Population dynamics of the bivalves
Gari solida, Semele solida and *Protothaca thaca*
from a small bay in Chile at 36°S *

H.-Jörg Urban[1], Bernardita Campos[2]

[1]Alfred-Wegener-Institut für Polar- und Meeresforschung, Columbusstr., D-27568 Bremerhaven, Germany
[2]Instituto de Oceanología, Universidad de Valparaíso, Casilla 13-D, Viña del Mar, Chile

ABSTRACT: *Gari solida* (Gray, 1828), *Semele solida* (Gray, 1828) and *Protothaca thaca* (Molina, 1782) are dominant members of the shallow-water, soft-bottom communities of the Peruvian-Chilean upwelling system. They are exploited commercially all over their distribution range. Reproduction, growth, mortality, and production of these species were studied from a small bay in Chile at 36° S. Results indicate an annual reproductive cycle with a short spawning season. The growth parameters of the non-oscillating von Bertalanffy function were: *G. solida*: L_∞ = 89.6 mm, K = 0.307 yr^{-1}, t_0 = 0.354 yr^{-1}; *S. solida*: L_∞ = 78.0 mm, K = 0.297 yr^{-1}, t_0 = 0.374 yr^{-1}; *P. thaca*: L_∞ = 82.2 mm, K = 0.174 yr^{-1}, t_0 = 0.069 yr^{-1}. Production estimates agree very well with data of other members of the Tellinacea and Veneracea taken from the literature. Annual somatic and gonad production amounted to 27.6 and 56.0 (*G. solida*), 4.8 and 8.6 (*S. solida*) and 16.9 and 14.5 (*P. thaca*) g AFDW m^{-2}. The following production/biomass ($P/\bar{B}$) ratios were obtained: for *G. solida* 0.334, for *S. solida* 0.188 and for *P. thaca* 0.269. Total mortality was estimated as 0.842 (*G. solida*), 0.924 (*S. solida*) and 0.584 yr^{-1} (*P. thaca*). The influence of latitudinal gradients on reproductive strategies is related to the results on reproduction cycles. Production and mortality estimates are discussed in relation to the influence of the fishery.

KEY WORDS: *Gari solida* · *Semele solida* · *Protothaca thaca* · Bivalvia · Population dynamics · Reproduction · Growth · Mortality · Production · Chile

INTRODUCTION

Owing to upwelling, the marine ecosystem off Peru and Chile is one of the most productive in the world (Ryther 1969). High primary production sustains a high level of secondary production. Besides a well-developed industrial exploitation of pelagic resources, a small-scale (artisanal) fishery of benthic invertebrates is of considerable importance for local consumption. The most important resource for this fishery is bivalves (mussels and clams). Approximately 10 shallow-water bivalve species are exploited commercially. However, despite their importance, little is known about the biology and ecology of these species and little information on the population dynamics is available in the literature, although this information is essential for any attempt at stock management. Therefore, in many

areas stocks are overexploited leading to a reduction of catches.

Urban (1992) presented a comparative study on the ecology of 8 commercially exploited bivalve species. Here we deal with the population dynamics of 3 of them, *Gari solida* (Gray, 1828), *Semele solida* (Gray, 1828) and *Protothaca thaca* (Molina, 1782). All 3 species are infaunal burrowers in sandy substrates of the intertidal and subtidal, down to 20 m depth. Their geographical distribution along the South American Pacific coast is as follows: *G. solida*, 14 to 54° S, *S. solida*, 12 to 45° S and *P. thaca*, 12 to 45° S (Urban 1994a). Over the distribution range local populations are formed. Often the 3 species are found in the same habitat, as was the case in the present study. *G. solida* and *S. solida* belong to the superfamily Tellinacea, while *P. thaca* belongs to the superfamily Veneracea. Both superfamilies are members of the order Veneroida.

The aim of the present paper is to report studies on the reproduction, growth, mortality and production of

Gari solida, S. solida and *P. thaca* from a small bay in Chile and to compare these results with data from the literature.

MATERIAL AND METHODS

Research area and sampling. The investigations were undertaken in the Bay of Dichato (36° 32' S, 73° 57' W), a small bay of approximately 12 km² (Fig. 1). Water temperature decreases to about 12 °C in winter and rises to 16 °C in summer. The investigation area, especially its distribution of substrate types, is described in Urban (1994b). At least 8 subtidal populations of different bivalve species exist in this area at different places (Urban 1992). The 3 bivalve species studied here are distributed almost exclusively near the entrance of the ocean in the north-western part of the bay (Fig. 1).

Samples were taken by SCUBA divers at monthly intervals at 2 to 5 m depths. On each sampling all bivalves present in 5 to 10 randomly selected squares (0.25 m²) were collected by hand. In addition, every 2 mo, 2 or 3

sediment cores of 25 × 25 cm area and 20 cm depth were dug out and sieved through 1 mm mesh to check for the presence of specimens smaller than 5 mm shell length, which the divers easily overlooked.

