

Reproductive cycle and cohort formation of *Venus antiqua* (Bivalvia: Veneridae) in the intertidal zone of southern Chile

Ciclo reproductivo y formación de una cohorte de *Venus antiqua*
(Bivalvia: Veneridae) en el intermareal del sur de Chile

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ABSTRACT

The reproductive cycle and generation of a new cohort of the clam *Venus antiqua* is described in relation to the annual food availability and temperature cycle at Yaldad Bay, Chiloé Island, southern Chile. The spawning period followed a seasonal pattern and was restricted to spring and summer (November 1990 to February 1991), whereas during autumn and winter the population was reproductively quiescent. First settlers were detected in January 1991, approximately thirty days after the main spawning event. Mean shell length at settlement was 0.26 mm; growth rate of this cohort was rapid till the end of summer (0.0021 to 0.0085 mm·d⁻¹), reaching an average length of 1mm at the end of March, whereas during autumn and winter (May to September) almost no shell growth was observed. The cohort recommenced growth in spring 1991 (October) and the clams quickly attained an average length of 6 mm (0.0248 to 0.0510 mm·d⁻¹) at the end of the first year (January 1992). Both the reproductive cycle and growth of this cohort at Yaldad Bay followed a seasonal pattern which was coupled to water temperature and food supply (chlorophyll *a* and organic seston).

Key words: Reproductive cycle, cohort formation, Bivalvia.

RESUMEN

Se describe el ciclo reproductivo y la generación de una cohorte de *Venus antiqua* en relación a la oferta alimentaria anual y al ciclo de temperatura en la Bahía Yaldad, Isla de Chiloé, sur de Chile. El período de desove en adultos siguió un patrón estacional, restringiéndose al período de primavera y verano (noviembre 1990 a febrero 1991), permaneciendo la población en estado de mínima actividad durante el otoño e invierno. Los primeros individuos asentados se detectaron en enero 1991, aproximadamente treinta días después de ocurrido el principal evento de desove. El asentamiento ocurrió a una talla media de 0,26 mm; la cohorte creció rápidamente hasta fines de verano (0,0021 a 0,0085 mm·d⁻¹) alcanzando a fines de marzo una talla promedio de 1 mm, mientras que prácticamente no se observó crecimiento durante el otoño e invierno (mayo a septiembre). El crecimiento de los individuos de la cohorte se reanudó en primavera (octubre 1991) alcanzando rápidamente una talla promedio de 6 mm (0,0248 a 0,0510 mm·d⁻¹) al final del primer año de vida (enero 1992). Tanto el ciclo reproductivo como el crecimiento de la cohorte siguió un patrón estacional fuertemente ligado al ciclo de temperatura del agua y a la oferta alimentaria (clorofila *a* y seston orgánico) en Bahía Yaldad.

Palabras clave: Ciclo reproductivo, formación de cohorte, Bivalvia.

INTRODUCTION

Marine bivalves from temperate latitudes generally follow a cyclical pattern of reproduction which can be divided into three stages: gametogenesis and vitellogenesis, spawning and fertilization, and larval de-

velopment and growth (Newell et al. 1982). Each species has a variety of genetic and environmental adaptations which coordinate these reproductive events with the environment in order to maximize reproductive success (Newell et al. 1982). The duration of each one of these stages can be annual, semi-annual or continuous, depend-

ing on the particular species and the environmental influences. Environmental factors will affect the number of cohorts produced annually as well as their subsequent growth and survivorship.

Whilst studies relating to the reproductive cycle and growth of bivalve species from the northern hemisphere are numerous (Ansell 1961, Ansell et al. 1964a, 1964b, Kautsky 1982a, 1982b, MacDonald & Thompson 1985a, 1985b, Harvey & Vincent 1989, 1990), few studies for the Chilean coast have integrated both these aspects with environmental variables. Such is the case of the infaunal filter-feeding bivalve *Venus antiqua* King & Broderip 1835, which inhabits intertidal and shallow sandy bottoms along the Pacific coast of South America from about 12° S to 54° S and along the Atlantic coast south of 31° S, including the Falkland Islands (Osorio et al. 1983). Individuals are iteroparous and follow an indirect reproductive strategy; size at first reproduction (46-48 mm length, Lozada & Bustos 1984) is attained at an age of 4 to 5 years, whereas commercial harvesting begins when clams reach 55 mm (5-6 years of age) (Clasing et al. 1994). Despite the wide distribution of *V. antiqua* and its significance to artisanal fisheries, only a few investigations on its biology and ecology have been carried out (see Jerez et al. 1991).

