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Growth, age and life span of the freshwater mussel *Diplodon chilensis chilensis* (Gray, 1828)

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With 5 figures and 2 tables in the text

Abstract

With comparative purposes, in two *Diplodon chilensis chilensis* populations, one from Lake Villarrica (39° 18′ S; 72° 05′ W) and the other from Huilquilco stream (38° 54′ S; 72° 35′ W) Southern Chile, annual growth rate, age and longetivity were determined using two methods: an experimental one (marking — recapturing) and a descriptive one (growth ring analysis). Both populations had different growth rates and longetivity, these differences being attributed to the influence of environmental conditions. The lake population exhibited a lower growth rate than the stream population whereas the latter had a shorter longetivity than the lake population. In small animals (< 35.0 mm) the results of the release and recapture experiments and the exponential equation data were more coincident with ring growth analysis than with results obtained with the von Bertalanffy equation. Although growth ring analysis evidenced some restrictions derived from irregularities on their formation, the results of the present study make recommendable the combined utilization of theoretical and experimental methods for reliable age and growth rate estimation in population studies.

Introduction

Within mollusks, bivalves have the longest life-span (Powel & Cummins, 1985), margaritiferids (freshwater bivalves) being those with the longest longetivity (Hendelberg, 1961; Stober, 1972; Bauer, 1983; Young & Williams, 1984). Growth rate and longetivity of individuals have been correlated to various factors; exogenous: temperature (Wilbur & Owen, 1964), eutrophy (Bauer, op cit), perturbations (Jones et al., 1978; Bretos, 1982) as well as endogenous: reproductive processes (Morton, 1969; Jones et al., op cit; Brousseau, 1979; Salzwedel, 1979), dietary changes (Sakai, 1960).

Variations in the annual growth rate of mollusks throughout their life cycle are evidenced through concentric marks or checks in valves or shells, known as growth rings. Even though growth rings can result from causes other than the normal mantle secretory activity such as handling or marking disturbances (Bretos, 1982) these marks constitute a reliable indicator to

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evaluate the annual growth rate, age and life span determination when the regularity of ring formation in the species under study is known.

Several methods have been carried out to determine age and growth in bivalves. The present study was undertaken to furnish data on annual growth rate, age and longetivity in *Diplodon chilensis chilensis* to determine the influence of environmental conditions on growth rate and longevity in this species and to compare an experimental method (marking-recapturing) with a descriptional one (study of growth rings).

Materials and methods

The present study was carried out in two areas with different environmental features:

1. Lake Villarrica: it is located at 39° 18′ S latitude and 72° 05′ W longitude in the pre-Andes mountains, at an altitude of 230 m. It is of glacial origin and has been characterized by Campos et al. (1983) as an oligotrophic, monomictic lake, with a winter circulation and a summer stagnation. The winter average temperature reaches 9.5 °C with small variations between surface and bottom. The maximal average temperatures registered in spring and summer reach 22 °C in the epilimnion and 9.5 °C in the hypolimnion. The physical and chemical parameters as well as phyto- and zooplankton have marked seasonal variations. *D. ch. chilensis* occurs in the sandy-gravely substrates of the lake.

2. Huilquilco stream: it is located at 38° 54′ S latitude and 72° 35′ W longitude. It is a first order stream (Strahler, 1957) belonging to the Imperial River basin. The stream flow is greatly influenced by a high rainfall, reaching its maximum volume and current in winter. In summer it has still and shallow waters. The vegetation on the banks is abundant all the year round. The bottom is composed of sand and gravel.

Methods

In February 1986, 500 specimens of *D. ch. chilensis* from lake Villarrica and 260 from Huilquilco stream were captured at random and their valves sawed at the posterior end and then realeased in their original habitat. Marked specimens were recaptured in February 1987 and their anterior-posterior length, umbo-mark length and mark-posterior valve end length were measured (Fig. 1). Growth and age were calculated following the methods described in Ricker (1975). The theoretical maximum average length (L_∞) was grafically determined according to Walford's method (Walford, 1946) and through correlation and regression on L_n (initial length) and L_{n+1} (final length) variables according to the equation $y = a + bx$. Since growth rate fits to a negative exponential relation, the equation $y = ae^{-bx}$ allowed to infer the annual growth rate of very small individuals which were not utilized in the experimental design. Finally, age and growth of individuals of each population were determined according to the von Bertalanffy equation $L_t = L_\infty (1 - e^{-K(t-t_0)})$ (Ricker, 1975). The results obtained with von Bertalanffy equation were compared with the analysis of growth rings measured in the recaptured specimens.