Maximum length on the anterior-posterior axis (shell length) was recorded from all individuals with vernier calipers. Sea surface temperature was recorded at each sampling. Subsamples of 30 to 40 individuals were taken from the monthly samples, and shell length and total wet weight (shell and body wet weight) were recorded. All soft parts were removed and dried at 60 °C to constant weight for body dry weight estimations. Ash-free dry weight (AFDW) was obtained by ignition of dried soft parts at 550 °C for 5 h. Further subsamples were taken for histological sections of ovaries (*Gari solida* only) and for shell ring measurements in order to estimate growth. Sampling began in January 1991 and lasted until May 1992. However, body weight cycles and annual production were calculated for the period April 1991 to March 1992. Therefore, the monthly length-frequency distributions from these months were pooled. Total sample size for the pooled samples was 3068 individuals for *G. solida*, 843 for *S. solida*, and 816 for *P. thaca*. The reproductive cycle, based on histological sections, was studied for the period June 1991 to May 1992.

Reproduction. The parameters of the relationship between length and weight (Eq. 1) were estimated by linear regression analysis on log-transformed data. Annual body dry weight cycles for a standard individual of 50 g total wet weight were calculated as

$$W = aL^b \tag{1}$$

where W is body dry weight (g), L is shell length (mm) and a and b are constants. An F-test was used to test for significant differences of regression lines of the length weight relationships between 2 successive months.

For histological sections soft parts were fixed in Bouin's solution, dehydrated in alcohol and then embedded in paraffin wax. Sections of 8 μm were stained in Harris' hematoxylin and eosin. In total 760 gonads and 2220 histological sections were prepared.

Different reproductive stages of the reproductive cycle were based on the morphological development of the germ lines in the acinus of the gonads. This parameter reflects the activity of the gametes. Five histological stages were distinguished:

Developing 1: Corresponds to the initial development of the acinus of the gonads. These are small with a rough basal membrane. Germ line principally represented by previtellogenic oocytes which stick to the wall of the acinus as well as the oogones. Oocytes which have passed through their meiotic stage show spherical and pallid germ vesicles with clear nucleolus and a basophilic cytoplasm. The large amounts of basophilic
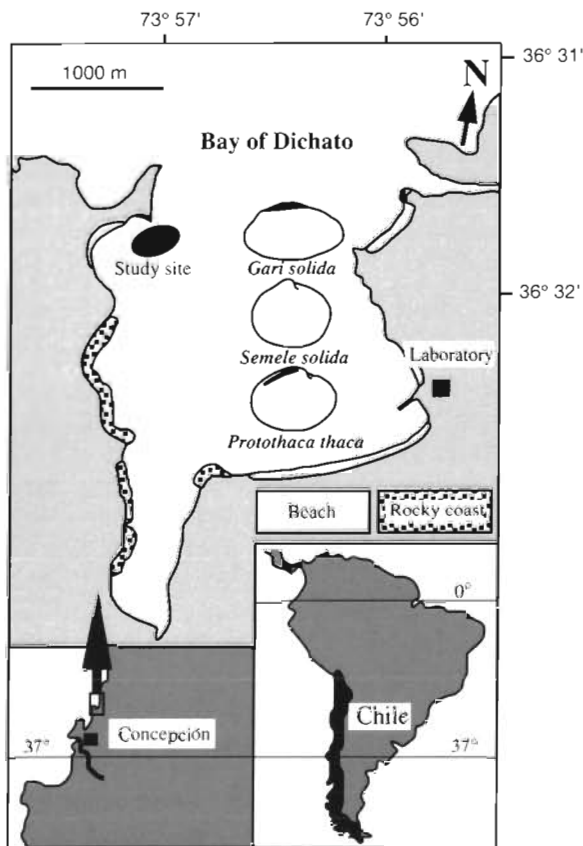

Fig. 1 Investigation area. Location of the sampling station and the names of the species studied are given

cytoplasm in some oocytes indicates incipient vitellogenesis. These latter oocytes can move towards the lumen as pedunculate vitellogenic oocytes, united by a fine cytoplasmatic stalk at the wall of the acinus.

Developing 2: The gonadal acinus increases in size with increasing numbers of vitellogenic oocytes sticking to the basal membrane, especially the number of the pedunculate oocytes. Free vitellogenic oocytes are found in the acinal lumen which are recognizable by (1) their prominent germ vesicles, (2) their abundant cytoplasm and (3) the development of a vitellin cover.

Ripe: The acinus is large. Free vitellogenic oocytes which fill the acinus are dominating. Germ cells clearly visible owing to a large ovoid to spherical germ vesicle with a prominent nucleolus, which typically shows a basophilic zone, and another characterized as an anfinucleolus (Raven 1961, Lucas 1971). Early germ line rarely represented by a few oogones and previtellogenic oocytes of small size.

Spent 1: Or stage of initial regression. The acinus is smaller and of irregular form indicating the beginning emission of female gametes in the stage of vitellogenic oocytes with intact germ vesicles. Germ cells which have completed their development present in low numbers, leaving free room in the acinus. Early germ line rarely present.

Spent 2: Or stage of total regression. The acinus is small with a rough basal membrane. Only few residual free oocytes (normally in the stage of degeneration) can be detected in the acinus. Normally, an intracinal tissue of somatic cells fills the acinal lumen. Early germ line represented only by a few oogones.