The large tidal amplitude (6.85 m maximum) found in the Chiloé Archipelago (Chile) has enhanced the formation of extensive tidal flats, which are characterized by their high biological productivity (Viviani 1979). In terms of biomass, the infaunal bivalve *Venus antiqua* is one of the dominant species in this environment. On the tidal flat of Yaldad Bay, the species is restricted to the lower half of the intertidal zone, where in past years it has reached average densities of 270 ind. \cdot m⁻² (R. Stead, personal observation). However, this bank was heavily exploited shortly after the start of this investigation, considerably reducing the abundance of individuals to less than 50 ind. \cdot m⁻². Due to the currently overexploited status of this resource in Chile (Reyes et al. 1991, Clasing et al. 1994), a more thorough understanding of reproductive timing and the forma-

tion and growth of post-larvae in the field will contribute towards improved stock management and mariculture practice.

The present study analyzes the reproductive cycle of *Venus antiqua* and its relationship with several important environmental variables in the generation of a new cohort in the natural habitat of this species.

MATERIAL AND METHODS

The study was carried out on the tidal flat at Yaldad Bay, Chiloé Island, southern Chile (43° 08'S; 73 44'W) (Fig. 1). The tidal flat (0.5 % slope) is exposed over a distance of 500 m during ELWS (semi-diurnal tides). The *Venus antiqua* bank is restricted to the lower half of the intertidal zone, which is constituted of gravelly muddy sand containing 2.4 % of combustibles (i.e., organic matter) with a mean grain size of 0.5 mm. Specimens were collected randomly by hand at monthly intervals from the study area at MLWS, between September 1990 and November 1991 (except April 1991); 10 male and 10 female clams within a shell length range of 50 to 55 mm were immediately selected for histological analysis. The gonads were preserved in aqueous Bouin's fixative and later embedded in paraffin wax. Tissue was cut in 7 μ m sections and stained with hematoxylin and eosin. Gonadal tissue sections were qualitatively examined and classified into one of four maturity stages (developing, ripe, spawning, post-spawning) according to the description of Lozada & Bustos (1984).

Growth of the individuals within a cohort was monitored by sampling the clams present in the upper 0.5 cm of the sediment. Sediment samples taken at monthly intervals (September 1990 to February 1992) each consisted of 25 subsamples obtained with a 2.1 cm diameter plastic corer tube introduced to a depth of 0.5 cm, i.e., a total sampled area of 85 cm². The sediment retained on a 125 μ m mesh sieve was examined under a dissecting microscope. Individuals identified as *Venus antiqua* were measured (maximum shell length) with a calibrated ocular graticule to an accuracy of 0.015 mm. Average shell length was cal-

