Zygochlamys patagonica beds on the Argentinian shelf. Part II: Population dynamics of Z. patagonica

Mario Lasta¹⁾, Juan Valero²⁾, Thomas Brey³⁾, Claudia Bremec^{1, 4)}

- 1) Instituto Nacional de Investigación y Desarollo Pesquero Mar del Plata, Argentina,
- 2) School of Aquatic and Fishery Sciences, University of Washington, Seattle, USA
- 3) Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, Germany
- 4) Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina

Abstract

۲

Population dynamics of the scallop *Zygochlamys patagonica* were investigated on the scallop bed "Reclutas" on the Argentinian shelf between 1995 and 1998. Successful recruitment was observed in 1994 and to a lesser extent in 1995, whereas no recruitment occurred between 1996 and 1998. Individual growth was described best by the von Bertalanffy growth model, $H_t = 74.70$ mm × $(1 - e^{-0.419(t-0.314)})$, based on natural growth ring readings. Annual formation of natural growth rings in the shell was validated by stable isotope ($\delta^{18}O$ and $\delta^{13}C$) analysis. The annual production–biomass ratio (P/B) decreased from 0.693 y⁻¹ in 1995 to 0.638 y⁻¹ in 1998, whereas production increased from 21.1 g SFWM·m⁻²·y⁻¹ to 77.2 g SFWM·m⁻²·y⁻¹. Muscle, soft tissue and gonad contributed 37 %, 56 % and 7 % to total production, respectively. On average, the annual P/B ratio was 0.679 y⁻¹ and the mortality rate, Z was estimated to be 1.039 y⁻¹.

Resumen

Bancos de vieiras Zygochlamys patagonica en la plataforma argentina. Parte II: Dinámica de poblaciones de Z. patagonica

La dinámica de poblaciones del bivalvo Zygochlamys patagonica se investigó en el banco de moluscos "Reclutàs" en la plataforma continental argentina entre 1995 y 1998. Se observó un reclutamiento exitoso en 1994 y menos intenso en 1995 mientras que en 1996 y en 1998 no se detectó reclutamiento. El crecimiento individual se describió mejor con el modelo de von Bertalanffy $H_t = 74.70 \text{ mm} \times (1 - e^{-0.419 (t - 0.314)})$ basado en observaciones de anillos de crecimiento. La formación anual de anillos de crecimiento naturales en la valva se validó con el análisis de isótopos

estables (δ^{18} O y δ^{13} C). La relación producción anual—biomasa (P/B) decreció de 0.693 y⁻¹ en 1995 a 0.638 y⁻¹ en 1998 mientras que la producción aumentó de 21.1 g SFWM·m⁻²·y⁻¹ a 77.2 g SFWM·m⁻²·y⁻¹. El músculo, el tejido blando y las gónadas contribuyeron con 37 %, 56 % y 7 % a la producción total, respectivamente. En promedio, la relación anual P/B fue 0.679 y⁻¹ y la tasa de mortalidad Z, 1.039 y⁻¹.

Kurzfassung

Zygochlamys-patagonica-Bänke auf dem argentinischen Schelf: Teil II: Populationsdynamik von Z. patagonica

Wir untersuchten die Populationsdynamik von Zygochlamys patagonica in der Muschelbank "Reclutas" auf dem argentinischen Schelf zwischen 1995 und 1998. Erfolgreiche Rekrutierungen wurden 1994 und in geringerem Umfang 1995 beobachtet, während zwischen 1996 und 1998 keine Rekrutierung stattfand. Das individuelle Wachstum wird am besten durch die von Bertalanffy Funktion $H_{\tau} = 74.70$ mm × $(1-e^{-0.419\,(t-0.314)})$ beschrieben. Die Analyse stabiler Isotope ($\delta^{18}O$ and $\delta^{13}C$) bestätigte die jährliche Anlage natürlicher Wachstumsringe in der Schale. Das Verhältnis von Produktion zu Biomasse (P/B) sank von $0.693~y^{-1}$ (1995) auf $0.638~y^{-1}$ (1998), während die Produktion von 21.1 g SFWM·m⁻²·y⁻¹ auf 77.2 g SFWM·m⁻²·y⁻¹ zunahm. Muskel, Weichkörper un %, 56 % und 7 % zur Gesamtproduktion bei. Das mittlere P/B-Verhältnis betrug $0.679~y^{-1}$ und die mittlere Sterblichkeitsrate lag bei $1.039~y^{-1}$.

Introduction

In 1995, beds of the scallop Zygochlamys patagonica, King and Broderip, 1832, were discovered on the Argentinian shelf between 39° and 43° S along the 100m isobath (Lasta and Bremec 1998) at a more northerly location than had previously been found. In 1996, a new scallop fishery was established using factory vessels (4 vessels, 50m long, with mechanical processing on board) (Lasta and Bremec 1998). From 1996 through to 2000, 15 108 tons of scallop flesh, which represent 177 758 tons of commercial scallop were landed (Lasta et al. 2001). Parts of the scallop beds identified as recruitment areas were protected from fishing, whereas the 2150 km² area investigated here was exploited slightly during subsequent years (swept areas: 1996: 0.5 %; 1997: 6.4 %, 1998: 0.2 % of total scallop bed area). The structure and productivity of the whole scallop bed macrofaunal community were investigated in the first part of this study by Bremec et al. (2000).

