



Population dynamics of *Venus antiqua* (Bivalvia: Veneracea) in the Bahía de Yaldad, Isla de Chiloé, Southern Chile*

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Abstract

Venus antiqua is a dominant member of intertidal and shallow subtidal soft bottom communities in southern Chile, where it is a significant resource for artisanal fisheries. Growth, mortality and productivity of *V. antiqua* were investigated at an intertidal flat in Bahía de Yaldad, Chiloé. Based on growth increment data obtained from a 20 months tagging-recapture experiment, the parameters of the seasonally oscillating von Bertalanffy function were estimated to be $L_{\infty} = 80.0$ mm, $K = 0.183$ y^{-1} , $C = 1.211$ and $t_0 = 0.995$. Production of *V. antiqua* is distinctly higher than in other species of the superfamily Veneracea. Annual production amounted to 40.69 g AFDM $\cdot m^{-2} \cdot y^{-1}$ (somatic tissue), 26.42 g AFDM $\cdot m^{-2} \cdot y^{-1}$ (shell organic matter) and 2.00 g AFDM $\cdot m^{-2} \cdot y^{-1}$ (gonad), respectively, corresponding to a P/B₀ ratio of 0.585 y^{-1} . Total mortality Z , natural mortality M and fishing mortality F were estimated to be 0.664 y^{-1} , 0.333 y^{-1} and 0.331 y^{-1} , respectively. The high exploitation rate E , 0.498 , indicates serious overexploitation of the stock despite the closure of the fishery.

Key words: Bivalvia; Chile; Population dynamic; Production; *Venus antiqua*

1. Introduction

The infaunal filter-feeding bivalve *Venus antiqua* (King & Broderip, 1835) inhabits intertidal and shallow subtidal soft bottoms along the Pacific coast of South America from about 12° S to 54° S, but also along the Atlantic coast south of 31° S, including the Malvinas (Falkland Islands) (Osorio et al., 1983). In Chile, the intertidal and subtidal banks of *V. antiqua* are exploited by local fishermen. During the last decade,

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annual landings were in the order of 30 000 tons, most of which came from banks around “Isla de Chiloé”. *Venus antiqua* is also a food source for several bird species (mainly seagulls) and the predatory gastropod *Xanthochorus cassidiformis* (de Blainville, 1832). However, despite the significance of this clam for artisanal fisheries only a few investigations on the biology and ecology of *V. antiqua* have been carried out (see Jerez et al., 1991 and references therein).

The purpose of this paper is to examine the population dynamics of *V. antiqua* in the Bahía de Yaldad at the Isla de Chiloé and to evaluate the present state of its exploitation.

2. Methods

2.1. Sampling area

The study was carried out at a *V. antiqua* bank located on a tidal flat at Bahía de Yaldad (43° 07' S, 73° 44' W, Fig. 1), Isla de Chiloé, which is the subject of an interdisciplinary study of the ecology of tidal flats in southern Chile and the impact of artisanal fisheries on the system (see Stead, 1992; Zimmermann et al., 1993; Asencio et al., in press a, b; Navarro et al., 1993). The tidal flat (0.5% slope) has an area of about 1 km² at low tide, and the *V. antiqua* stock is concentrated in a 200 m wide band along MLWN. The amplitude of spring tides just exceeds 5 m, with a semidiurnal regime throughout the year. Sediment in the area of the *V. antiqua* bank is heterogenous and characterized as gravely muddy sand (according to Folk, 1980), with the gravel fraction composed mainly (> 50%) of broken bivalve shells. Water temperature during the study period ranged from 6.0 °C in winter to 16.5 °C in summer. Salinity fluctuated around 28‰, occasionally dropping below 25‰ after strong rainfalls.

During previous years the *V. antiqua* bank was heavily exploited by local fishermen, with monthly catches reaching 6 tons wet mass and more (information provided by local dealers). However, exploitation was prohibited by the national authorities (Servicio Nacional de Pesca) in 1991, shortly after the start of this investigation, because all clams were below minimum size for legal extraction (55 mm).

2.2. Sampling

Specimens used for the establishment of length-mass relations were collected in December 1990, January, April, August 1991 and January 1992.

To estimate population density and biomass, quantitative samples were collected along a transect reaching from the low water level to the high water level at 13 dates between April 1990 and August 1991. Each transect consisted of five stations, and at each station two sediment cores of 25 × 25 cm area and 20 cm depth were dug out and sieved through 1.5 mm mesh size. All specimens of *V. antiqua* found were counted and measured.

To obtain growth increment data, specimens of *V. antiqua* were sampled, measured, marked with a number on the periostracum (black drawing ink covered with “Loctite Super Bonder Extra”) and returned to the original site at 10 dates between Novem-