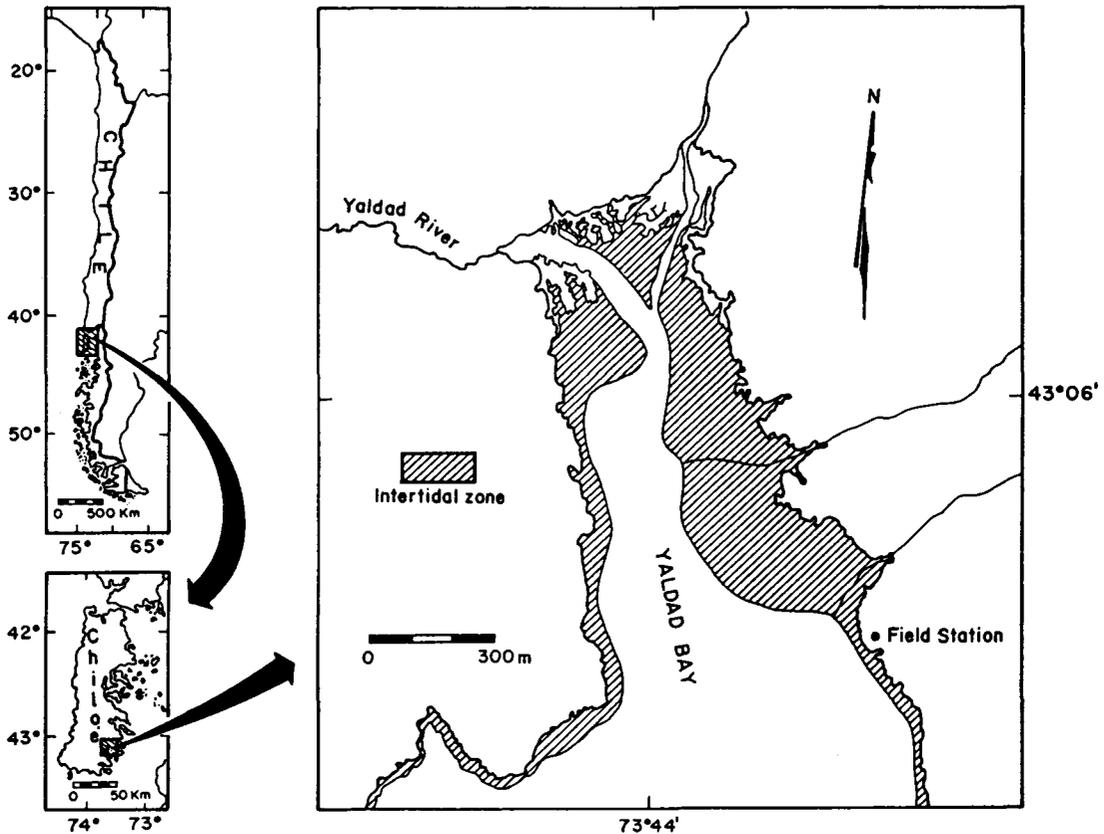


Fig. 1: Location of the study site at Yaldad Bay, Chiloé island, Chile.

Localización del sitio de estudio en Bahía Yaldad, Isla de Chiloé, Chile.

culated from all individuals collected on each sampling occasion, whereas growth rate of the cohort was estimated by obtaining the difference in average shell length between two consecutive samplings ($\Delta L = L_2 - L_1$) and dividing by the number of days between them ($\Delta t = t_1 - t_2$).

Salinity and water temperature were monitored on each sampling occasion using a WTW LF 191 conductivity meter and a 0.1 °C precision thermometer, respectively.

In order to determine the seasonal variability of food available for reproduction and growth, seston and pigment quantification (chlorophyll *a* and phaeopigments) were estimated using the techniques described by Strickland & Parsons (1972). Water samples (1-2 l) obtained every hour throughout one tidal cycle (6 hours) were pumped from a distance of 10 cm above the clam bed and then filtered through a 333 μm nitex mesh sieve to eliminate larger

zooplankton and debris, before filtering through prewashed, precombusted, preweighed Whatman GF/C filters. The obtained samples were stored in darkness at -20 °C until analysis.

RESULTS

Reproductive cycle

Histological analysis revealed slightly different reproductive patterns for male and female clams (Fig. 2). Only one important reproductive period (i.e., over 50 % of the population in the spawning stage) was observed throughout the year. In both sexes spawning was restricted to spring and summer, with the highest frequencies of spawning individuals (93 % females, 83 % males) occurring in December 1990. The reproductive period (i.e., spawning) in females