Water masses in the shelf and slope area develop a shelf-break front due to differential heating during the spring and summer, including the development of strong thermo- and pycnoclines (30 to 40 m depth). Bottom water temperature at 100 m depth is about 6 to 8 °C during this time. Thermo- and pycnoclines are destroyed by vertical mixing due to convective processes during autumn and winter, thus leading to about 1 to 2 °C higher bottom water temperatures (Guerrero and Piola 1997) which are about the upper temperature limit of Z. patagonica (Heilmayer *et al.* 2001). Primary production ranges between 0.1 and 2.7gC·m⁻²·d⁻² and amounts to about 350 gC·m⁻² annually (Carreto *et al.* 1995; Negri 1993).

This study is an investigation into the growth, production and mortality of *Z. pata-gonica* on the scallop bed "Reclutas". Since this bed remained relatively undisturbed by fisheries during the investigation period, this study may provide unbiased baseline data on the natural population "dynamics" of this new and economically important fishery in the Southwest Atlantic.

Materials and methods

Sampling

The scallop bed "Reclutas" was sampled regularly between 1995 and 1998. All samples were taken in the region 39°04' to 39°35' S and 55°44' to 56°10′ W (about 2150 km²) and in 85 to 141 m water depth (Figure 1). Between January 1995 and August 1998, 73 samples were collected using a bottom otter trawl as deployed by the commercial fishery (12.6 m mouth opening, 10 cm mesh size in the cod end). On average one trawl took 11 min, covered about 15 700 m² and yielded about 470 kg of scallops. Between August and November 1998, 38 samples were collected using a rectangular dredge (2.5 m

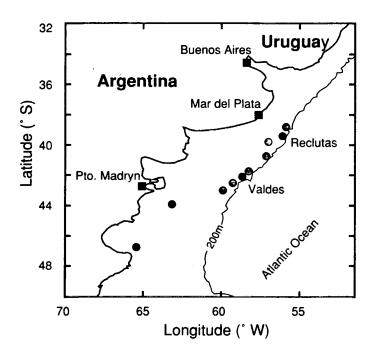


Figure 1: Position of major beds of Zygochlamys patagonica (dots) on the Argentinian shelf. This study was carried out on the bed "Reclutas". Gear efficiency was studied on the bed "Valdes".

mouth opening, 2.5 cm mesh size in top net, 3.5 cm in bottom net). On average one trawl took 10 min, covered 2640 m² and yielded about 100 kg of scallops. Average gear efficiency in the scallop fishery was estimated experimentally to be about 30 % for the bottom otter trawl (Valdes scallop bed, Lasta and Iribarne 1997) and about 18 % for the dredge (*Chlamys tehuelcha* scallop beds, Iribarne *et al.* 1991).

The unsorted total catch was weighed with an accuracy of ± 1 kg. One 10 kg sample was taken randomly from the unsorted catch and scallop and bycatch weights were determined (accuracy ± 0.1 kg). On the basis of this proportion the total scallop catch was estimated. Total height, from the umbo to the opposite shell edge, of the scallops in the sub-sample was measured with a calliper to the nearest millimeter. 200 individuals, covering the whole size range, were collected and frozen at -20° C for laboratory measurements. In the laboratory, total wet weight was determined after removal of epibionts by brushing the shell surface. Muscle, gonad and residual soft tissue were weighed (accuracy ± 0.01 g) separately after dissection.

Data analysis

Size-mass relations (log(M) = a + b log(H)) were established for whole animals, soft tissue mass, muscle mass and gonad mass, the latter for both the period of lowest (March to April) and highest (August to September) gonad mass. To analyze seasonal variation in condition, a relative condition index (RCI) was calculated for muscle as well as the gonad mass of individuals \geq 45 mm height (N = 2361). RCI was calculated by CI = Mass/Height^b,

where b is the exponent of the corresponding overall size-mass relationship (Table 1), and normalized by RCI = (CI - mean CI)/S.D. of CI. Average scallop abundance and biomass per m² were estimated from trawled area, trawl efficiency, number of scallops per trawl, height-frequency distribution of scallops and mass-height relation of scallops.

Growth ring reading and analysis

Only the left (upper) shells were used for identification of external shell growth rings because the right-hand valves showed a higher degree of abrasion. In order to remove epibionts, shells were treated with a 5 % NaOCl solution for 60 min, rinsed in water and then dried. Cleaned shells were inspected under a stereomicroscope using light transmitted vertically through the shell as well as reflected light directed horizontally. Shells with evidence of physical damage were discarded.

Interpretation of growth rings and the identification of annual growth rings were assisted by previous work on this species (Waloszek and Waloszek 1986) and other scallops (Dare 1995). The number of annual bands and the median dorso-ventral (height) linear distances of the annual bands were recorded, thus providing estimates of size at age. Only the actual size-at-age of each individual was used for further analyses.

The von Bertalanffy growth model

$$H_t = H_{\infty} (1 - e^{-K(t - t_0)})$$

was fitted to the data by a maximum likelihood method (Hilborn and Mangel 1997). This method provides maximum likelihood estimates of H_{∞} , K, t_0 and s^2 (assuming normal distribution of the error) and allows the estimation of confidence intervals for each parameter (Hilborn and Mangel 1997).