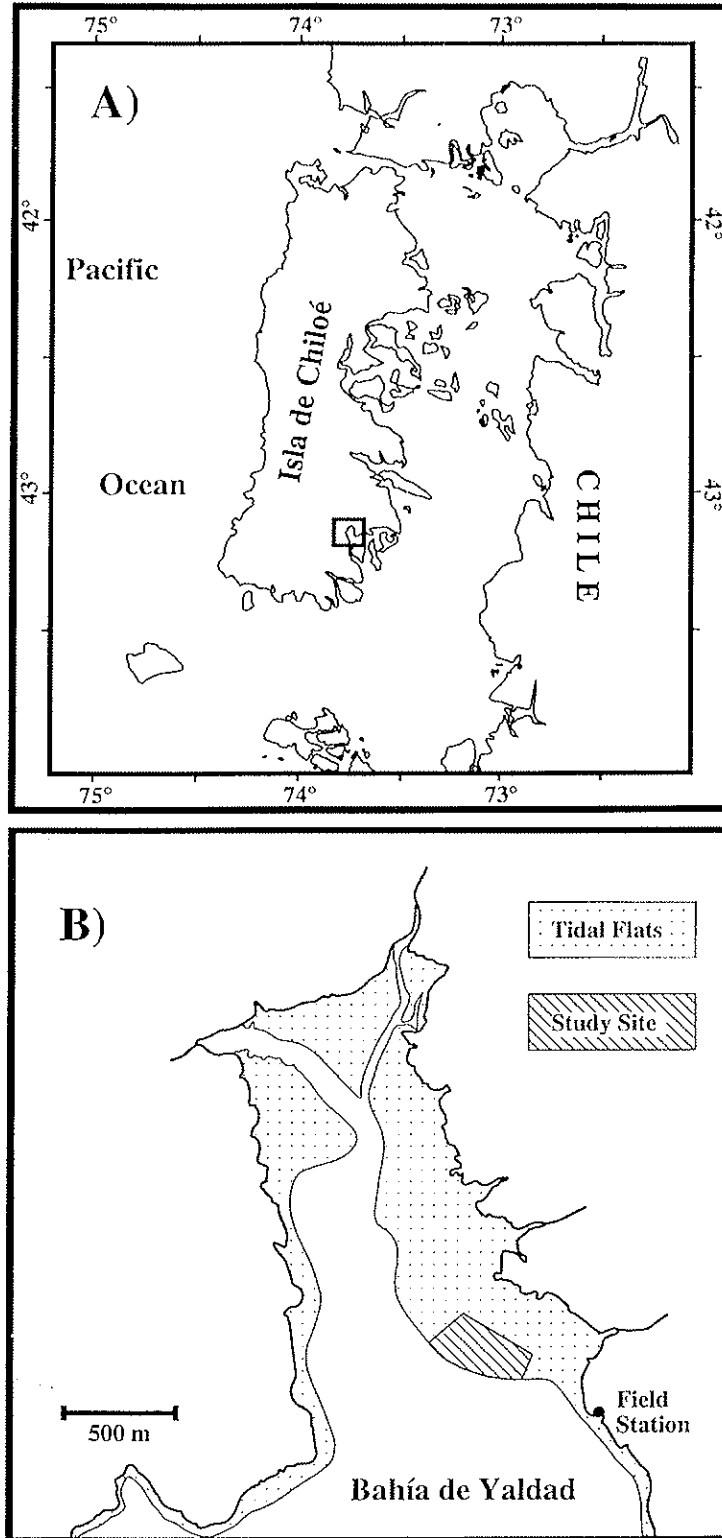


Fig. 1. The investigation area. (A) Island of Chiloé, (B) Bay of Yaldad.

ber 1990 and September 1991. At 10 dates between May 15th 1991 and July 3rd 1992, specimens were recovered, measured and returned again to the tidal flat. The sampling schedule is given in Table 1.

Possible effects of repeated recovery on growth were checked by dividing all marked specimens in August 1991 into two groups of 200 animals each. The first group was recovered periodically, whereas the second group was left undisturbed until July 29th 1992, when the complete experimental area was intensely searched for all remaining clams. The growth increments of both groups were compared by ANOVA.

Growth of the newly settled cohort (i.e. age class 0) was followed in 1990/1991 and in 1991/1992 (Stead, 1992). Subsequent mean length data were used as additional size increment data pairs in the growth analysis.

2.3. Length-mass relations

Length was measured to an accuracy of 0.1 mm. Shell, somatic tissue and gonad tissue were weighed separately. Ash-free dry mass (AFDM) was determined by drying at 80 °C for 24 h (DM) and subsequent ignition at 500 °C for 24 h (ash). Analysis of covariance [$\log(M)$ vs $\log(L)$ and vs month] was used to test for differences among different sampling months, and length-mass (L - M) relations of the form

$$M = a \times L^b$$

Table 1
The number of newly marked and re-marked specimens of *V. antiqua* per sampling date

Date	Newly marked	Re-measured
5 Nov. 1990	83	0
3 Dec. 1990	88	0
15 Jan. 1991	37	0
1 March 1991	28	0
30 March 1991	25	0
15 May 1991	36	135
14 June 1991	32	0
13 July 1991	55	0
10 Aug. 1991	164	236
10 Sept. 1991	59	0
10 Oct. 1991	0	202
23 Nov. 1991	0	216
18 Jan. 1992	0	202
18 Feb. 1992	0	142
18 March 1992	0	138
15 April 1992	0	105
16 May 1992	0	105
3 Jul. 1992	0	97
Total	607	1578

were established by an iterative nonlinear fitting algorithm (SIMPLEX, see Press et al., 1986).

2.4. Growth analysis

Growth was described by a seasonally oscillating von Bertalanffy growth curve according to Pauly & Gaschutz (1979) as modified by Hoenig & Choudary (1982) and Somers (1988):

$$\begin{aligned}L_t &= L_\infty \times (1 - e^{-K \times (t - t_0) + A + B}) \\A &= C \times \sin(2\pi \times (t - t_s))/2\pi \\B &= C \times \sin(2\pi \times (t_0 - t_s))/2\pi\end{aligned}$$

where L_∞ is asymptotic length, K is the growth constant, t_0 is age at which length is zero, C is the amplitude of growth oscillation, and t_s is the starting point of the oscillation with respect to $t=0$. The parameters of this function were estimated by fitting a re-arranged function (Appeldoorn, 1987) to the size increment data pairs using the SIMPLEX algorithm:

$$\begin{aligned}L_2 &= L_\infty \times (1 - (1 - L_1/L_\infty) \times e^{-K \times (t_2 - t_1) - A' + B'}) \\A' &= C \times \sin(2\pi \times (t_1 - t_s))/2\pi \\B' &= C \times \sin(2\pi \times (t_2 - t_s))/2\pi\end{aligned}$$

For t_0 no estimate can be obtained from growth increment data.