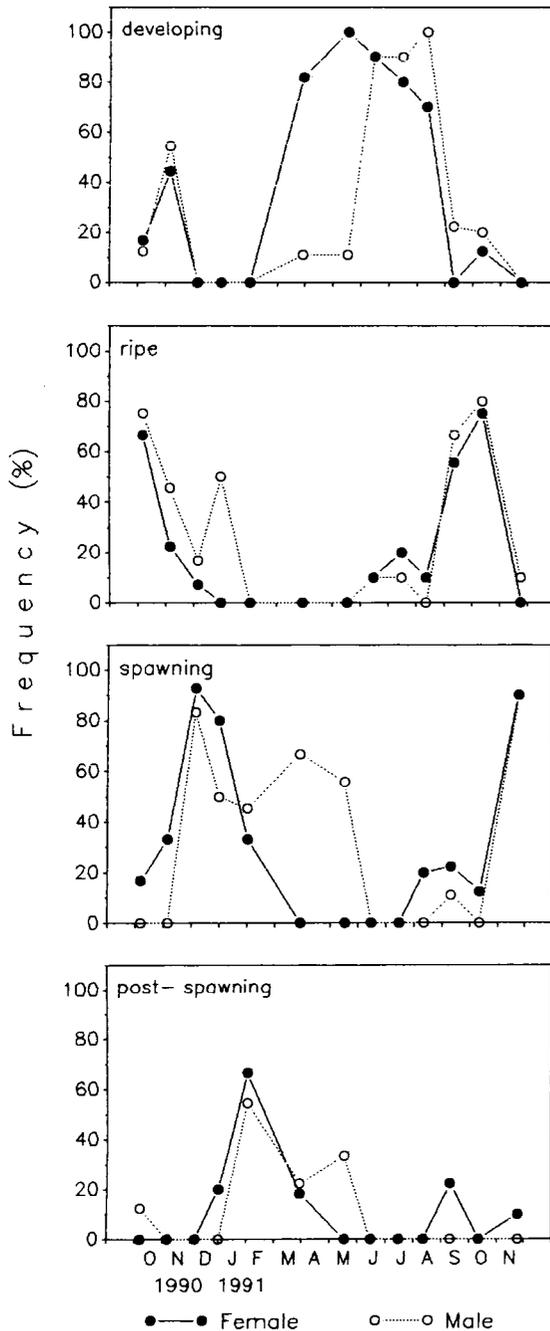


Fig. 2: Gametogenic phases of female and male *Venus antiqua*. The values represent the percentage frequency of clams in each reproductive phase (100 % = 10 specimens).

Estados gametogénicos de hembras y machos de *Venus antiqua*. Los valores representan el porcentaje de frecuencia de individuos en cada estado reproductivo (100% = 10 individuos)

lasted until mid-summer (January 1991); males followed a similar pattern until January, but quickly recovered in February and

extended the spawning phase until mid-autumn (May 1991). Spawning in both sexes was followed by a period of reproductive quiescence, which was prolonged in females (approximately 6 months; February to July) compared to males (3 months; June to August). Gonad maturation restarted in late winter - early spring (August-September 1991) in most of the adult population, and by October a large proportion of individuals were ripe. By November 1991, 90 % of the population was in the spawning stage, 1 month earlier than, but following a pattern similar to the previous year.

Settlement and growth

The first post-settled individuals were collected on 16 January 1991, when shell lengths ranged between 330 and 665 μm . Measurement of the prodissoconch II ring of specimens < 500 μm long (n= 34) showed that settlement had occurred at an average size of 264 μm (1 S.D. = $\pm 12.8 \mu\text{m}$). The cohort grew rapidly until the end of summer (2.09 to 8.55 $\mu\text{m}\cdot\text{d}^{-1}$, January - March 1991), whereas during autumn and winter (May-August) a very low growth rate was observed (Table 1). In spring, individuals recommenced growth and attained an average size of 6 mm after the first year's lifespan (January 1992) (Table 1).

Temperature and salinity

Water temperature showed a seasonal pattern, the lowest values occurring during the winter months (9.8 C in July 1991) and increasing towards summer (17 C in January 1992). Salinity was stable throughout the present study, fluctuating around 28 (Fig. 3 A).

Seston

Organic and inorganic seston followed a pattern similar to that of temperature during most of the study period. Highest values (48 $\text{mg}\cdot\text{l}^{-1}$, total seston) were observed at the end of spring 1990 (November-December), and were most probably due to the effect of resuspension of bottom deposits observed during strong prevailing winds from the north. The rest of the study

Table 1

Mean shell length (μm) and mean growth rate ($\mu\text{m d}^{-1}$)
of *Venus antiqua* spat settled between January and March 1991 at Yaldad Bay.