Stable oxygen and carbon isotope ratios ($\delta^{18}O$ and $\delta^{13}C$) can be used to analyze seasonal variation in growth in living or fossil calcareous species (see Forester *et al.* 1973; Krantz *et al.* 1987; Wefer and Berger 1991). Following previous attempts by Jones *et al.* (1983), Krantz *et al.* (1984), Donner and Nord (1986), Brey and Mackensen (1997) and others, it was decided to use $\delta^{18}O$ and $\delta^{13}C$ in the shell to test whether or not growth rings are formed annually in *Zygochlamys patagonica*. For isotope analysis, carbonate samples of ca. 50 µg each were drilled from the outer shell layer of three individuals in an equally spaced dorsoventral series using a small dental drill (bit size 0.5 mm). Oxygen and carbon isotopes of these samples were measured with a Finnigan MAT251 mass spectrometer coupled to an automatic carbonate preparation device. The precision of measurements was better than ± 0.06 % for $\delta^{13}C$ and ± 0.080 for $\delta^{18}O$, based on routine measurements of a laboratory working standard. Data are related to the Pee Dee Belemnite (PDB) standard through repeated analyses of National Bureau of Standard (NBS) isotopic reference material 19 (Hut 1987).

Production and mortality calculations

To compensate for the differences in sample size, sample distance and time, the size-frequency distributions were transformed prior to production and mortality calculations: (i) within each sample, numbers per 1 mm size class were transformed into percent of sample; (ii) transformed samples were pooled into quarterly samples; (iii) average size-frequency distributions for each year and for the complete investigation period were formed

by pooling the corresponding quarterly samples.

Production of soft and muscle tissue was calculated by the massspecific growth rate method according to Crisp (1984) from the size-frequency distribution, the size-growth function and the appropriate size-mass ratio. Gonad production (PG) was calculated from the size-frequency distribution and the size specific seasonal difference in gonad mass obtained from the size-gonad mass relationship for the period of lowest (March to April) and highest (August to September) gonad mass. Production-biomass ratios (P/B) were found by dividing P by the biomass, B of the corresponding size-frequency sample. Production per square meter was calculated by multiplying P/B with an estimate of biomass derived from trawled area and catch efficiency (see above).

Total mortality rate, Z was estimated by a size-converted catch curve (Pauly 1984) assuming constant mortality rate and using the overall (1995 to 1998) size-frequency distribution and the Von Bertalanffy growth function parameters.

Results

During the four consecutive years of observation, mean shell height and body mass increased from 34.1 mm and 2.96 g wet mass (WM) in 1995 to 47.2 mm and 7.95 g WM in 1998 (Figure 2). Based on the area trawled and trawlefficiency information, average

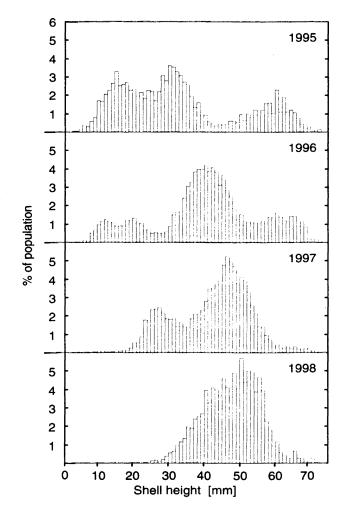


Figure 2: Height frequency distribution of *Zygochlamys* patagonica on the bed "Reclutas" during four consecutive years.

Table 1: Size-mass relations in Z. patagonica.

log(g wet mass) = $a + b \cdot log(mm \text{ height})$. ¹⁾ Whole animal, but epibionts removed from shell surface, ²⁾ Soft parts without muscle and gonads, ³⁾ Minimum gonad weight in March to April (individuals > 35mm height), ⁴⁾ Maximum gonad weight in August to September (individuals > 35mm height).

ΥΥ	а	b	r²	N
Whole Animal ¹⁾	-3.988	2.910	0.984	3898
Muscle	-5.077	3.149	0.952	3898
Soft Tissue ²⁾	-4.595	2.978	0.995	3898
Gonad	-8.293	4.441	0.512	2997
Gonad (Min)3)	-8.845	4.652	0.661	500
Gonad (Max)4)	-7.116	3.921	0.601	729

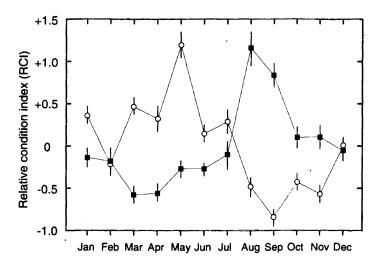


Figure 3: Annual cycle of relative condition index RCI of muscle (circles) and gonad (squares). Plot shows averages ± 95 % confidence intervals (bars). Data refer to individuals >= 45mm height sampled during the period March 1995 to February 1999. RCI is computed by CI = Mass/Height^b, where b is the exponent of the shell size-mass relation, and normalized by RCI = (CI - mean CI)/S.D. of CI.