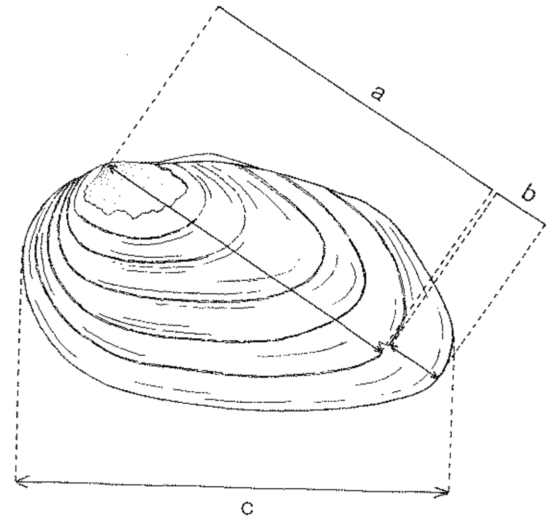

Fig. 1. Valve marking method. a) umbo — mark length; b) mark — posterior valve end length and c) anterior — posterior length.

Results

Lake Villarrica: 269 animals were recaptured in February 1987, with a shell length that ranged from 25 to 63 mm. In addition, 9 empty valves were found which were discarded because there was no data on the death date of the animals. The results calculated with Walford's method (Fig. 2) and with von Bertalanffy equation (Fig. 3) show that individuals of this population have a theoretical maximum average shell length of 57.57 mm length which would be reached at the age of 40 years. The results of measurements of growth rings in 20 recaptured animals are shown in Table 1. Only animals of less than 40 mm in length, in which growth rings are clearly defined, were considered.

Huilquilco Stream: a total of 33 animals were recaptured. Their shell lengths ranged from 24 to 46 mm. According to Walford's methods and the von Bertalanffy equation, this population has a theoretical maximum average shell length of 65.82 mm which would be reached at the age of 30 years (Figs. 4 and 5). It was not possible to determine growth rate in this population through the study of annual growth rings because the animals did not have well defined rings. Therefore, it was not possible to determine accurately the growth rate in the animal's first years of life.

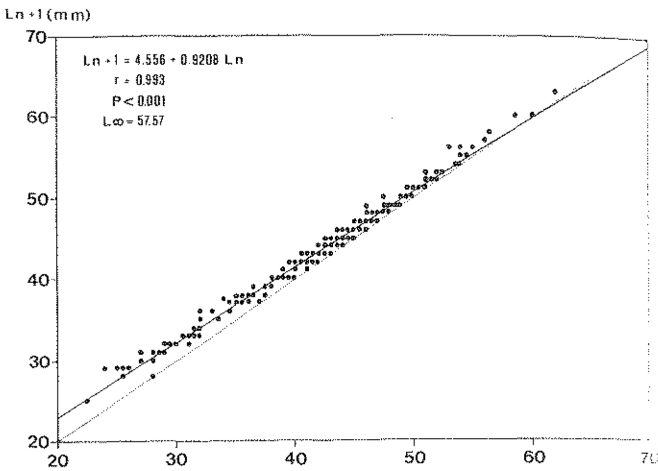

Fig. 2. Walford's graphic for *Diplodon chilensis chilensis* at Lake Villarrica.

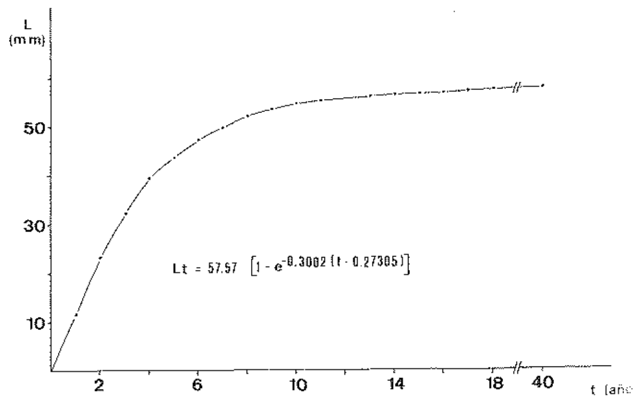

Fig. 3. Growth curve of valve length for *Diplodon chilensis chilensis* at Lake Villarrica