Talla media (μm) y tasa de crecimiento promedio ($\mu\text{m d}^{-1}$)
de postlarvas de *Venus antiqua* asentadas entre enero y marzo de 1991 en Bahía Yaldad.

sampling date	length [μm] $\bar{x} \pm (1 \text{ S.D.})$	n	growth rate ($\mu\text{m} \cdot \text{d}^{-1}$)
1990			
16 January	463.54 (74.46)	50	
3 March	865.17 (162.43)	178	8.5453
29 March	919.93 (162.43)	159	2.0946
15 May	975.00 (150.14)	19	1.1717
14 June	997.63 (188.63)	19	0.7543
16 July	1040.87 (40.00)	5	1.3513
10 August	1060.55 (42.50)	6	0.7872
10 September	1097.50 (95.46)	4	1.1919
11 October	1865.23 (23.46)	8	24.7581
23 November	3684.00 (700.00)	50	42.3023
20 December	4476.00 (800.00)	87	29.3333
1991			
20 January	6058.00 (1037.00)	99	51.0323
19 February	7158.00 (1565.00)	67	36.6667

period was characterized by a low organic and inorganic seston concentration with values below $4 \text{ mg}\cdot\text{l}^{-1}$ and $8 \text{ mg}\cdot\text{l}^{-1}$ respectively (Fig. 3 B).

Pigments

Chlorophyll *a* reached a maximum concentration during late spring 1990 (November-December) and summer 1991-1992 (February) following a seasonal cycle similar to that found for seston and temperature. The main peak observed during spring 1990 was greater ($40 \mu\text{g}\cdot\text{l}^{-1}$) and more prolonged than the main peak for summer 1991-1992 ($22 \mu\text{g}\cdot\text{l}^{-1}$) (Fig. 3 C) although the magnitude of the former can be partly attributed to the effect of bottom resuspension. Fluctuation of phaeopigment concentration was similar to that of chlorophyll *a*, with highest values occurring during spring 1990 (November-December) as a consequence of the resuspension of bottom detritus. Phaeo-pigment values throughout the rest of the year were relatively low (Fig. 3 C).

DISCUSSION

Reproductive cycle

The reproductive cycle of *Venus antiqua* at Yaldad Bay is the first to be described for an intertidal population of this species in Chile. There was a single reproductive period which extended from November 1990 to the end of February 1991 (Fig. 2, spawning). These results are broadly comparable with those reported by Lozada & Bustos (1984) who observed at Ancud Bay, Chile one important spawning period during December and January followed by two minor events (< 1 month) in April and August respectively (Fig. 4 A). Weber (1992), observed that *Venus antiqua* from Metri, Seno de Reloncaví, spawned on two occasions during the year: at the end of summer (February to March 1991) and at the end of winter to the beginning of spring (mid August to mid October 1991) (Fig. 4 B). However, both these studies were carried out on subtidal populations, where environmental factors tend to be more stable, especially with