Growth. Annual shell growth rings on the surface of the valves of approximately 30 individuals were measured with vernier calipers. It was easy to distinguish between disturbance rings and annual rings due to the stronger and clearer appearance of the latter. Two data sets were obtained: (1) Individual growth increment data arranged as tagging recapture data with constant time intervals ($t = 1$ yr), and (2) mean lengths for each age were calculated from all individuals to obtain age-length data. For growth estimation the non-oscillating von Bertalanffy growth function, VBGF (von Bertalanffy 1938), was used:

$$L_t = L_\infty (1 - e^{-K(t - t_0)}) \quad (2)$$

where L_t is length at age t, L_∞ is the asymptotic length (mm), K is the growth constant (yr^{-1}), t is the age (yr) and t_0 is the age at zero length.

Growth parameters were estimated using Fabens' (1965) method by fitting a rearranged function of the VBGF to size increment data pairs (i.e. tagging recapture data) using the Simplex algorithm:

$$L_2 = L_1 + (L_\infty - L_1)(1 - e^{-K(t_2 - t_1)}) \quad (3)$$

where L_1 is the length at the beginning and L_2 the length at the end of the time interval.

With this method only L_∞ and K can be estimated. In order to estimate t_0 as well, the original VBGF (Eq. 2) was fitted to age-length data with the Simplex algorithm.

Methods of estimating growth such as those described above may lead to erroneous values of L_∞. For example too-low values will be obtained if large individuals are missing in the tagging recapture data set. As L_∞ and K are inversely related (Pauly 1979) in such a case, erroneously high K-values will also be obtained. A method for calculating L_∞ from an alternative data source (length-frequency data) is the Wetherall method (see below under methods for mortality estimations). Preliminary results of Fabens' method and the VBGF fitted to age-length data showed that L_∞ deviated considerably from L_{max}, the largest individual present in the pooled length-frequency data. Much better results were obtained with the Wetherall method, which gave values consistently a little higher than L_{max}. The 2 routines for growth estimations were therefore rerun with fixed values of L_∞, calculated after Wetherall.

Mortality. Total mortality Z was calculated by the single negative exponential model:

$$N_t = N_0 e^{-Zt} \quad (4)$$

(where t is the time and N_0 is the number of individuals at $t = 0$) and the length-converted catch curve running the ELEFAN II routine of the 'Compleat ELEFAN' program (Gayanilo et al. 1988) on the pooled length-frequency data. Based on the VBGF parameter in this routine, lengths are converted to ages after the following model:

$$N_i/\Delta t_i = N_0' e^{-Zt_i} \quad (5)$$

where N_i is the number of individuals in length class i, Δt_i is the time required to grow through this size class and t_i is the age of the middle length class i. Mortality Z is calculated by linear regression analysis:

$$\text{Log}_e(N_i/\Delta t_i) = a + bt_i; \quad Z = -b \quad (6)$$

Another method, available in the routine ELEFAN II of the 'Compleat ELEFAN' program is the modified Wetherall et al. method (Pauly 1986, modified after Wetherall 1986), which obtains L_∞ and the parameter Z/K from length-frequency data. The Wetherall method rearranges Beverton & Holt's (1956) Z-equation based on length data to a linear regression equation:

$$\bar{L} - L' = a + bL'; \quad Z/K = -(1 + b)/b; \quad L_\infty = -a/b \quad (7)$$

where $\bar{L}$ is the mean length of individuals of length L' and longer and L' is the length for which all individuals of that length and longer are under full exploitation.

Production. Based on the results of the annual repro-
duction and body weight cycles, annual gonad produc-
tion ($P_{gon.}$, in g AFDW m^{-2}) was calculated from length
weight relations (Eq. 1) of the lowest body weight
before and the highest body weight during the spawn-
ing season on monthly samples:

$$P_{gon.} = \sum N_i (W_{i(gon.dur)} - W_{i(gon.pre)}) \tag{8}$$

where $W_{i(gon.dur)}$ and $W_{i(gon.pre)}$ are gonad weights dur-
ing and before the spawning season in length class i.

The length of first maturity was calculated after
Eversole (1989) as 25 % of the maximum length (L_{max})
present in the pooled length-frequency data.

Annual somatic production (P, in g AFDW m^{-2}) was
calculated by the weight-specific growth rate method
(Crisp 1984) from the mean of quantitative samples,
pooled length-frequency data, the VBGF parameter
and the length-weight relationship:

$$P = \sum N_i W_i G_i \tag{9}$$

where N_i is the mean number of individuals (N m^{-2}), W_i
the mean body weight (g AFDW) in length class i, and
G_i the weight-specific growth rate (yr^{-1}):

$$G_i = bK[(L_\infty/L_i) - 1] \tag{10}$$

where b is the exponent of the length-weight relation-
ship (Eq. 1), L_∞ and K are VBGF parameters and L_i is
the mean length in length class i.

Annual mean biomass ($\bar{B}$, in g AFDW m^{-2}) was cal-
culated as follows:

$$\bar{B} = \sum N_i W_i \tag{11}$$

The annual $P/\bar{B}$ ratio was calculated from annual
somatic production P and annual mean biomass $\bar{B}$.