2.5. Production

Somatic production was calculated by the mass-specific growth rate method (see Crisp, 1984) from (1) an average length-frequency sample based on the pooled samples, (2) the von Bertalanffy growth function and (3) the length-mass relation:

$$P = \sum N_i \times M_i \times G_i \quad [\text{g AFDM} \cdot \text{m}^{-2} \cdot \text{y}^{-1}]$$

N_i and M_i are the average number of animals ($N \text{ m}^{-2}$) and mean individual somatic mass in size class i , and G_i is the mass-specific growth rate:

$$G_i = b \times K \times ((L_\infty/L_i) - 1) \quad [\text{y}^{-1}]$$

where b is the exponent of the length-mass relation, K , L_∞ are parameters of the von Bertalanffy function, and L_i is the mean length in class i . Annual P/\bar{B} ratio was calculated from production P and biomass \bar{B} :

$$\bar{B} = \sum N_i \times (M_i + \text{MG}_i) \quad [\text{g AFDM} \cdot \text{m}^{-2}]$$

where MG_i is annual average individual gonad mass in length class i .

Gonad production was computed from the length-gonad mass relations in the pre-spawning and the post-spawning periods and the pooled length-frequency distributions:

$$PG = \sum N_i \times (MG_{i,pre} - MG_{i,post})$$

where $MG_{i,pre}$ and $MG_{i,post}$ are gonad mass in length class i before and after spawning, respectively.

2.6. Natural, fishing & total mortality and exploitation rate

Natural mortality rate M had to be estimated on an empirical basis. In unexploited populations M equals total mortality Z since fishery mortality F is zero. Allen (1971) showed that in a steady state population the somatic P/\bar{B} ratio is equal to the total mortality rate Z , if mortality can be described by the single negative model and if individual growth follows a von Bertalanffy function. Hence natural mortality of *V. antiqua* can be estimated from empirical relations between population parameters and annual P/\bar{B} ratio in unexploited benthic invertebrate populations. We estimated maximum age A_{Max} from an empirical relationship between A_{Max} and the growth constant K of the von Bertalanffy function in mollusc populations (Table 3), and M from empirical relations between P/\bar{B} ratio and A_{Max} (Table 3).

A size-converted catch curve was used to compute total mortality rate Z of the single negative exponential mortality model:

$$N_i = N_0 \times e^{-Z \times t_i}$$

This curve was calculated from the size-frequency distribution of the pooled quantitative samples and the von Bertalanffy growth function by the ELEFAN (Electronic Length Frequency Analysis) program of D. Pauly and co-workers (see Brey et al., 1988, 1990; Gayanilo et al., 1989):

$$(N_i/\Delta t_i) = N_0' \times e^{-Z \times t_i}$$

N_i is the number of animals in size class i , Δt_i is the time required to grow through this size class and t_i is the relative age of the mid-size of class i . Total mortality Z is computed by the linear regression:

$$\log_e(N_i/\Delta t_i) = a + b \times t_i; \quad Z = -b$$

Fishing mortality rate F and actual exploitation rate E were computed by

$$F = Z - M \text{ and } E = F/Z.$$

3. Results

3.1. Length-mass relations

Neither in ash free dry mass of somatic tissue ($p = 0.07$) and of the shell ($p = 0.55$) nor in the inorganic shell mass (i.e. ash, $p = 0.68$) significant differences in the length-

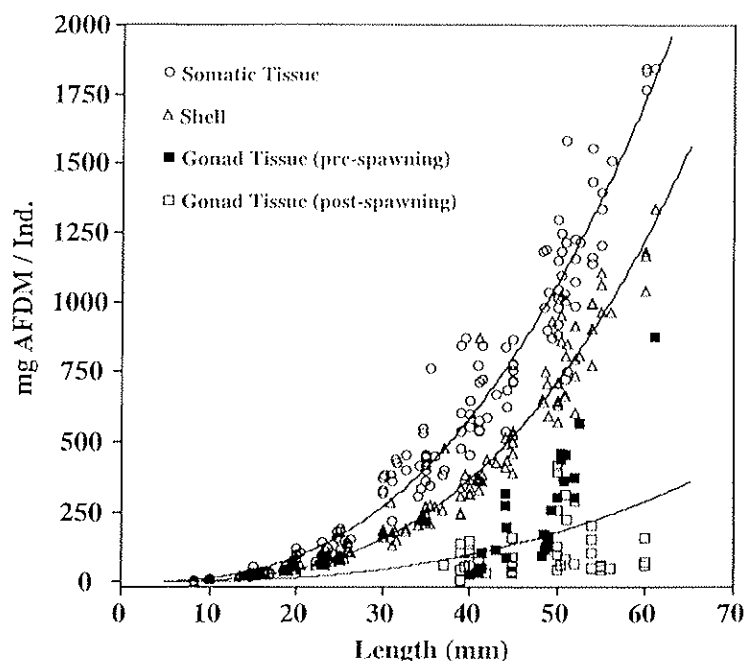


Fig. 2. Length-mass relations in *V. antiqua* ($M = a \times L^b$). The corresponding parameter values are given in Table 2. Note the common relation for pre- and post-spawning gonad tissue. O, Somatic tissue; Δ , shell organic matter; \square , gonads.

mass relations among the different months could be detected. Fig. 2 and Table 2 show the length-mass relations for the combined data. Gonad mass was determined in a few animals (≤ 15) per sampling date only. To increase the reliability of the length-gonad

Table 2
Length-mass relations in *V. antiqua*

(A) Somatic and shell mass

Mass	<i>N</i>	<i>a</i>	<i>b</i>	<i>r</i> ²
Somatic tissue (mg AFDM)	152	0.030	2.678	0.947
Shell (mg AFDM)	152	0.006	2.771	0.946
Inorganic shell (mg Ash)	152	0.117	3.020	0.975

(B) Gonad mass

Date	<i>N</i>	<i>a</i>	<i>b</i>	<i>r</i> ²
Dec. 90, Jan. 91, Jan. 92	44	0.035	2.049	0.109
April 91, Aug. 91	23	4.66×10^{-11}	7.488	0.577
All sampling dates	67	0.005	2.678	0.137

Mass = $a \times \text{length}^b$.

Units of length are mm.

$r^2 = 1 - \text{residual sum of squares} / \text{total sum of squares}$.