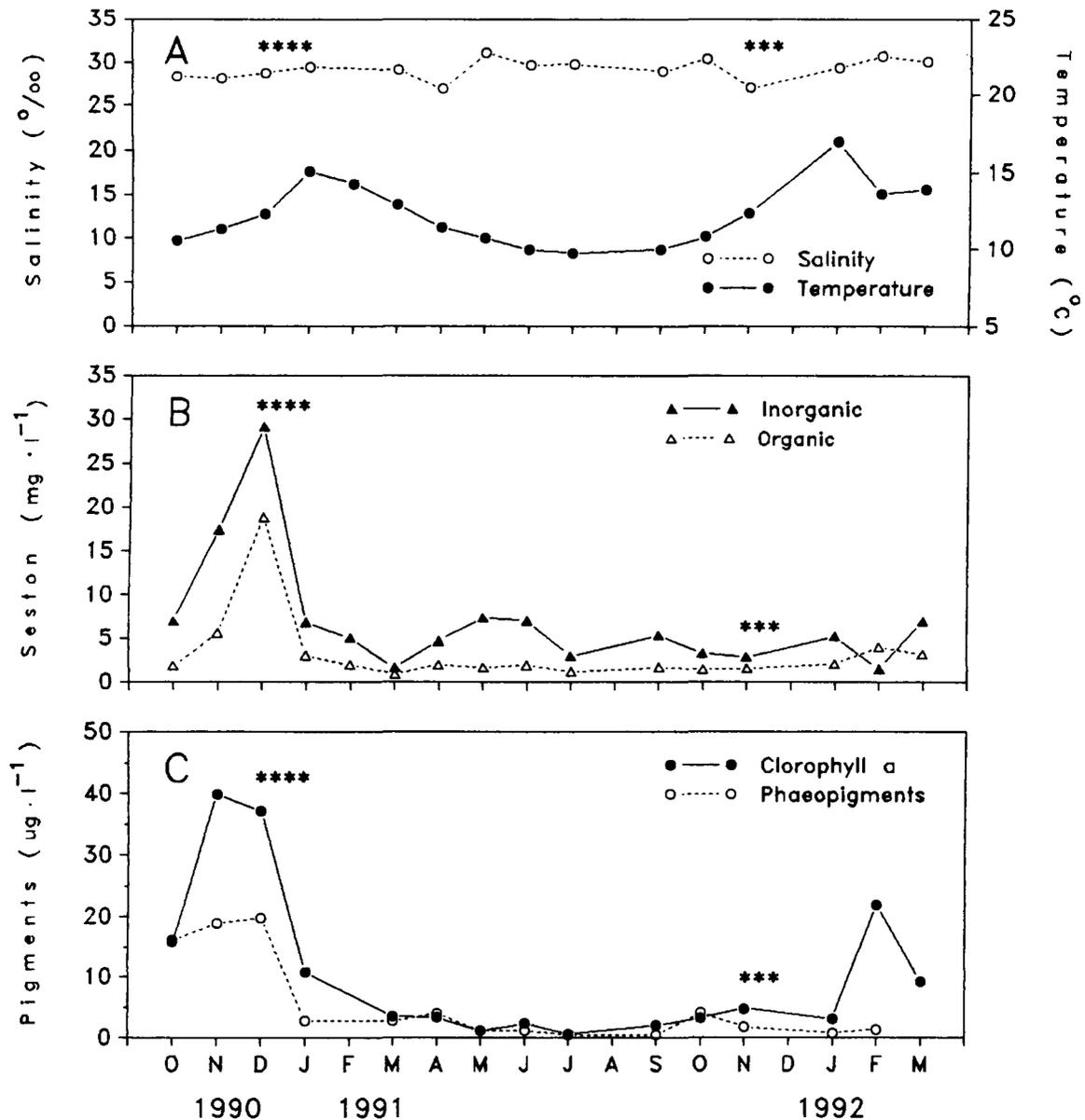


Fig. 3: Seasonal fluctuation of: (A) salinity and temperature, (B) organic and inorganic seston, and (C) chlorophyll *a* and phaeopigment concentration, measured at the tidal flat of Yaldad Bay. Asterisks indicate period of female clam spawning.

Fluctuación estacional de: (A) salinidad y temperatura, (B) seston orgánico e inorgánico, y (C) concentración de clorofila *a* y feopigmentos, medidos en la planicie mareal de Bahía Yaldad. Los asteriscos indican el período de desove en hembras.

and food availability (note that all three studied populations occurred at a similar latitude). Several authors stress that such factors are of great importance in determining bivalve reproductive capability (Bricelj & Malouf 1980, Newell et al. 1982, Mac-

Donald & Thompson 1985b, Brousseau 1987, Emmet et al. 1987).