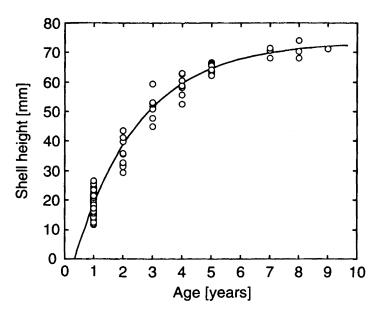


Figure 4: Von Bertalanffy growth function fitted to 197 size-at-age data for *Zygochlamys. patagonica*. Growth function parameters (incl. lower and upper 95 % confidence limit) are: $H_{\infty} = 74.70 \text{ mm} (71.40-78.52), K = 0.419 (0.363-0.481), and t_0 = 0.314 (0.238-0.382).$

scallop abundance and biomass were estimated to range between 18 ind. m^{-2} and 61 gW·m⁻² (1995) and 24 ind.·m⁻² and 220 g WM·m⁻² (1998).

Size-mass ratios for whole animals, muscle, soft tissue and gonads are shown in Table 1. The proportion of whole animal body mass present as shell free body mass (SFWM) increased with shell height from 38 % (3.5 mm) to 60 % (70 mm). Both muscle and gonad mass show a distinct seasonal cycle. The lowest and highest muscle RCI values were found in September and May, respectively, whereas gonad RCI was lowest in March to April and highest in August to September (Figure 3).

Shells with growth rings obscured or disrupted by shell damage, abrasion or epibionts were not used for age assessment. The proportion of these individuals increased with size (8 % for the range 14 to 40 mm, 57 % for individuals larger than 40 mm). A von Bertalanffy growth function fitted best the size-at-age data obtained from growth ring readings in 197 suitable individuals (Figure 4):

$$H_t = 74.70 (1 - e^{-0.419 (t - 0.314)})$$

 $N = 197; R^2 = 0.998.$

95 % confidence limits of the growth function parameters were H_{∞} : 71.40 to 78.52, K: 0.363 to 0.481 and t_0 : 0.238 to 0.382.

The comparison between shell growth rings and stable isotope profiles revealed a distinct coincidence between both parameters (Figure 5). Most growth rings are situated on or just before local δ^{18} O minima (*i. e.* temperature maxima) and local δ^{13} C minima (*i. e.* periods of sedimentation of pelagic primary producers). Growth ring A4 has no corresponding δ^{18} O minimum, and there are some local minima in either δ^{18} O or δ^{13} C which are not accompanied by a growth ring.

Production data referring to the pooled data from 1995 to 1998 are shown in Figure 6. Individual muscle (soft tissue) production reached its maximum between 50 and 52 mm (49 and 51 mm) shell height, amounting to 1.22 (1.80) g SFWM·ind⁻¹. Individual gonad production increased exponentially with shell height, amounting to 0.86 g·ind⁻¹ at 72.5 mm. The annual P/B ratio of the population was 0.679 y⁻¹, corresponding to an annual total production of 45.5 g SFWM·m⁻²·y⁻¹. Muscle, soft tissue and gonad contributed 37.3 %, 56.2 % and 6.5 % to total production, respectively. When calculated separately for each year (Figure 2), the annual P/B ratio decreased from 0.693 y⁻¹ in 1995 to 0.638 y⁻¹ in 1998, whereas annual production increased from 21.1 gSFWM·m⁻²·y⁻¹ to 77.2 g SFWM·m⁻²·y⁻¹.

The total mortality rate, Z of Zygochlamys patagonica was estimated to be 1.039 y⁻¹ by the size converted catch curve

(Figure 7).

Discussion

The distinct difference between mortality rate, $Z(1.039 \text{ y}^{-1})$ and P/B ratio (0.679 y⁻¹) (Allen 1971), as well as the development of the height frequency distribution (Figure 2), indicate that the Zygochlamys patagonica population on the bed "Reclutas" was not in a steady-state during the four year period of observation. According to the height frequency distribution (Figure 2), successful recruitment took place in 1994 and to a much lesser extent in 1995, whereas no recruitment occurred between 1996 and 1998. Judging from the height frequency distribution in 1995 (Figure 2) and the growth function, the last successful recruitment prior to 1994 occurred in 1991. In several suspension feeding bivalve species negative interactions between

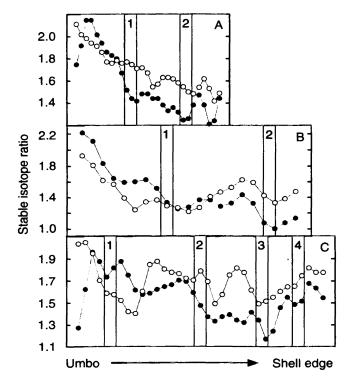


Figure 5: Comparison of visible growth rings on the shell surface (grey bars) with stable isotope profiles (weighed moving average $(x_1+2x_2+x_3)/4$; circles: $\delta^{18}O$, dots: $\delta^{13}C$) in three individuals of *Zygochlamys patagonica* (A: 33 mm height, 30 samples; B: 50 mm height, 23 samples; C: 56 mm height, 35 samples). Width of plot is proportional to bivalve height.

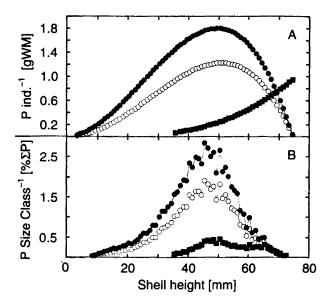


Figure 6: Annual production (average of years 1995 to 1998) in *Zygochlamys patagonica*. A: Individual production; B: Production per size class as a percentage of total population production (somatic tissue + muscle + gonads). Dots: tissue; Circles: muscle; Squares: gonads.