RESULTS

Reproduction

For *Gari solida*, Fig. 2 shows the overlay of annual
body weight cycle and sea surface temperature as well
as the reproduction cycle based on histological sec-
tions. During a short period (between November 1991
and January 1992) principally developing 2 and ripe
ovaries are present while during a much longer period
(June to October 1991 and February to May 1992)
spent 2 and developing 1 ovaries dominate. This
clearly indicates an annual reproduction cycle with a
short reproductive period between October and Janu-
ary/February with a possible second short spawning
event in March/April. The body weight cycle corre-
lates very well with the water temperature cycle: in
winter, from April to October 1991, the temperatures
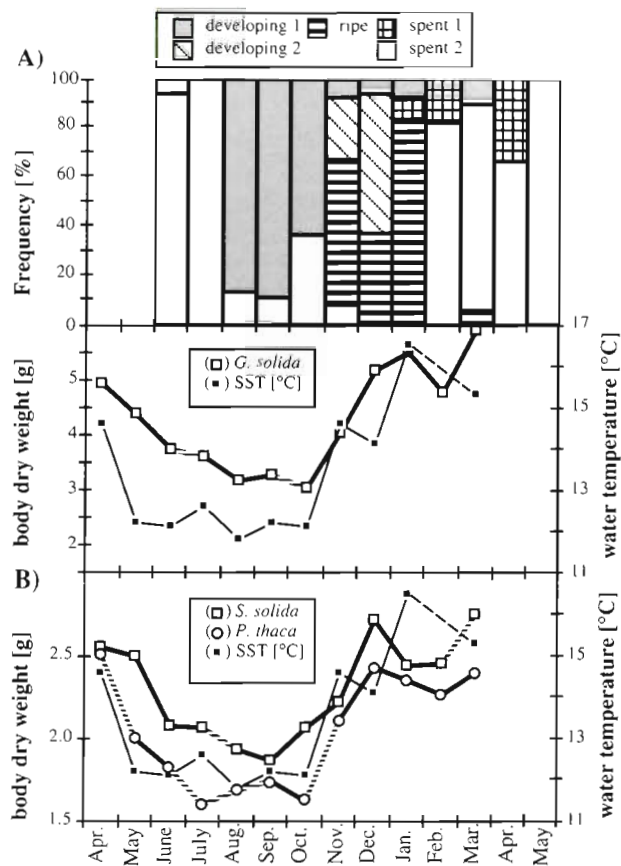and body weights decline, and rise during spring and

Fig. 2. (A) *Gari solida*. Reproductive cycle, based on histolog-
ical sections of ovaries, for the period June 1991 to May 1992;
and overlay of body dry weight cycle for a 50 g wet weight
standard individual and the sea surface temperature (SST) cy-
cle for the period April 1991 to March 1992. (B) *Semele solida*
and *Protothaca thaca*. Overlay of body dry weight cycle for a
50 g wet weight standard individual and the SST cycle for the
period April 1991 to March 1992. Solid lines (weight cycles):
significant differences (p ≤ 0.05) between 2 successive
months; broken lines: nonsignificant differences

summer from November 1991 to March 1992. High
body weights therefore seem to be related to repro-
ductive activities which might be triggered by low
temperatures in winter. The body weight and water
temperature cycles of *Semele solida* and *Protothaca
thaca* follow the same pattern as for *G. solida*. A similar
reproduction cycle for *S. solida* and *P. thaca* is there-
fore indicated. For *G. solida* and *S. solida*, except for
2 times (June/July, September/October and July/Aug-
ust, February/March, respectively), the body-weight
changes between 2 successive months were signifi-
cantly different (p ≤ 0.05). For *P. thaca* significant dif-
ferences were found only in the months May/June,
September/October and then from November to the
end of the study period (March).

Table 1. *Gari solida*, *Semele solida* and *Protothaca thaca*. Parameters of the length (mm) – body dry weight (g) relationship for 3 Chilean bivalve species before and during the spawning season. log(Weight) = a + b log(Length)

Species	Month	a	b	r^2	n
G. solida	Oct 1991	−5.093	3.074	0.99	28
	Jan 1992	−4.323	2.792	0.98	32
S. solida	Sep 1991	−5.270	3.169	0.99	36
	Dec 1992	−4.525	2.824	0.98	31
P. thaca	Oct 1991	−6.490	3.957	0.98	30
	Dec 1992	−5.225	3.292	0.97	28

Based on these results, annual gonad production was calculated as the difference between the lowest annual body weight before and the highest body weight during the spawning season by linear regression analysis for each length class, accordingly. The linear regression parameter for the length-weight relationships for the lowest and the highest body weights are given in Table 1.

Growth and mortality

The results for the VBGF parameter are given in Table 2. With tagging recapture data, low L_∞- and high K-values were obtained, while with age-length data higher L_∞- and low K-values were obtained, owing to the inverse relationship of L_∞ and K (see 'Material and methods'). However, estimated with fixed L_∞-values after Wetherall (Table 3), the K-values are very similar. Non-oscillating VBGF growth curves, calculated with these mean K-values from both data sets, are shown together with age-length data in Fig. 3. The fit of growth curves and data is very good. Fig. 4 shows the size-converted catch curves and the obtained estimates of Z. These values are compared with the Z-

Table 3. *Gari solida*, *Semele solida* and *Protothaca thaca*. Z-values (mortality) estimated with the catch curve method (Z_{cc}) and after Wetherall (1986) (Z_{Weth}). Also given are the VBGF parameters used as input data for the catch curve method: L_∞ (estimated after Wetherall), K and t_0 from Fig. 3