Brousseau (1987) observed that certain populations of *Mya arenaria* could spawn twice each year, and concluded that the second spawning event is facultative and

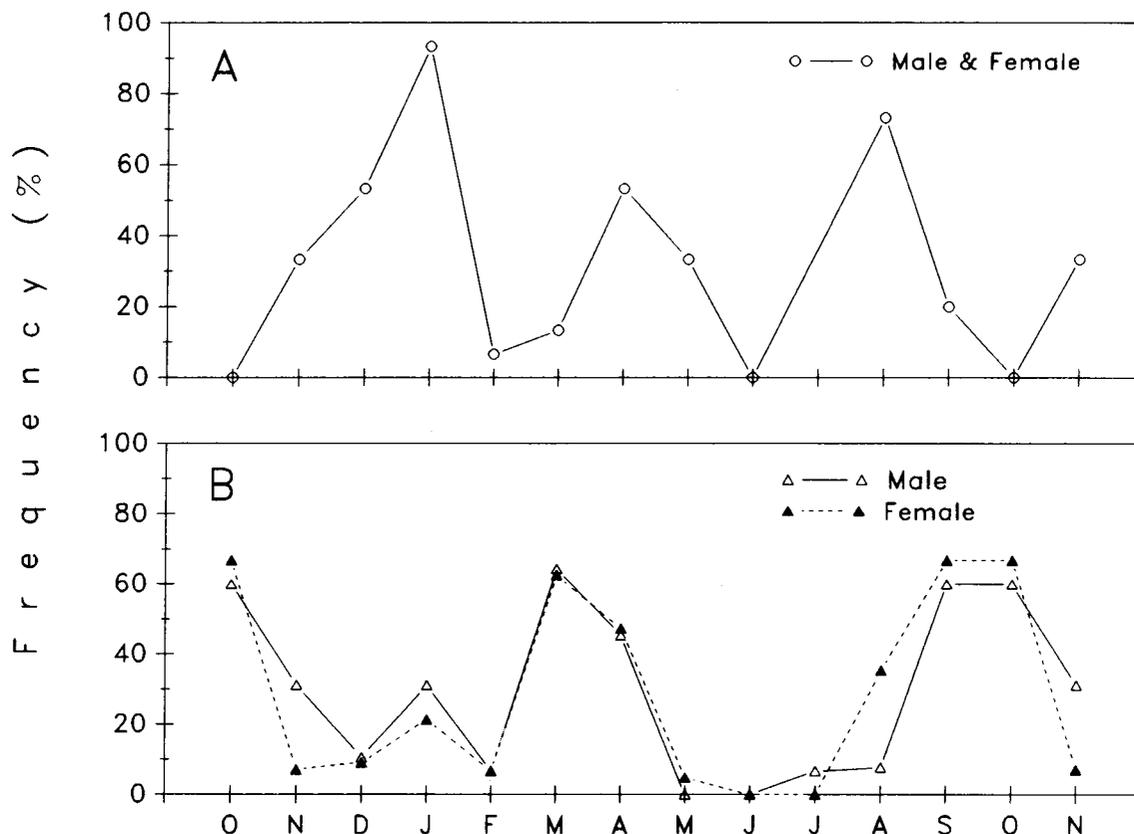


Fig. 4: Frequency of spawning adult *Venus antiqua* clams reported for: (A) Ancud Bay, Chiloe Island, Chile (Adapted from Lozada & Bustos 1984), (B) Metri, Seno de Reloncavi, Chile (Adapted from Weber 1992).

Frecuencia de adultos de *Venus antiqua* en desove reportado para: (A) Bahía Ancud, Isla de Chiloe, Chile (Adaptado de Lozada & Bustos 1984), (B) Metri, Seno de Reloncavi, Chile (Adaptado de Weber 1992).

occurs only under environmentally favorable conditions. Akberali & Trueman (1985) pointed out that intertidal bivalves are periodically confronted with stressful conditions, which results in prolonged valve closure. During these unfavorable periods bivalves cease to feed, reproduce and grow (Bayne & Newell 1983, Akberali & Trueman 1985, Wilson & Elkaim 1991).