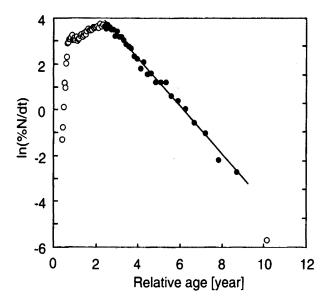


Figure 7: Mortality in *Zygochlamys patagonica* as described by a size converted catch curve. Dots: data used in regression, circles: data excluded from regression. ln(%N/dt) = 6.379 - 1.039t; N = 28; $r^2 = 0.992$.

adults and settling larvae have been observed, either because larvae avoid patches already occupied by adults or because the adults filter settling larvae out of the water, causing high larval mortality (e.g. Woodin 1976, Williams 1980, Vahl 1982). This, however, seems not to be the case in Z. patagonica. Strong recruitment occurred in all dense scallop beds monitored during 2000 (Lasta, unpublished data). Moreover, Bogazzi and Lasta (2000) observed that juveniles (3 to 30 mm height) selectively settled on living scallops (13) to 80 mm height) and were not found on dead shells and other substrata. Hence, there may be as yet unknown large scale hydrographic or ecological phenomena responsible for the irregularities in recruitment. Interannual variability in temperature is a likely candidate, because the upper temperature limit of Z. patagonica is around 9 °C (Heilmayer et al. 2001). This temperature may be exceeded to a sufficient degree during most winters as to lead to reproduction or recruitment failure, thus keeping the population in a nonsteady state continuously.

The annual cycles of somatic and gonad mass in Z. patagonica (Figure 3) seem to be typical for scallop species. Maximum gonad mass or gonad condition index is reached in spring/summer in many species, e.g. in Patinopecten caurinus (British Columbia, MacDonald and Bourne 1987) or in Placopecten magellanicus (Newfoundland, MacDonald and Thompson 1988). Maximum somatic mass or somatic condition index is usually observed in autumn, e.g. in Patinopecten caurinus (British Columbia, MacDonald and Bourne 1987) or in Pecten maximus (Clyde Sea, Comely 1974).

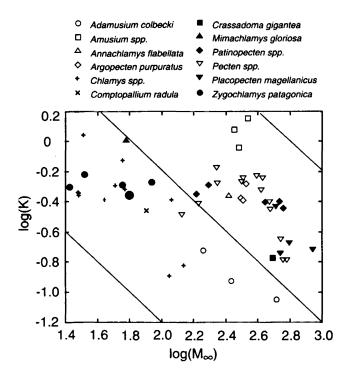


Figure 8: Auximetric grid comparing growth performance of several scallop species. Units of K are y^{-1} , units of M_{∞} are kJ. Body mass was converted to kJ using factors taken from Brey (1999). Diagonal lines represent lines of equal growth performance $P = \log(K \times M_{\infty})$. Data sources: Brey (1999), Lefort (1994), Pranovi *et al.* (1994), Waloszek and Waloszek (1986) and references therein. Large dot: this study.

The estimated growth parameters of the von Bertalanffy model (Figure 4) are close to those reported in previous studies on Z. patagonica on the Argentinian shelf (Waloszek and Waloszek 1986; Orensanz et al. 1991) and Magellan Strait (Valladares and Stotz 1996). They differ, however, from growth parameters reported for other populations of Zygochlamys in Tierra del Fuego and the Magellan Strait (Trautmann 1979; Ríos et al. 1980; Guzmán et al. 1987; Valladares and Stotz 1996), with H_{∞} ranging between 105 and 133 mm. Waloszek (1991) and Valladares and Stotz (1996) consider these populations to be Z. vitrea (King & Broderip, 1832), a larger species coexisting with Z. patagonica in the Magellan Strait. Measured by the index $P = \log(K \times M_{\infty})$ (Munro and Pauly 1983; Pauly 1979), growth performance of Z. patagonica falls in the range of its closest relatives among the scallops, Chlamys spp. (see Waller 1991) as shown by an auximetric plot of log(K) versus $\log(M_{\infty})$ (Figure 8). Unfortunately, Z. vitrea could not be included in Figure 8 because no data on M_{∞} were available.

In their study on the productivity of the epifaunal community on the scallop bed "Reclutas", Bremec *et al.* (2000) estimated annual production of *Z. patagonica* to be between 0.3 and 0.9 g C_{org} ·m⁻²·y⁻¹. This estimate, however, was based on fewer samples and on a P/B ratio derived from an empirical relation. Hence, we assume the present calculation of 45.5 g SFWM·m⁻²·y-1 (= 4.02 g C_{org} ·m⁻²·y⁻¹; with ca. 0.09 g C_{org} ·g SFWM⁻¹ according to Brey 1999) to be more reliable. In terms of total production, the *Z. patagonica*