Species	Z_{cc}	Z_{Weth}	L_∞	K	t_0
G. solida	0.846	0.838	89.6	0.307	0.354
S. solida	0.916	0.931	78.0	0.297	0.374
P. thaca	0.628	0.540	82.2	0.174	0.069

values estimated after Wetherall in Table 3. For *Gari solida* and *Semele solida* the different values agree very well (0.85/0.84 and 0.92/0.93, respectively), while in *Protothaca thaca* a higher variability can be observed (0.63/0.54). The results indicate slightly higher growth and mortality rates for *G. solida* and *S. solida* and the reverse for *P. thaca*.
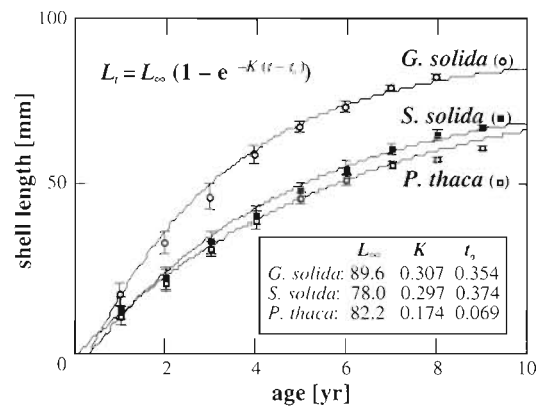

Fig. 3. *Gari solida*, *Semele solida* and *Protothaca thaca*. Non-oscillating growth curves of the von Bertalanffy growth function (VBGF) and age-length data of 3 Chilean bivalve species. VBGF parameters (asymptotic length, L_∞; growth constant, K; age at zero length. t_0) are given in the inset. Vertical bars indicate standard deviations of the mean lengths

Table 2. *Gari solida*, *Semele solida* and *Protothaca thaca*. Von Bertalanffy growth function (VBGF) parameters of 3 Chilean bivalve species estimated from 2 data sets: tagging-recapture data (with Fabens method) and age-length data (with the VBGF and the Simplex algorithm). L_∞: asymptotic length (mm); K: growth constant (yr^{-1}); t_0: age at zero length

Species	L_∞	K	t_0	r^2	L_∞[a]	K[b]	t_0[b]	r^2	n
Tagging-recapture data									
G. solida	86.1	0.349	–	0.96	89.6	0.319	–	0.95	8
S. solida	85.3	0.187	–	0.98	78.0	0.219	–	0.99	9
P. thaca	70.0	0.253	–	0.99	82.2	0.184	–	0.98	9
Age-length data									
G. solida	106.3	0.193	0	0.95	89.6	0.295	0.354	0.99	51
S. solida	100.6	0.127	0	0.99	78.0	0.213	0.374	0.99	89
P. thaca	78.7	0.174	0	0.98	82.2	0.164	0.069	1.00	109

[a] Estimated after Wetherall on pooled length-frequency distribution data
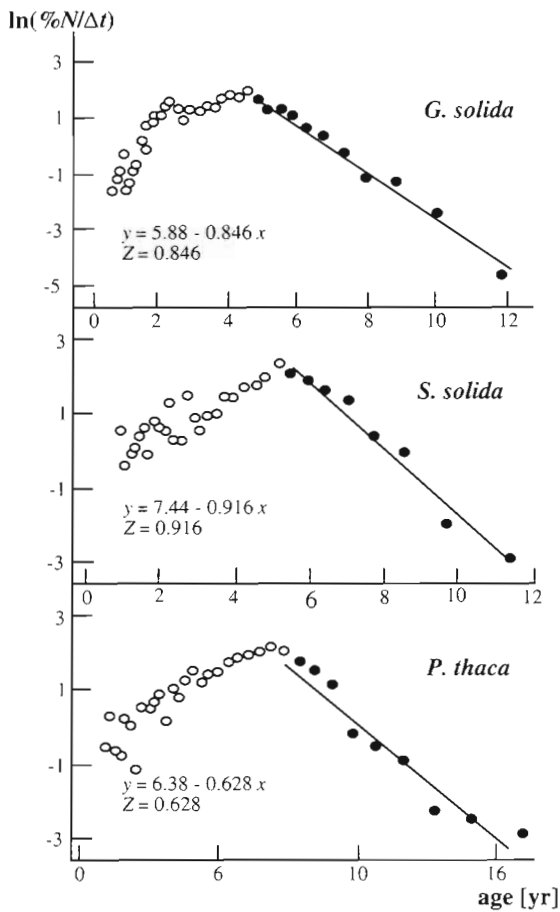[b] Estimated with fixed L_∞ (after Wetherall)

Fig. 4. *Gari solida, Semele solida* and *Protothaca thaca.* Length-converted catch curves of 3 Chilean bivalve species based on pooled length-frequency samples (from April 1991 to March 1992) and calculated with the ELEFAN II program. The VBGF parameters L_∞, K and t_0 required for this method are given in Table 3. Solid symbols: used for calculations of Z (mortality); open symbols: excluded from calculations. Linear regression equation and estimated Z-values are given