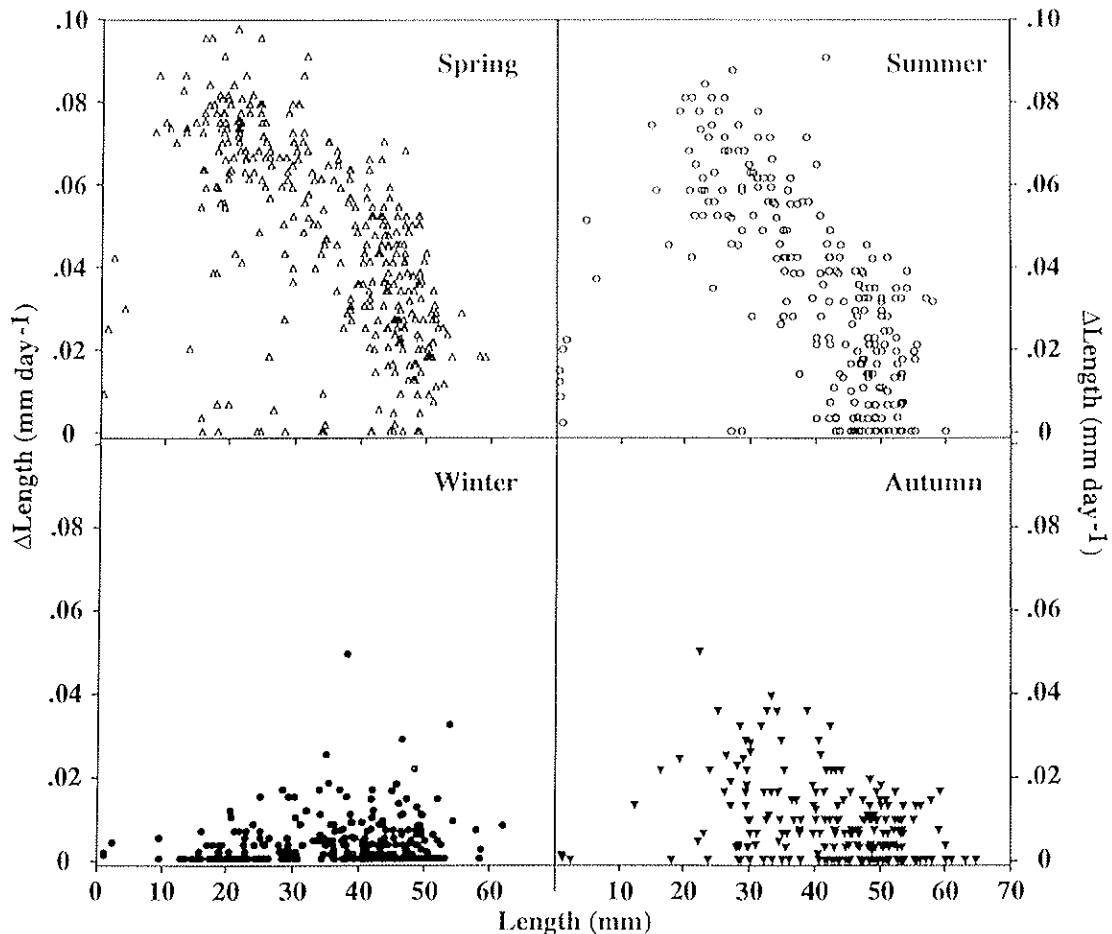


Fig. 4. Plot of the daily length increment versus initial length based on 1154 data pairs of L_1 , L_2 from all seasons.

growth during a certain period due to technical reasons (sinus function), in reality there is zero growth during this time (Figs. 4 & 5).

3.2.1. Productivity

Individual somatic tissue production as well as shell organic matter production increase steadily up to about $310 \text{ mg AFDM} \cdot \text{ind}^{-1} \cdot \text{y}^{-1}$ and $240 \text{ mg AFDM} \cdot \text{ind}^{-1} \cdot \text{y}^{-1}$ at 50–55 mm length and then decrease again. Calculated gonad production starts at about 40 mm length and increases exponentially towards the highest length classes, exceeding total non-gonad production above 55 mm length (Fig. 6).

Annual production of the population was computed to be $40.69 \text{ g AFDM} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$ (somatic tissue), $26.42 \text{ g AFDM} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$ (shell organic matter) and $2.00 \text{ g AFDM} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$ (gonad), respectively. Fig. 7 shows the distribution of production among the length classes. Mean annual biomass amounts to $118.06 \text{ g AFDM} \cdot \text{m}^{-2}$ (mean abundance = $227.6 \text{ ind} \cdot \text{m}^{-2}$), hence annual P/\bar{B} ratio is calculated to be 0.585 y^{-1} .

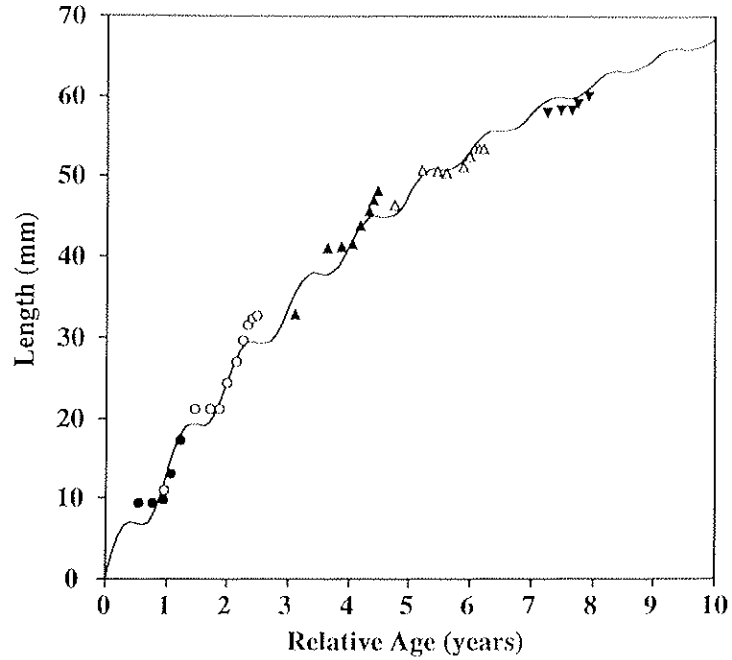


Fig. 5. Seasonally oscillating von Bertalanffy growth curve fitted to 1154 data pairs of L_1 , L_2 (L_∞ fixed at 80 mm, $K = 0.183$, $C = 1.211$, $t_s = 0.995$; $N = 1154$, Residual sum of squares = 562.4, $[1-RSS/TSS] = 0.996$). Superimposed are subsequent growth-increment data of five specimens of *V. antiqua*. Each symbol refers to a different specimen. The number of data points differs among specimens due to the different sampling schedules. The x-axis is denoted relative age since age at length zero (t_0) is unknown.