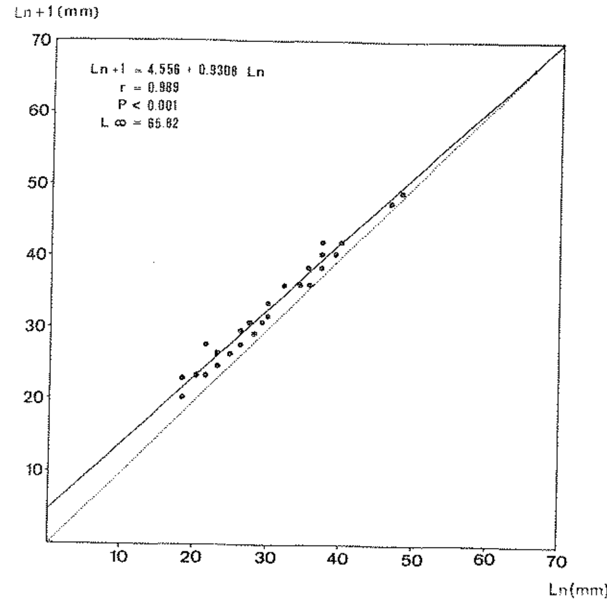

Fig. 4. Walford's graphic for *Diplodon chilensis chilensis* at Huilquilco stream.

In Table 2 shell length values are shown that the specimens from both pop-ulations in the first years of life according to the negative exponential equation theoretically would reach.

Discussion and Conclusions

D. ch. chilensis as all the unionids so far studied, has a differential annual growth rate depending on the size of the individuals. Thus large sized-specimens grow slower than small ones do (Lewandowsky & Stanczykowska, 1975; Hugeon & Morton, 1983). From the present study it was possible to verify that marking-recapturing [and exponential equation applied to the data (Table 4)] and growth ring analysis (Table 1) are more adequate methods for describing growth pattern that the von Bertalanffy equation in small specimens (< 35.0 mm). On the other hand growth ring analysis was restricted to certain populations and to animals smaller than 35.0 mm mainly due to:

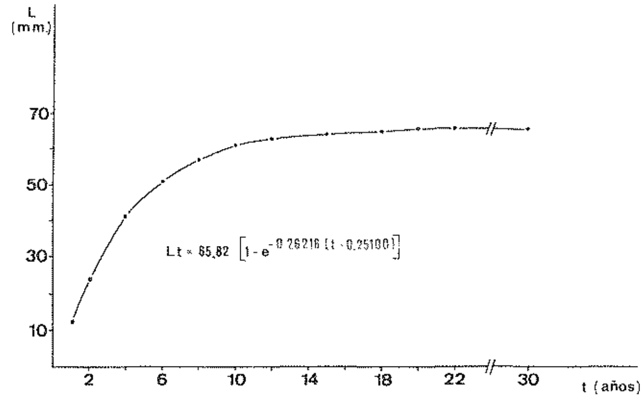

Fig. 5. Growth curve of valve length for *Diplodon chilensis chilensis* at Huilquilco stream.

a) the slow growth rate evidenced by individuals larger than 45 mm in which an overlapping of growth rings was observed, deciphering of them being confusing,
b) one of the populations under study (i.e. Huilquilco) didn't show clearly defined rings and
c) the frequent wearing away of the valves. For these reasons, the combined use of both of the described methods (growth rings and marking-recapturing) is advisable to assure reliable and accurate results in growth rate determination.

Annual growth patterns have been studied on several unionids (Negus, 1966; Morton, 1969; Lewandowsky & Stanczykowska, 1975; Dugeon & Morton, 1983) these studies having reported the formation of light bands on the valves as result of fast growth in certain periods of the year. The period of fast growth has been correlated to increasing water temperature, whereas dark bands have been interpreted as growth interruptions or slowings ascribable to environmental changes, mainly water temperature decrease (Williams & Owen, 1964), reproductive period (Morton, 1969; Jones et al., 1978; Brousseau, 1979; Salzwedel, 1979) diet changes, handling of animals or other kind of disturbances (Bretos, 1980, 1982; Jones et al., op. cit.).

At the time of marking the experimental animals, carried out in the lake Villarrica during the summer season (February 1986) their valve margins exhibited a slow growth ring, thus indicating the occurrence of a slowing of shell growth in summer, coincident with spawning and brooding of glochidia. This

Table 1. Annual growth rate (mm) as calculated from annual rings measurement for *Diplodon chilensis chilensis* from Lake Villarrica.