Production

The parameters of the linear regression analysis of the length-weight (AFDW) relationship used for the calculation of somatic production are given in Table 4. Individual somatic and gonad production of *Gari solida* and *Semele solida* follow a similar pattern (Fig. 5). Somatic production increases to its highest value at 50 to 55 mm length (*G. solida* ~1.0 and *S. solida* ~0.4 g AFDW ind.$^{-1}$ yr^{-1}) and decreases thereafter. Gonad production begins at 20 to 25 mm length at a level little below somatic production, increasing exponentially and exceeds somatic production at 45 mm length. Its highest values are ~4.0 g AFDW ind.$^{-1}$ yr^{-1} at 85 mm for *G. solida* and ~1.0 g AFDW ind.$^{-1}$ yr^{-1} at 75 mm for *S. solida*. Somatic production of *Protothaca thaca*

Table 4. *Gari solida, Semele solida* and *Protothaca thaca.* Parameters of the length (mm) to ash-free body dry weight (g) relationship for 3 Chilean bivalve species. log(AFDW) = $a + b$ log(Length)

Species	a	b	r^2	n
G. solida	−4.659	2.837	0.96	35
S. solida	−5.032	3.004	0.95	34
P. thaca	−6.020	3.658	0.97	32

reaches its highest level at 60 mm length (~0.6 g AFDW ind.$^{-1}$ yr^{-1}). Gonad production of this species follows the curve of somatic production, reaching its highest values at 60 mm length with 0.7 g AFDW ind.$^{-1}$ yr^{-1}. Contrasting to the latter 2 species, gonad production of *P. thaca* does not increase exponentially.

The distribution of annual somatic and gonad production and the abundance among the length classes
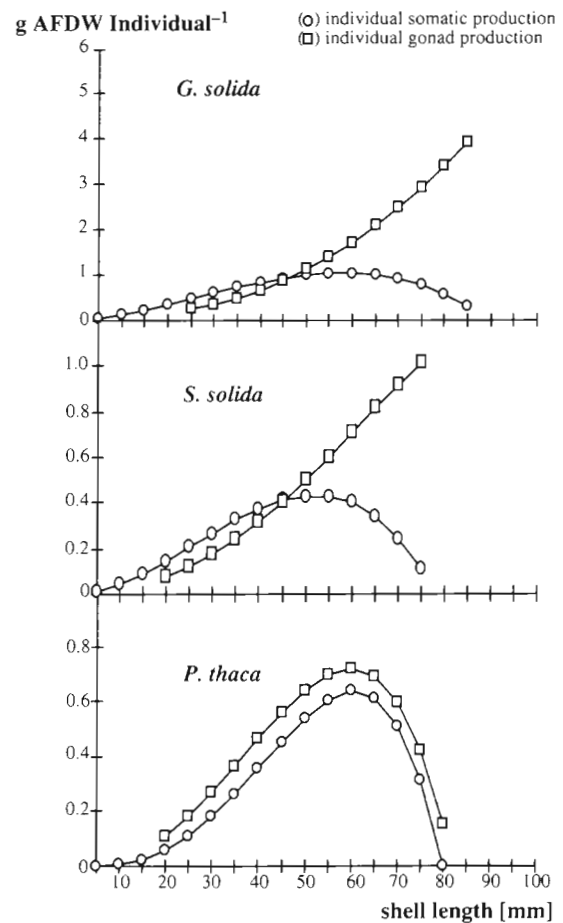

Fig. 5. *Gari solida, Semele solida* and *Protothaca thaca.* Individual production of somatic tissues and individual gonad production for different length classes of 3 Chilean bivalve species
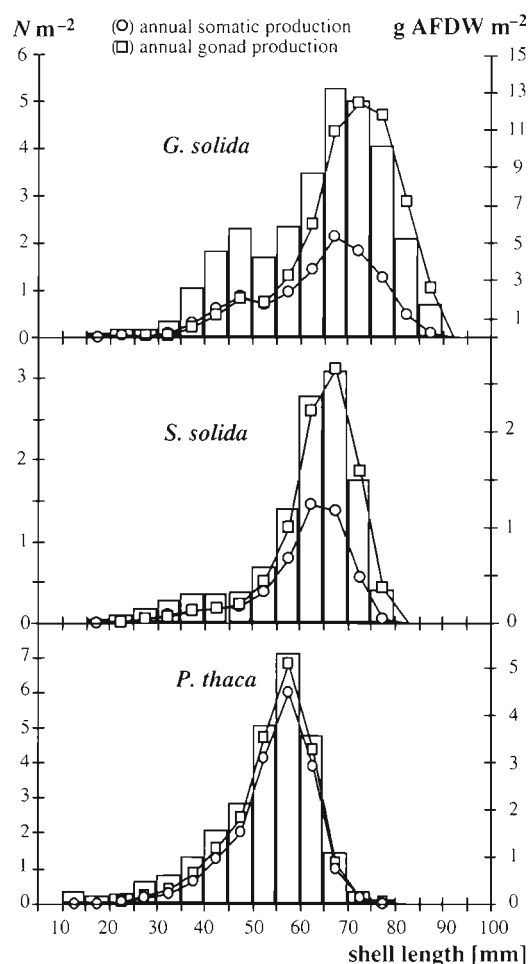
Fig. 6. *Gari solida*, *Semele solida* and *Protothaca thaca* Distribution of annual production of somatic tissues, annual gonad production and mean abundance for different length classes of 3 Chilean bivalve species