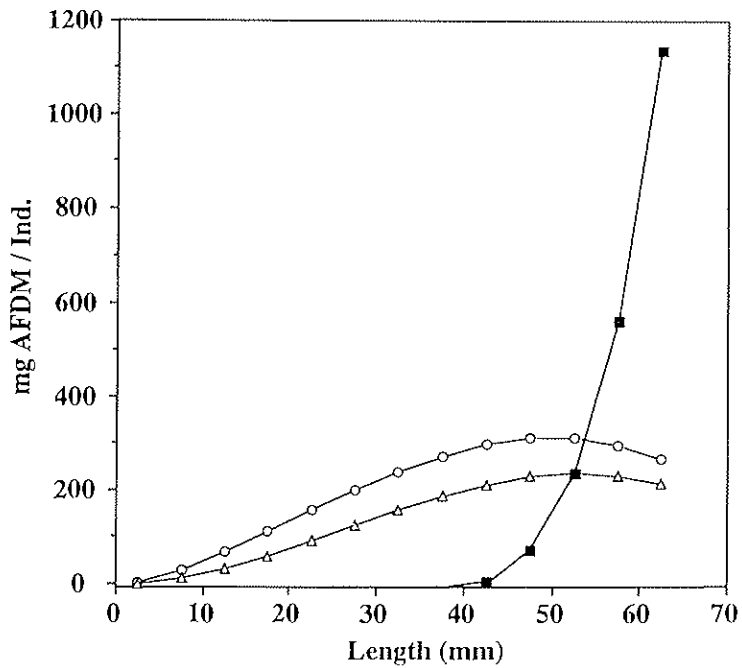


Fig. 6. Relation between length (mm) and individual somatic and gonad production ($\text{mg AFDM} \cdot \text{y}^{-1}$). \circ , somatic tissue; \triangle , shell organic matter; \square , gonads. See chapter "methods" for computation procedures.

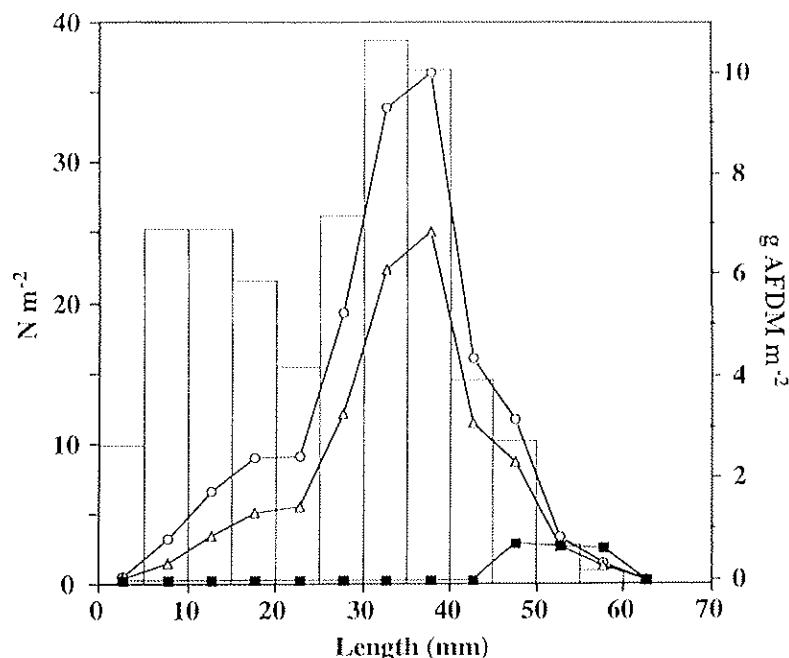


Fig. 7. Distribution of annual production ($\text{g AFDM} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$) among the length classes of the *V. antiqua* population. \circ , somatic tissue; Δ , shell organic matter; \blacksquare , gonads.

3.3. Mortality and exploitation rate

Maximum age A_{Max} of *V. antiqua* at Yaldad was estimated to be 10.4 years by the empirical relation between A_{Max} and K (Table 3), which is a reasonable estimate with respect to our growth curve (Fig. 5). Subsequently, natural mortality rate M was estimated to 0.333 y^{-1} (mean of 0.341, 0.423, 0.236 from equations in Table 3).

Total mortality Z was estimated to be 0.664 y^{-1} by the size converted catch curve shown in Fig. 8. Hence, fishing mortality F was 0.331 y^{-1} and exploitation rate E was 0.498.

Table 3

Empirical relations between the growth constant K of the von Bertalanffy and maximum age (A_{Max}) as well as between A_{Max} and annual P/\bar{B} ratio in unexploited benthic invertebrate populations

Author	X	Y	Intercept a	Slope b	Number of data	r^2
Brey (unpubl.) ¹	K	A_{Max}	0.450	-0.768	89	0.566
Brey (unpubl.) ¹	A_{Max}	P/\bar{B}	0.682	-1.130	219	0.767
Hoernig (1983)	A_{Max}	P/\bar{B}	0.625	-0.982	134	0.820
Warwick (1980) ²	A_{Max}	P/\bar{B}	0.538	-0.112	85	0.567

$\log_{10}(Y) = a + b \times \log_{10}(X)$; ¹ Molluscs only; ² $\log_{10}(Y) = a + b \times X$.