population on the bed "Reclutas" falls within the range reported from other scallop beds. Annual production of scallops is between 0.7 g $C_{org} \cdot m^{-2} \cdot y^{-1}$ in *Placopecten magellanicus* (Newfoundland, Canada, MacDonald and Thompson 1986) and 15.3 g $C_{org} \cdot m^{-2} \cdot y^{-1}$ in *Chlamys islandica* (Balsfjord, Norway, Vahl 1981 a,b). However, the annual P/B ratio derived for *Z. patagonica* ($P_{total}/B = 0.679 \cdot y^{-1}$, $P_{somatic}/B = 0.635 \cdot y^{-1}$) shows the highest value of all scallop populations investigated so far. The major reason for this high P/B ratio is the low mean body mass in this population over the period of investigation (Figure 9), as body mass is generally the major determinant of P/B in poikilothermic animals (Brey 1999). Obviously the size structure of the *Z. patagonica* population is more strongly dominated by smaller individuals than the size structure of other scallop populations with comparable growth performance (compare Figure 8 and Figure 9).

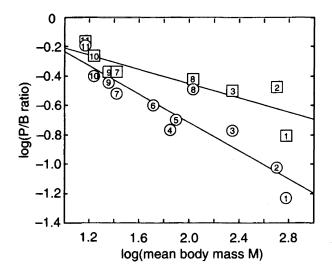


Figure 9: Annual P_{total}/B ratio (squares) and P_{somatic}/B ratio (circles) of scallop populations related to mean body mass (kJ). 1, 8: Patinopecten caurinus (MacDonald and Bourne 1987), 2, 3: Placopecten magellanicus (MacDonald and Thompson 1986), 4: Adamusium colbecki (Stockton 1984), 5: A. colbecki (Berkman 1990), 6: Mizuhopecten yessoensis (Golikov and Scarlato 1970), 7: Chlamys islandica (Vahl 1981a,b), 9, 10: C. varia (Conan and Shaffe 1978; Shafee and Conan 1984), 11: Zygochlamys patagonica (this study). Body mass was converted to kJ acc. to Brey (1999).

Regression lines:

 $log(P_{total}/B) = 0.034 - 0.244 log(M)$ N = 8 $r^2 = 0.734$ $log(P_{somatic}/B) = 0.246 - 0.482 log(M)$ N = 11 $r^2 = 0.845$

References

Allen, K. R., 1971: Relation between production and biomass. Journal of the Fisheries Research Board of Canada 28: 1537–1581.

Berkman, P. A., 1990: The population biology of the Antarctic scallop, *Adamussium colbecki* (Smith 1902) at New Harbor, Ross Sea. In: Kerry, K.R., Hempel, G. (eds.): Antarctic ecosystems. Ecological change and conservation, Berlin: Springer, p. 281–288.

- Bogazzi, E.; Lasta, M., 2000: Capacidad bisógena y natatoria de la vieira patágonica *Zygochlamys* patagonica. Resúmenes de las IV Jornadas Nacionales de Ciencias del Mar, 11–15 Setiembre 2000, Puerto Madryn, Argentina: p. 42.
- Bremec, C.; Brey, T.; Lasta, M.; Valero, J.; Lucifora, L., 2000: *Zygochlamys patagonica* beds on the Argentinian shelf. Part I: Energy flow through the scallop bed community. Archive of Fishery and Marine Research 48: 295–303.
- Brey, T., 1999: Growth performance and mortality in aquatic macrobenthic invertebrates. Advances in Marine Biology 35: 153–223.
- Brey, T.; Mackensen, A., 1997: Stable isotopes prove shell growth bands in the Antarctic bivalve *Laternula elliptica* to be formed annually. Polar Biology 17: 465–468.
- Carreto, J. I.; Lutz, V. A.; Carignan, M.O.; Cucchi Colleoni, A.D.; De Marco, S.G., 1995: Hydrography and chlorophyll a in a transect from the coast to the shelf-break in the Argentinian Sea. Cont. Shelf Res. 15: 315–336.
- Comely, C. A., 1974: Seasonal variation in weights and biochemical content of the scallop *Pecten maximus* L. in the Clyde Sea area. Journal du Conseil 35: 281–285.
- Conan, G.; Shafee, M. S., 1978: Growth and biannual recruitment of black scallops, *Chlamys varia* (L.) in Lavénoc area, Bay of Brest. J. Exp. mar. Biol. Ecol. 35: 59–71.
- Crisp, D. J., 1984: Energy flow measurements. In: Holme, N.A., McIntyre, A.D. (eds.): Methods for the study of marine benthos. Blackwell Scientific, Oxford, p. 284–372.
- Dare, P. J., 1995: Use of external shell microgrowth patterns for determining growth and age in the scallop, *Pecten maximus* (L.). 8th International Pectinid Workshop, Cherbourg (France) May 22–29, 1991. IFREMER, Actes de Colloques 17: 211–217.
- Donner, J.; Nord, A. G., 1986: Carbon and oxygen stable isotope values in shells of *Mytilus edulis* and *Modiolus modiolus* from holocene raised beaches at the outer coast of the Varanger Peninsula, north Norway. Palaeogeogr. Palaeoclimat. Palaeoecol. 56: 35–50.
- Forester, R. M.; Sandberg, P. A.; Anderson, T. F., 1973: Isotopic variability of cheilostome bryozoan skeletons. In: Larwood, G.P., (ed.), Living and fossil Bryozoa. New York: Academic Press, p. 79–94.
- Golikov, A. N.; Scarlato, O. A., 1970: Abundance, dynamics and production properties of populations of edible bivalves *Mizuhopecten yessoensis* and *Spisula sachalinensis* related to the problem of controllable submarine farms at the Western shores of the Sea of Japan. Helgoländer Wiss. Meeresunters. 20: 489–513.
- Guerrero, R., A.; Piola, A. R., 1997: Masas de agua en la plataforma continental. In: Boschi, E. E. (ed.), El Mar Argentino y sus recursos pesqueros. I. Antecedentes históricos de las exploraciones en el mar y las características ambientales. Mar del Plata, INIDEP, p. 107–118.
- Guzmán, L.; Ríos, C.; Ibarra, M.; Oyarzún, S., 1987: Investigación bancos de ostiones y "locos". 2. Recurso "ostión" *Chlamys (Zygochlamys) patagonica* (King & Broderip). Informe Técnico. Informes Instituto de la Patagonia 38: 1–86.
- Heilmayer, O.; Bremec, C.; Brey, T.; Lasta, M.; Valero, J.; 2001. Why are there no Patagonic scallops (*Zygochlamys patagonica*) north of the Rio Plata estuary? 13th. International Pectinid Workshop, Coquimbo, Chile, April 18–24, 2001: 103.
- Hilborn, R.; Mangel, M., 1997: The Ecological Detective: Confronting Models with Data. Monographs in population biology 28. Princeton, New Jersey: Princeton University Press, 315 p.
- Hut, G., 1987: Stable isotope reference samples for geochemical and hydrological investigations. International Atomic Energy Agency Report No. 42, Vienna, Sept. 16–18, 1985.
- Iribarne, O. O.; Lasta, M. L.; Vacas, H. C.; Parma, A. M.; Pascual, M. S., 1991: Assessment of abundance, gear efficiency and disturbance in a scallop dredge fishery: results of a depletion experiment. In: Shumway, S. E., Sandifer, P. A. (eds.), Scallop biology and culture. The world aquaculture society, selected papers from the 7th international pectinid workshop, p. 244–248.

