal of the*

Marine Biological Association of the United Kingdom 59, 605–621.

Underwood A.J. (1997) *Experiments in ecology*. Cambridge: Cambridge University Press.

Valladares C. and Stotz W. (1996) Crecimiento de *Chlamys patagonica* (Bivalvia: Pectinidae) en dos localidades de la Región de Magallanes, Chile. *Revista Chilena de Historia Natural* 69, 321–338.

Waloszek D. and Waloszek G. (1986) Ergebnisse der Forschungsreisen des FFS 'Walther Herwig' nach Südamerika, LXV. Vorkommen, Reproduktion, Wachstum und mogliche Nutzbakeit von *Chlamys patagonica* (King & Broderip, 1832) (Bivalvia, Pectinidae) auf dem Schelf von Argentinien. *Archiv für Fishchereiwissenschaft* 37, 69–99.

Zaba B.M. (1981) Glycogenolytic pathways in the mantle tissue of *Mytilus edulis* L. *Marine Biology Letters* 2, 67–74.

and

Zar J.H. (1999) *Biostatistical analysis*. 4th edn. Englewood Cliffs, New Jersey: Prentice-Hall, Inc.

Correspondence should be addressed to:
Silvana Campodónico
Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP)
Paseo V. Ocampo No.1
(B7602HSA) Mar del Plata
Argentina
email: scampodo@inidep.edu.ar