are shown in Fig. 6. The length-frequency distribution indicates a unimodal distribution for *Semele solida* and *Protothaca thaca* in the range of the higher length classes (*S. solida*: 55 to 75 mm, *P. thaca*: 50 to 65 mm). Only for *Gari solida* do 2 modes seem to exist (35 to 55 and 55 to 85 mm). However, all 3 populations seem to

consist mainly of old adult individuals with a small number of recruits. The annual production estimates are given in Table 5. Annual somatic production and mean biomass of *G. solida* amount to the highest values of all 3 species studied (27.6 and 82.6 g AFDW m^{-2} yr^{-1}), followed by *P. thaca* (16.9 and 62.9 g AFDW m^{-2} yr^{-1}) and finally *S. solida* (4.8 and 25.5 g AFDW m^{-2} yr^{-1}). Annual gonad production approximately doubles somatic production in *G. solida* and *S. solida* (56.0 and 8.7 g AFDW m^{-2} yr^{-1}, respectively), while for *P. thaca* it almost equals somatic production (14.5 g AFDW m^{-2} yr^{-1}). The following $P/\bar{B}$ ratios were calculated: *G. solida* = 0.334, *S. solida* = 0.188, *P. thaca* = 0.269.

DISCUSSION

Reproduction

Ishiyama & Chávez (1990) studied the reproduction cycle of *Gari solida* from Pisco, Peru (14° S) based on histological sections. They found a biannual cycle with reproductive activities in spring (October/November) and late summer (February/March) related to the annual temperature cycle, stating for *G. solida* continuous and synchronous gonad activities during the whole year. After each spawning cycle gonads recuperate rapidly to begin a new reproductive cycle. Campos et al. (1993) reported a continuous gametogenesis with several reproductive cycles and spawning events per year for *Semele solida* from Tongoy, Chile (30° S). Henríquez et al. (1981) found similar continuous and synchronous gonad activities for *Protothaca thaca* from San Jorge Bay, Chile (23° S) with spawning activities in August, February, March and May. These findings seem to contradict our own results which clearly indicate an annual reproductive cycle with a short spawning period in summer and a longer resting period in winter.

The examples for a continuous or biannual reproductive cycle were found in northern latitudes, nearer to the equator, while our own research area is located more towards the south (37° S). Towards the south, annual ambient conditions during winter become unfavourable, thus, spawning seasons have to become shorter and can change from biannual to annual. Chaparro & Winter (1983), citing Lozada (1968), found a short spawning season during spring and summer and a longer resting period in winter for the mytiloid species *Aulacomya ater*, from Putemún, Chile, and *Mytilus chilensis* from Chiloe, Chile (43° S). Similar exam-

Table 5. *Gari solida*, *Semele solida* and *Protothaca thaca*. Summary of production estimation for 3 Chilean bivalve species

	G. solida	S. solida	P. thaca
Annual gonad production (g AFDWm^{-2})	56.0	8.6	14.5
Annual somatic production (g AFDW m^{-2})	27.6	4.8	16.9
Annual biomass (g AFDW m^{-2})	82.6	25.5	62.9
Annual $P/\bar{B}$ ratio	0.334	0.188	0.269
Mean abundance (n m^{-2})	30.7	13.3	27.3
Mean body weight (g AFDW)	2.69	1.91	2.30

ples for annual reproductive cycles and spawning in summer are also available for clams from the North-American Pacific coast. *Protothaca staminea* from British Columbia, Canada (48° 57' N) spawns between May and September (Quayle 1943) and those from Oregon, USA (44° 39' N) between March and August (Robinson & Breese 1982) while *Clinocardium nuttallii* from Washington, USA (48° 35' N) spawns between July and November (Gallucci & Gallucci 1982). Thus, latitudinal effects and unfavourable ambient conditions related to them could explain the different reproductive strategies of the populations cited above. In contrast, Lozada & Bustos (1984), who studied the reproduction of *Venus antiqua* (which is closely related to *P. thaca*) from Chiloe, Chile (43° S, only 6° more to the south than our own research area), also found biannual reproductive (and body weight) cycles similar to those of the 3 populations cited above. It therefore seems that the explanation stated above is not generally the rule. Species-specific differences or locally different ambient conditions (e.g. currents, upwellings, nutrients) could dominate over a possible general latitudinal pattern. Clasing et al. (1994) explained the very high annual somatic production of *V. antiqua* from Chiloe by a comparatively long period of high primary production as well as the high nutritional value of suspended organic matter.