Rings → Individuals	Accumulated antero-posterior length (mm) 1	2	3	4	5	6	7	8	9	10
1	11.0	13.6	16.0	22.4	28.5	31.0*	33.4			
2	11.0	18.0	23.4	28.4*	31.4					
3	12.6	16.6	23.0	28.5	34.3	36.0*	37.5			
4	11.6	14.4	16.2	18.8	24.0	28.4	31.6*	33.2		
5	9.0	13.4	20.2	26.8	28.4*	32.0				
6	8.2	12.6	17.0	24.5	27.4*	30.8				
7	10.4	14.0	20.6	26.8	30.8	33.0*	34.7			
8	11.2	13.6	17.0	21.6	27.3	31.0	32.5	34.9	36.0*	37.6
9	11.4	14.9	19.6	25.8	30.4*	32.4				
10	8.3	14.0	19.9	25.4	29.6*	34.0				
11	(–)	15.2	20.6	28.6	32.0	34.9	38.8	40.9*	43.4	
12	11.0	15.0	19.0	25.2	31.7	34.0*	36.0			
13	10.0	15.4	21.0	25.4*	28.6					
14	(–)	16.0	20.8	24.1	26.8	28.6	30.8*	32.6		
15	10.0	17.0	23.2	29.5	35.4	40.6*	43.3			
16	11.8	13.0	17.0	23.6	29.0	35.1	40.0*	44.0*	46.6	
17	(–)	13.0	18.4	23.0	29.0	32.8	34.5*	37.5		
18	(–)	13.5	18.0	24.2	27.6	29.6*	32.4			
19	10.4	14.4	20.8	24.2	29.9	35.2	37.5	39.4*	41.4	
20	(–)	17.8	22.6	27.7	31.6	33.6	35.4	36.6*	36.6	
N	15	20	20	20	20	18	14	8	5	
Mean	10.5	14.7	19.7	25.2	29.6	32.9	35.6	37.3	40.8	
sd	1.22	1.60	2.31	2.67	2.64	2.95	3.53	3.91	4.51	
Growth increment	4.2	5.0	5.5	4.4	3.3	2.7	1.7	3.5		

* = mark, (–) = eroded.

Table 2. Estimated age as calculated from the negative exponential equation: $\Delta L = a\ e^{-bLn}$ for *Diplodon chilensis chilensis* from Lake Villarica and Huilquilco stream.

Age (years)	Lake Villarrica ($\Delta L = 7.97\ e^{-0.0325Ln}$) Length (mm)	Huilquilco stream ($\Delta L = 6.74\ e^{-0.0353Ln}$) Length (mm)
0	1.00	1.00
1	7.97	7.50
2	13.11	13.26
3	17.31	17.48
4	20.85	21.12
5	23.90	24.32
6	26.53	27.18
7	28.89	29.76
8	31.00	32.12
9	32.91	34.29
10	34.64	36.29

was confirmed with the analysis of the valves of specimens caught in Lake Villarrica in January 1985 (summer) which had a thin dark band in the valve edges, being this band more evident at the anterior margin of the valves. Specimens examined in July 1985 (winter) exhibited a light band formation whereas a dark band was insinuated in the margin of the valves in specimens caught in November 1985. This observation together with reports of PEREDO & PARADA (1986) suggest that in *D. ch. chilensis* energy during spring and summer is preferently canalized to reproduction (spawning and brooding) and for growing in fall and winter. These results do not agree with those reported for other unionids (NEGUS, 1966) in which growth is positively correlated to water temperature increase during summer. On the other hand, the results of the present study agree with those of DUGEON & MORTON (1983) in *Anodonta woodiana* and with those of HAUKIOJA & HAKALA (1978) who reported that the period of fast growth in *Anodonta piscinalis* is previous to the reproductive period, that is in winter.

Specimens caught in the Huilquilco stream did not show distinct slow and fast growth rings as specimens from Lake Villarrica did, suggesting that specimens of the Huilquilco population do not have a seasonal growth pattern, or if they have, it is not evidenced in ring formation. This could be ascribed to the more stable environmental conditions in Huilquilco stream compared with those of Lake Villarrica. This steady growth exhibited by specimens from Huilquilco stream could explain the higher annual growth rate and the larger size reached by the individuals of this population. From this, it can be concluded that in *D. ch. chilensis* there are interpopulation differences with respect to growth rates and life span due to the influence of the peculiar conditions of lotic and lentic environments. Results indicate an inverse relationship between life span and growth rate in *D. ch. chilensis*. A similar relationship has been reported for *A. piscinalis* (HAUKIOJA & HAKALA, 1978).