- Jones, D. S.; Williams, D. F.; Arthur, M. A., 1983: Growth history and ecology of the Atlantic surf clam, Spisula solidissima (Dillwyn), as revealed by stable isotope and annual shell increments. J. Exp. Mar. Biol. Ecol. 73: 225–242.
- Krantz, D. E.; Jones, D. S.; Williams, D. F., 1984: Growth rates of the sea scallop, *Placopecten magellanicus*, determined from the ¹⁸O/¹⁶O record in shell calcite. Biol. Bull. 167: 186–199.
- Krantz, D. E.; Williams, F. D.; Jones, D. S., 1987: Ecological and paleoenvironmental information using stable isotope profiles from living and fossil molluscs. Palaeogeogr. Palaeoclimat. Palaeoecol. 58: 249–266.
- Lasta, M. L.; Bremec, C., 1998: Zygochlamys patagonica in the Argentine Sea: a new scallop fishery. J. Shellfish Res. 17: 103–111.
- Lasta, M. L.; Iribarne, O.O., 1997: Southern Atlantic scallop (*Zygochlamys patagonica*) fishery: assessment of gear efficiency through a depletion experiment. J. Shellfish Res. 16: 59–62.
- Lasta, M.; Bogazzi, E.; Bremec, C. 2001: Development and present status of the patagonic scallop fishery (*Zygochlamys patagonica*) in the Argentine Sea. 13th. International Pectinid Workshop, Coquimbo, Chile, April 18–24, 2001: 109–110.
- Lefort, Y., 1994: Growth and mortality of the tropical scallops: *Annachlamys flabellata* (Bernardi), *Comptopallium radula* (Linné) and *Mimachlamys gloriosa* (Reeve) in southwest lagoon of New Caledonia. J. Shellfish Res. 13: 539–546.
- MacDonald, B. A.; Bourne, N. F., 1987: Growth, reproductive output, and energy partitioning in Weathervane scallops, *Patinopecten caurinus*, from British Columbia. Can. J. Fish. Aquat. Sci. 44: 152–160.
- MacDonald, B. A.; Thompson, R. J., 1986: Production, dynamics and energy partitioning in two populations of the giant scallop *Placopecten magellanicus* (Gmelin). J. Exp. Mar. Biol. Ecol. 101: 285–299.
- MacDonald, B. A.; Thompson, R. J., 1988: Intraspecific variation in growth and reproduction in latitudinally differentiated populations of the giant scallop *Placopecten magellanicus* (Gmelin). Biol. Bull. 175: 361–371.
- Munro, J.L.; Pauly, D., 1983: A simple method for comparing the growth of fishes and invertebrates. Fishbyte 1: 5–6.
- Negri, R. M., 1993: Fitoplancton y producción primaria en el área de la plataforma bonaerense próxima al talud continental. INIDEP Tech. Rep., Mar del Plata 1: 1–7.
- Orensanz, J. M.; Parma, A. M.; Iribarne, O. O., 1991: Population dynamics and management of natural stocks. In: Shumway, S. E. (ed.), Scallops: Biology, ecology and aquaculture. Amsterdam: Elsevier, p. 625–689.
- Pauly, D., 1979: Gill size and temperature as governing factors in fish growth: a generalization of von Bertalanffy's growth formula. Berichte aus dem Institut für Meereskunde Kiel 63: 1–156.
- Pauly, D., 1984: Length converted catch curves: A powerful tool for fisheries research in the tropics. Part 2. Fishbyte 2: 17–19.
- Pranovi, F.; Marcato, S.; Zanellato, R., 1994: Analisi biometriche e biologia di popolazione nel mollusco antartico *Adamussium colbecki* a Baia Terra Nova, Mare di Ross. Esratto degli Atti dell'Istituto veneto di Sci., Let. e Arti 152 (CLII): 123–136.
- Ríos, C.; Guzmán, C.; Campodónico, I., 1980: Antecedentes sobre crecimiento y morfometría del ostión de magallanes *Chlamys* (*Zygochlamys*) patagonica (King & Broderip). Informe Técnico. Informe del Instituto de la Patagonia, 18 pp.
- Shafee, M. S.; Conan, G., 1984: Energetic parameters of a population of *Chlamys varia* (Bivalvia: Pectinidae). Mar. Ecol. Prog. Ser. 18: 253–262.
- Stockton, W. L., 1984: The biology and ecology of the epifaunal scallop *Adamussium colbecki* on the west side of McMurdo Sound, Antarctica. Mar. Biol. 78: 171–178.
- Trautmann, S., 1979: Estudio preliminar de edad y crecimiento en el ostión (*Chlamys patagonica* King, 1831) en base a lectura de anillos. Informe Práctica profesional Ingeniería (E) en Acuicultura. Universidad de Chile, sede Osorno, 23 pp.