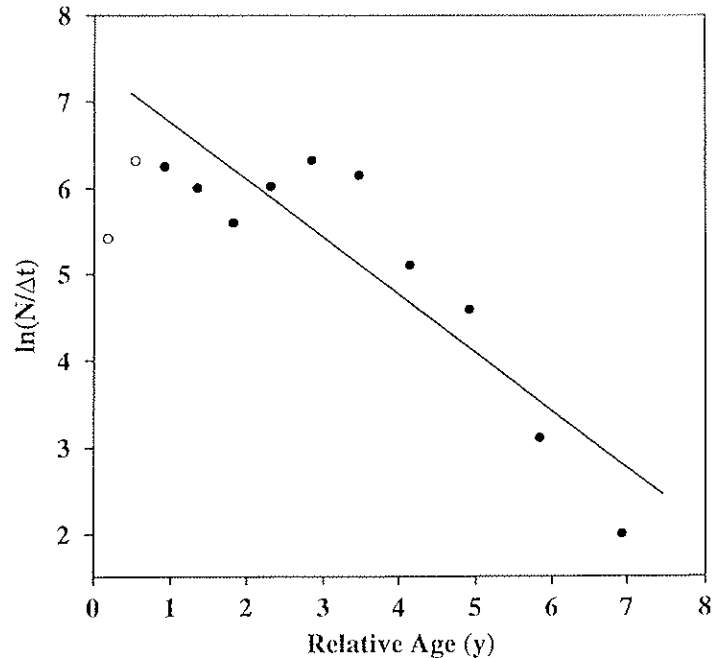


Fig. 8. Size converted catch curve of *V. antiqua* based on the pooled length-frequency samples (Fig. 7) and the von Bertalanffy growth function (Fig. 5). ●, Points included in catch curve calculation, ○, points excluded. $\log_e(N_i/\Delta t_i) = 7.393 - 0.664 \times t_i$, $r^2 = 0.801$.

4. Discussion

4.1. Growth

The computed oscillating von Bertalanffy growth curve (Fig. 5) shows an excellent fit to the data with the exception of specimens ≤ 10 mm length (age class 0), where growth seems to be generally overestimated by the above function. This indicates that a growth function with inflexion point such as the Gompertz function may fit the data better in this particular size range. Our first estimate of L_∞ , 71.22 mm, underestimates the true L_∞ , since specimens up to 80 mm length are known from subtidal areas of the Bahía de Yaldad as well as from other areas of southern Chile (Bustos et al., 1981; Jerez et al., 1991). In the intertidal of Yaldad, however, these large specimens do not occur due to the impact of artisanal fishermen. Hence, they are missing from our growth increment data set (Fig. 4), leading to an under-estimation of L_∞ , as indicated by the almost equally good fit of the growth curve obtained with L_∞ fixed at 80 mm.

Our growth parameter values differ clearly from those estimated for a population of *V. antiqua* in the Bahía de Ancud, ≈ 150 km north of Yaldad. From growth ring readings, Bustos et al. (1981) estimated a non-oscillating von Bertalanffy growth curve with $L_\infty = 78.7$ mm and $K = 0.421 \text{ y}^{-1}$. Jerez et al. (1991) estimated $L_\infty = 102$ mm and $K = 0.421 \text{ y}^{-1}$ by a method based on the analysis of length-frequency samples. Bustos et al. (1981) assumed *V. antiqua* to form two growth rings per year as stated by Estay et al. (1979), but did not validate this assumption. There is new evidence from recent

investigations that *V. antiqua* in the sublittoral of the Bahía de Ancud forms only one growth ring per year during autumn/winter (C. Rojas, pers. comm.), as observed in our experiments in Bahía de Yaldad, too. Consequently, Bustos et al. (1981) may have overestimated the growth constant K by about 100%. We therefore conclude that *V. antiqua* around Isla de Chiloé will reach size at first reproduction (46–48 mm, Lozada & Bustos, 1984) at an age of 4–5 years, whereas size of permitted legal extraction (55 mm) will be reached at 5–6 years of age.

The observed strong seasonal pattern of growth in *V. antiqua* with highest growth rates in spring and summer and lowest growth rates during winter may be related to the similar annual pattern of primary production in southern Chile waters (Navarro et al., 1993).

4.2. Productivity

Annual somatic P/\bar{B} ratio of *V. antiqua* in the intertidal of Yaldad, 0.572 y^{-1} , is in the upper range of values referring to various species of the superfamily Veneracea, if the relation between population P/\bar{B} ratio and mean body mass is taken into account (Fig. 9). The above-average P/\bar{B} ratio may be explained best by increased mortality due to human exploitation, since P/\bar{B} ratio and mortality rate are more or less equivalent (Allen, 1971). Under natural conditions, P/\bar{B} ratio is expected to be equal to natural