With respect to other unionaceans, *Margaritifera margaritifera*, the most primitive unionacean, exhibits a long life span with interpopulation differences according to the geographic location, ranging from 45 to 110 years (HENDELBERG, 1961; STOBER, 1972; BAUER, 1983; YOUNG & WILLIAMS, 1984). For different species of *Anodonta* and *Unio*, having also interpopulation variation longevities of 10 to 15 years have been reported (BRANDER, 1956; COMFORT, 1957; NEGUS, 1966; DUGEON & MORTON, 1983).

Molluscan life spans have been correlated to the conditions of the environment in which they occur. Thus, species living in productive (eutrophic) habitats and still waters have short life spans like *Anodonta* and *Unio*. On the other hand, *M. margaritifera* which occurs in cool oligotrophic habitats with low calcium availability, exhibits a low growth rate and a long life span. The available data of the present study agree with the last pattern since *D. ch. chilensis* from lake Villarrica, a long-lived species within unionaceans, according to CAMPOS et al. (1985, 1987) lives in environmental conditions similar to those reported for *M. margaritifera*. The above mentioned correlation would also explain the interpopulation differences in life span shown by *D. ch. chilensis* since Huilquilco stream inhabited by specimens with shorter longetivity has more eutrophic waters than Lake Villarrica, as indicated by the abundance of hydrophytes in the sampling area.

Some molluscs start reproducing once they have finished growth (GILBERT, 1973; SPIGHT et al. 1974) whereas others continue to grow during or inbetween reproductive periods (CALOW, 1981; BAYNE, 1975, 1976). In the latter, there is a competition for the available resources between reproduction and growth in terms of energy allocation. In *D. ch. chilensis* from Lake Villarrica, such competition would be attenuated since although the individuals grow throughout their lives and reproduce once they reach sexual maturity until they die, they have developed a strategy which allow them to optimize their energy utilization; thus, energy in spring and summer is mainly channelized during the breeding period to reproductive processes and to growth demands in fall and winter. Since *D. ch. chilensis* is a seasonal breeder with continuous gonadal activity (PEREDO & PARADA, 1986) some of the energy would also be conveyed in autumn to reproductive processes.

Resumen

A fin de comparar la tasa de crecimiento anual, edad y longevidad de *Diplodon chilensis chilensis* se estudiaron dos poblaciones que habitan ambientes diferentes (lago Villarrica y riachuelo Huilquico) mediante un método experimental (marcaje y recaptura) y uno descriptivo (análisis de los anillos de crecimiento). Los resultados indican que ambas poblaciones presentan una tasa de crecimiento anual y longevidad diferentes atribuibles a las condiciones ambientales en las que ellas se encuentran. La población léntica mostró una tasa de crecimiento menor que la población lótica mientras que la longevidad fue mayor en la población léntica. En animales menores a 35 mm los resultados obtenidos de los experimentos de marcaje y recaptura y de la ecuación exponencial fueron más coincidentes con el análisis de los anillos de crecimiento que los obtenidos con la ecuación de von Bertalanffy. Aún cuando el uso de los anillos de crecimiento presenta restricciones derivadas de las irregularidades de su formación, los resultados del presente estudio hacen recomendable el uso combinado de los métodos teóricos y experimentales para tener resultados más confiables para la estimación de la edad y crecimiento de los individuos en las poblaciones estudiadas.

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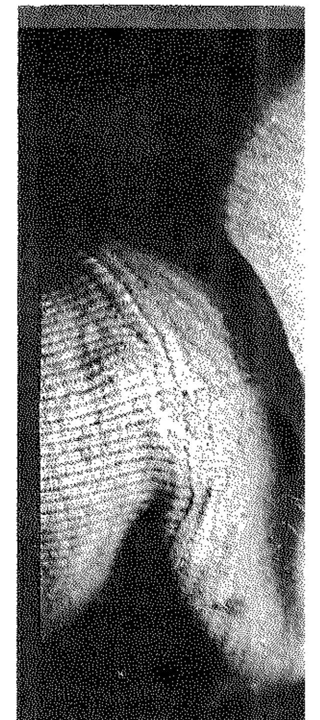

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