- Vahl, O., 1981a.: Energy transformations by the iceland scallop, *Chlamys islandica* (O. F. Müller) from 70° N. I. The age-specific energy budget and net growth efficiency. J. Exp. Mar. Biol. Ecol. 53: 281–296.
- Vahl, O., 1981b: Energy transformations by the iceland scallop, *Chlamys islandica* (O.F. Müller) from 70° N. II. The population energy budget. J. Exp. Mar. Biol. Ecol. 53: 297–303.
- Vahl, O., 1982: Long-term variations in recruitment of the Iceland scallop, *Chlamys islandica* from northern Norway. Netherl. J. Sea Res. 16: 80–87.
- Valladares, C.; Stotz, W., 1996: Crecimiento de *Chlamys patagonica* (Bivalvia: Pectinidae) en dos localidades de la Región de Magallanes, Chile. Revista Chilena Historia Natural 69: 321–338.
- Waller, T. R., 1991: Evolutionary relationships among commercial scallops. In: Shumway, S.E. (ed.), Scallops: Biology, ecology and aquaculture. Amsterdam: Elsevier, p. 1–74.
- Waloszek, D., 1991: *Chlamys patagonica* (King & Broderip, 1832), a long "neglected" species from the shelf off the Patagonia Coast. In: Shumway, S. E. and Sandifer, P. A. (eds.): World Aquaculture workshops 1: 256–263.
- Waloszek, D.; Waloszek, G., 1986. Ergebnisse der Forschungsreisen des FFS 'Walther Herwig' nach Südamerika, LXV. Vorkommen, Reproduktion, Wachstum und mögliche Nutzbarkeit von Chlamys patagonica (King and Broderip, 1832) (Bivalvia, Pectinidae) auf dem Schelf von Argentinien. Arch. Fish. Wiss. 37: 69–99.
- Wefer, G.; Berger, W. H., 1991: Isotope paleontology: growth and composition of extant calcareous species. Marine Geology 100: 207–248.
- Williams, J. G., 1980: The influence of adults on the settlement of spat of the clam, *Tapes japonica*. J. Mar. Res. 38: 729-741.
- Woodin, S. A., 1976: Adult-larval interaction in dense infaunal assemblages: Patterns of abundance. J. Mar. Res. 34: 25–41.

Acknowledgements

This study is part of a joint Argentinian-German project (No. ARG 002/98 MAR) funded by the Comisión de Ciencia y Técnica, Argentina, and the International Office of the Federal Ministry for Research and Technology (Bundesministerium für Forschung und Technologie - BMFT), Germany. Juan Valero was supported by scholarships from the Fulbright Program and the University of Washington, Seattle, WA, USA. We are indebted to Angel Marecos for technical assistance. This is INIDEP Contribution N° 1196.

Authors' addresses: Lic. Mario Lasta (corresponding author), Instituto Nacional de Investigación y Desarollo Pesquero c.c. 175. Paseo V. Ocampo I, 7600 Mar del Plata, Argentina, T. +54-223-4860806, F. +54-223-4861830, e-mail: mlasta@inidep.edu.ar; Lic. Juan Valero, School of Aquatic and Fishery Sciences, University of Washington, P. O. Box 355020, Seattle, WA 98195-5020, USA, e-mail: juan@u.washington.edu; Dr. Thomas Brey, Stiftung Alfred Wegener Institut für Polar und Meeresforschung, P. O. Box 120161, 27515 Bremerhaven, Germany, e-mail: tbrey@awibremerhaven.de; Dr. Claudia Bremec, Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Mar del Plata, Argentina, e-mail: cbremec@inidep.edu.ar

Communicated by W. Arntz; received: 19th July 2001; accepted: 26th October 2001; print proof received from author: 27th November 2001