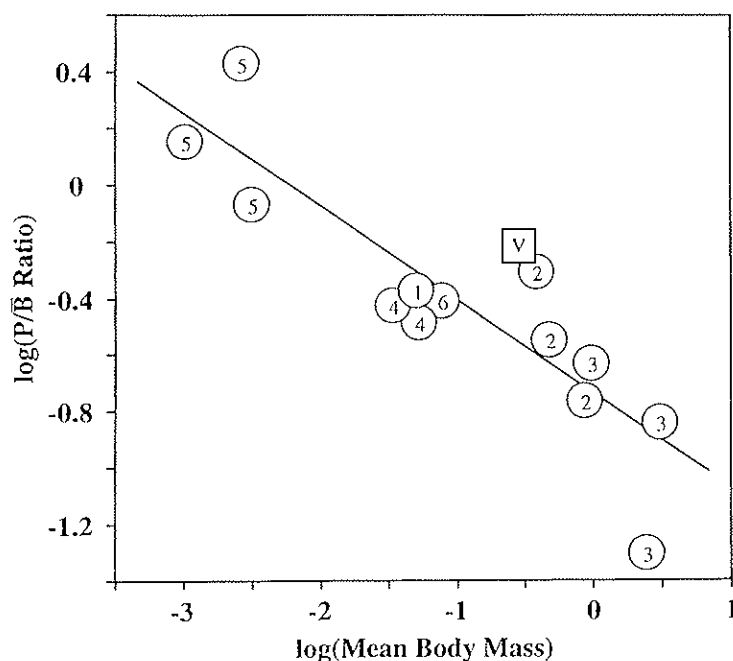


Fig. 9. Somatic productivity of *V. antiqua* at Yaldad compared to other species of the superfamily Veneracea. The relation between P/\bar{B} ratio and mean body mass (converted to kJ) is described by $\log(P/\bar{B}) = -0.738 - 0.329 \times \log(\text{Mass})$, $N = 14$, $r^2 = -0.746$. 1, *Chione cancellata*, Florida/USA, Moore & Lopez (1969); 2, *Mercenaria mercenaria*, Southampton/UK, Hibbert (1976); 3 *Mercenaria mercenaria*, Georgia/USA, Walker & Tenore (1984); 4, *Venerupis aurea*, Southampton/UK, Hibbert (1976); 5, *V. ovata*, Morlaix Bay/France, Dauvin (1985); 6, *V. striatula*, Bristol Channel/UK, Warwick et al. (1978); [V] *V. antiqua*, Yaldad, this study.

mortality rate M , which has been estimated to 0.331 y^{-1} . This figure would fit much better in the plot of $\log(P/\bar{B})$ vs $\log(\text{body mass})$, even if mean body mass is expected to increase due to reduced mortality.

Annual somatic production, $42 \text{ g AFDM} \cdot \text{m}^{-2}$, is three times higher in *V. antiqua* than in that species coming closest to this figure, the population of *Mercenaria mercenaria* at Southampton, $14 \text{ g AFDM} \cdot \text{m}^{-2}$ (recomputed from Hibbert, 1976). Two factors are likely to be significant for this high production: the comparatively long period of high primary production at Bahía de Yaldad, $\approx 10 \text{ wk}$; and the high levels as well as high nutritional value of suspended organic matter at this particular tidal flat (Navarro et al., 1993). Especially bacteria appear to provide a significant additional food source for *V. antiqua* throughout the year (Zimmermann et al., 1993).

4.3. Mortality and state of exploitation

In that part of the *V. antiqua* population at Yaldad living in the intertidal, fishing mortality F (0.331 y^{-1}) equals natural mortality M (0.331 y^{-1}), and the resulting exploitation rate of 0.5 indicates a high fishing pressure on the stock, despite the closure of the fishery since 1991. Gulland (1971) suggested $E = 0.5$ (i.e. $F = M$) to represent optimum exploitation conditions in fish stocks. However, Beddington & Cooke (1983), Caddy & Csirke (1983), Francis (1974) and others showed that this assumption generally overestimates potential yield by a factor of 2 or even higher, i.e. $E = 0.5$ is far above optimum exploitation conditions. These considerations are likely to be valid for benthic invertebrate stocks, too, since there are no differences in the underlying principles of population dynamics and fisheries. Hence, *V. antiqua* in the Bahía de Yaldad seems to be in a state of overexploitation, comparable to the Bahía de Ancud, where *V. antiqua* was found to be exploited by a rate 40% above optimum level (Jerez et al., 1991).

It is obvious from this study that the measures taken against overexploitation by the authorities are ineffective to control the fishery. Unfortunately, these are not isolated phenomena. Although total landings of *V. antiqua* in southern Chile keep on rising (Anonymus, 1991), the production to yield ratio is descending rapidly and average size of extracted specimens is also diminishing. These observations indicate continuous overexploitation of the traditional fishing areas around Isla de Chiloé (Reyes et al., 1991). Hence, there is an urgent need for effective management of the *V. antiqua* stocks and the *Venus* fishery to prevent the coastal ecosystem from permanent damage and to maintain the significance of this species for the local artisanal fisheries.