The *Venus antiqua* population studied is comparable with other intertidal bivalve populations (Seed & Brown 1977, Feder et al. 1979, Harvey & Vincent 1989) in that reproductive output is limited to one single time of the year; in contrast to subtidal populations of the same species in which reproduction is more continuous, suggesting an adaptive strategy to this type of en-

vironment (sensu Newell et al. 1982). However, the prolonged spawning period observed in male clams (approximately 6 months, 2 events) indicates that they quickly recover after spawning. The occurrence of a second spawning event (although probably of less importance than the first), is similar to the pattern described by Lozada & Bustos (1984) and Weber (1992) for other subtidal populations of *V. antiqua*. This suggests that male clams are perhaps less affected by tidal exposure than females and may require less energy for the production of gametes. However from an ecological point of view, the extended spawning behaviour of male clams is of little value unless it occurs in response to subtidal *Venus anti-*

qua females with similar prolonged spawning periods. Prolonged spawning of males only, has also been observed in an intertidal population of the venerid clam *Protothaca staminea* (Feder et al. 1979).

Settlement and growth

The main spawning period (December 1990), was followed after approximately 30 days by the beginning of the settlement period (Table 1), which extended from January to March 1991 (R. Stead, unpublished data). These results coincide with laboratory experiments where larvae took between 23 and 28 days to settle (R. Stead, unpublished data). The new cohort exhibited maximum growth rates from the moment of settlement until the beginning of March, by which time clams were five times larger than at the time of their settlement (Table 1). A period of slower growth during autumn and winter is then followed by rapid growth during spring (Table 1). The same growth pattern was observed by Clasing et al. (1994) in *Venus antiqua* juveniles (> 2 years old) and adult clams from Yaldad Bay. The seasonal growth and reproductive cyclical pattern are strongly related to the seasonality of water temperature, particulate organic matter (POM) and chlorophyll *a* concentration, although low chlorophyll *a* and POM concentration at the end of the study (October - November 1991) are inconsistent with this interpretation. However, Navarro et al. (1993) concluded that chlorophyll *a* peaks in November - December 1990 and February 1992 at Yaldad Bay (Fig. 3 C) were produced by high diatom concentrations ($30 \cdot 10^6$ cells \cdot l $^{-1}$), whereas microflagellate blooms ($21 \cdot 10^6$ cells \cdot l $^{-1}$) in July and November 1991 were not reflected in high chlorophyll *a* values; high microflagellate concentrations may therefore explain growth and gonad development during the second year (October and November 1991).

The influence of temperature and food on growth and reproduction in bivalves is well documented (e.g., Bayne & Worrall 1980, MacDonald & Thompson 1985a, 1985b, Harvey & Vincent 1989, Jaramillo & Navarro 1995) and although some au-

thors have suggested that only food supply is important in controlling these processes (Bayne & Newell 1983, Brey & Hain 1992), spawning of *V. antiqua* at Yaldad Bay started during both years at similar water temperatures (12.4 °C and 12.5 °C, in 1990 and 1991 respectively), suggesting a strong influence of temperature on reproduction. According to Mackie (1984), the maturation of gametes is induced either by annual temperature fluctuations or a threshold temperature, whereas the act of spawning is initiated when temperatures exceed a critical level characteristic for each species (e.g., 10-12 °C in *Mytilus edulis*), but again the characteristics can vary from one locality to another and depend also on the nutritive value of food available (Seed & Suchanek 1992). On the other hand, growth of *Venus antiqua* spat can be maintained during periods of low natural food supply (autumn and winter) by adding cultured microalgae, despite the decrease in water temperature (P. Katz, personal communication), emphasizing the important role of food supply on the growth of this species.

Our results demonstrate that young clams are faced with low natural food supply upon recruitment, largely limiting growth to their first three months of life and therefore making them more vulnerable to predation (sensu Kraeuter & Castagna 1989). For aquaculture or repopulation of overexploited areas like Yaldad Bay, the artificial production of "seedlings", at the end of winter, followed by their transfer to the natural environment at the beginning of spring, would enable these individuals to take advantage of the greater food supply during spring and summer, thus allowing them to grow to a larger size (with possibly better survival rates) before encountering unfavorable winter conditions. This strategy would also reduce the interval before the onset of commercial harvesting, which starts when clams reach 55 mm in shell length.

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