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6. References

- Allen, K.R., 1971. Relation between production and biomass. *J. Fish. Res. Board Canada*, Vol. 28, pp. 1537–1581.
- Anonymus, 1991. Anuario estadístico de Pesca. Ministerio de Economía Fomento y Reconstrucción. Servicio Nacional de Pesca (Sernap), 214 pp.
- Appeldoorn, R.S., 1987. Modification of a seasonally oscillating growth function for use with mark-recapture data. *J. Cons. Int. Explor. Mer.*, Vol. 43, pp. 194–198.
- Asencio, G., E. Clasing, C. Herrera, R. Stead & J.M. Navarro, in press a. Desarrollo larval in vitro de *Anphiascopsis cinctus* Claus 1866 y *Laophonte parvula* Sars 1908 (Copepoda, Harpacticoidea). *Rev. Chilena Hist. Nat.*
- Asencio, G., E. Clasing, C. Herrera, R. Stead & J.M. Navarro, in press b. Copépodos Harpacticoideos de las Comunidades de *Venus antiqua* y *Mulinio* sp. en la planicia mareal de Yaldad, Quellón, Chiloé. *Rev. Chilena Hist. Nat.*
- Beddington, J.R. & J.G. Cooke, 1983. The potential yield of fish stocks. *FAO Fish. Tech. Pap.*, Vol. 242, pp. 1–47.
- Brey, T., M. Soriano & D. Pauly, 1988. Electronic length frequency analysis. A revised and expanded user's guide to ELEFAN 0, 1 and 2. (2nd edition). *Berichte Inst. Meereskunde Kiel*, Vol. 177, 31 pp.
- Brey, T., W.E. Arntz, D. Pauly & H. Rumohr, 1990. *Arctica* (*Cyprina*) *islandica* in Kiel Bay (Western Baltic): Growth, production and ecological significance. *J. Exp. Mar. Biol. Ecol.*, Vol. 136, pp. 217–235.
- Bustos, H., M. Guarda, C. Osorio, E. Lozada, I. Solis, M. Diaz & E. Valenzuela, 1981. Estudio biológico-pesquero del recurso almeja en la Bahía de Ancud. II Investigaciones específicas. Instituto Fomento Pesquero, Chile, 356 pp.
- Caddy, J.F. & J. Csirke, 1983. Approximations to sustainable yields for exploited and unexploited stocks. *Océanogr. Trop.*, Vol. 18, pp. 3–15.
- Crisp, D.J., 1984. Energy flow measurements. In, *Methods for the study of marine benthos*, edited by N.A. Holme & McIntyre, A.D. Blackwell, London, pp. 284–372.
- Dauvin, J.-C., 1985. Dynamique et production d'une population de *Venus ovata* Pennant (Mollusque-Bivalve) de la Baie de Morlaix (Manche Occidentale). *J. Exp. Mar. Biol. Ecol.*, Vol. 91, pp. 109–123.
- Estay, A.E., J.C. Flores & M.S. Guarda, 1979. Estudio sobre edad y crecimiento de la "almeja" *Ameghinomya antiqua* King 1831 en el estuario del río Maullín (41° 36' S, 73° 39' W). Tesis, Universidad de Chile, Sede Osorno, Chile, 82 pp.
- Folk, R., 1980. *Petrology of sedimentary rocks*. Hemphill Publ. & Co. Austin, Texas, 182 pp.
- Francis, C.R., 1974. Relationship of fishing mortality to natural mortality at the level of maximum sustainable yield under the logistic stock production model. *J. Fish. Res. Board. Can.*, Vol. 31, pp. 1539–1542.
- Gayanilo, F.C., M. Soriano & D. Pauly, 1989. *A draft guide to the complete ELEFAN*. International Center for Living Aquatic Resources Management (ICLARM), The Philippines, 89 pp.
- Gulland, J.A., 1971. *The fish resources of the oceans*. FAO/Fishing News Books, Surrey, England, 255 pp.
- Hibbert, C.J., 1976. Biomass and production of a bivalve community on an intertidal mudflat. *J. Exp. Mar. Biol. Ecol.*, Vol. 25, pp. 249–261.
- Hoening, N., 1983. Empirical use of longevity data to estimate mortality rates. *Fish. Bull.*, Vol. 82, pp. 898–903.
- Hoening, N. & R.H. Choudary, 1982. A statistical study of seasonal growth models for fishes. Tech. Rep. Dept. Comp. Sci. Stat., University of Rhode Island, Kingston, USA, 22 pp.
- Jerez, G., F. Ponce & D. Rivas, 1991. Análisis de la explotación del recurso almeja (*Venus antiqua antiqua* King y Broderip, 1835) en la Bahía de Ancud, Chile. *Invest. Pesq. (Chile)*, Vol. 36, pp. 3–16.
- Lozada, E. & H. Bustos, 1984. Madurez sexual y fecundidad de *Venus antiqua antiqua* King & Broderip 1835 en la Bahía de Ancud (Mollusca: Bivalvia: Veneridae). *Rev. Biol. Mar. Valparaíso*, Vol. 20, pp. 91–112.
- Moore, H.B. & N.N. Lopez, 1969. The ecology of *Chione cancelata*. *Bull. Mar. Sci.*, Vol. 19, pp. 131–148.
- Navarro, J.M., E. Clasing, G. Urrutia, G. Asencio, R. Stead & C. Herrera, 1993. Biochemical composition and nutritive value of suspended particulate matter over a tidal flat of southern Chile. *Estuarine Coastal Shelf. Sci.*, Vol. 37, pp. 59–73.
- Osorio, C., D. Frassinetti & E. Bustos, 1983. Taxonomía y morfometría de *Venus antiqua* King y Broderip, 1835 (Mollusca, Bivalvia, Veneridae). *Tethys*, Vol. 11, pp. 49–56.

- Pauly, D. & G. Gaschütz, 1979. A simple method for fitting oscillating length growth data, with a program for pocket calculator. Int. Council. Explor. Sea. Council Meeting 1979:G:24, Demersal Fish Cttee., 26 pp.
- Press, W.H., B.P. Flanner, S.A. Teukolsky & W.T. Vetterling, 1986. *Numerical recipes. The art of scientific computing*. Cambridge University Press, Cambridge, 818 pp.
- Reyes, A., E. Arias, C. Rojas, N. Barahona, E. Lozada, A. Sepúlveda & A. Carmona, 1991. Estado de situación y perspectivas del recurso pesquerías bentónicas III, IV y X región. Diagnóstico de las principales pesquerías nacionales 1991. SGI – Instituto Fomento Pesquera, Santiago, Chile 92/6, 57 pp.
- Somers, L.F., 1988. On a seasonally oscillation growth function. *Fishbyte*, Vol. 6, pp. 8–11.
- Stead, R.A., 1992. Asentamiento de *Venus antiqua* (Bivalvia: Veneridae) en el intermareal arenoso de Bahía Yaldad, Chiloé. Tesis, Universidad Austral de Chile, Valdivia, Chile, 56 pp.
- Walker, R.L. & K.R. Tenore, 1984. The distribution and production of the hard clam, *Mercenaria mercenaria*, in Wassaw Sound, Georgia. *Estuaries*, Vol. 7, pp. 19–27.
- Warwick, R.M., 1980. Population dynamics and secondary production of benthos. In, *Marine benthic dynamics*, edited by K.R. Tenore & B.C. Coull, University of South Carolina Press, Columbia, pp. 1–24.
- Warwick, R.M., C.L. George & J.R. Davies, 1978. Annual macro-fauna production in a *Venus* community. *Estuarine Coastal Mar. Sci.*, Vol. 7, pp. 215–241.
- Zimmermann, R., E. Clasing & C. Herrera, 1993. El rol potencial de la biomasa bacteriana como alimento para *Venus antiqua*. Resúmenes XIII Jornadas Ciencias del Mar, Viña del Mar, Chile, March 26th–May 28th 1993, 137 pp.