Growth and mortality

Urban (1991) estimated the growth of *Gari solida* and *Semele solida* from Pisco, Peru (14° S). He found the following VBGF parameters: *G. solida*, $L_\infty = 86$ mm, $K = 0.72$ yr^{-1}; and *S. solida*, $L_\infty = 85$ mm, $K = 0.48$ yr^{-1}. The L_∞-values agree well with the own values presented here while the K-values are much higher. However water temperatures are about 5 °C higher than in Chile (Urban 1994) and ambient conditions sustain a biannual reproduction cycle (see above), therefore, higher K-values can be expected in Peru. Vega (1979) studied the growth of *Protothaca thaca* in the Bay of Concepción, Chile (37 °S), very close to our own research area. His final (corrected) values are $L_\infty = 95.3$ mm and $K = 0.16$ yr^{-1}, owing to his assumption that 2 growth rings were formed per year. However, the present results did not confirm this assumption. His uncorrected values ($L_\infty = 80.7$ mm, $K = 0.29$ yr^{-1}) agree better with our own results. Comparing the growth of the 3 species indicates higher growth ($K \approx 0.3$ yr^{-1}) for *G. solida* and *S. solida* and slower growth ($K = 0.17$) for *P. thaca*. Taking into account the uncorrected K-value of Vega (1979) may indicate a similar growth for *P. thaca* as for the other 2 species. So far, no explanation for the different K-values of *P. thaca* is available.

Mortality values (Z) are highest for *Semele solida* ($Z = 0.92$ yr^{-1}), followed by *Gari solida* ($Z = 0.84$ yr^{-1}) and lowest for *Protothaca thaca* ($Z = 0.58$ yr^{-1}). During the study period the 3 populations found at the sampling site were not exploited intensively. Only a few local fishermen were observed at irregular intervals to collect individuals for consumption in the nearby village. Different Z-values could be explained by selection: *G. solida* and *S. solida* are collected more at the sampling site than *P. thaca* because a larger population of *Venus antiqua* is exploited more intensively only 1000 m away (the fishermen do not distinguish between *P. thaca* and *V. antiqua*, which are morphologically very similar).

Production

To the authors' knowledge, no other production estimates for the 3 species studied here exist so far. Clasing et al. (1994) estimated somatic and gonad production of *Venus antiqua* from Chiloe, Chile (42° S). *V. antiqua* is a shallow-water infaunal bivalve closely related and morphologically very similar to *Protothaca thaca*. Although Clasing et al. (1994) recorded a higher biomass they found an annual gonad production of only 2.0 g AFDW m^{-2} yr^{-1} which is considerably lower than our own results (56.0, 8.6 and 14.5 g AFDW m^{-2} yr^{-1}, respectively). Clasing et al. (1994) assumed only 1 spawning period per year. According to Lozada & Bustos (1984), *V. antiqua* has a biannual reproductive cycle, thus, their reproductive output could have been underestimated by 50%. In contrast to our 3 populations (Fig. 6), the amount of small individuals in the *V. antiqua* population from Chiloe is high. These young individuals devote most of their energy to somatic production and little to gonad production, which would be a further explanation for the low value of gonad production of *V. antiqua*. Finally, the method for gonad production applied in this study is based on weight changes before and during the spawning season. It is thereby assumed that all material stored during the weight increase in summer is devoted to reproduction. As this assumption is not correct — energy is devoted to growth and maintenance — the present gonad production is probably overestimated.

In Fig. 7 our own results on annual somatic production are compared with data found in the literature on other Tellinacea and Veneracea by plotting the $P/\bar{B}$ ratio against the mean body weight. It can be seen clearly that our own data (1) agree very well with the data taken from the literature and (2) are in the lower range of the $P/\bar{B}$ data presented. As stated above, only a small number of recruits were present during the study period. Thus, the 3 populations consist of older

Fig. 7. Comparison of somatic production of 3 Chilean bivalve species, *Gari solida* (Gs), *Semele solida* (Ss) and *Protothaca thaca* (Pt) with other species of the superfamilies Veneracea and Tellinacea (taken from the literature) by plotting the $P/\bar{B}$ ratio against mean body weight (MBW).

Literature sources:
(Va) *Venus antiqua*, Chiloe, Chile (Clasing et al. 1994)
1: *Donax vittatus*, South Wales, UK (Warwick et al. 1978)
3: *Scrobicularia plana*, Cornwall, UK (Warwick & Price 1975)
4, 5: *Abra alba*, Kiel Bight, Germany (Rainer 1985)
6–10: *Abra alba*, English Channel, France (Dauvin 1986)
11. *Abra nitida*, Northumberland, UK (Buchanan & Warwick 1974)
12, 13: *Abra nitida*, North Sea, Sweden (Josefson 1982)
15: *Macoma balthica*, Nova Scotia, Canada (Burke & Mann 1974)
16, 17: *Macoma balthica*, North Sea, Denmark (Madsen & Jensen 1987)
18: *Macoma balthica*, Cornwall, UK (Warwick & Price 1975)
19, 20: *Macoma calcarea*, Arctic Sea, Greenland (Petersen 1978)
21–28: *Tellina fabula*, German Bight, Germany (Salzwedel 1980)
29, 30: *Tellina fabula*, Yorkshire, UK (Rees 1983)

$$\text{Log }(P/\bar{B}) = -0.432 - 0.221 \text{ Log (MBW)}$$
$$r = 0.77, \; n = 53$$

31: *Tellina fabula*, South Wales, UK (Warwick et al. 1978)
33–35: *Callista brevisiphonata*, Sea of Japan, Russia (Selin & Selina 1988)
36, 37: *Chione cancellata*, Florida, USA (Moore & Lopez 1969)
38: *Dosinia elegans*, Florida, USA (Moore & Lopez 1970)
39–41: *Mercenaria mercenaria*, Southampton, UK (Hibbert 1976)
42, 43: *Mercenaria mercenaria*, Geor-
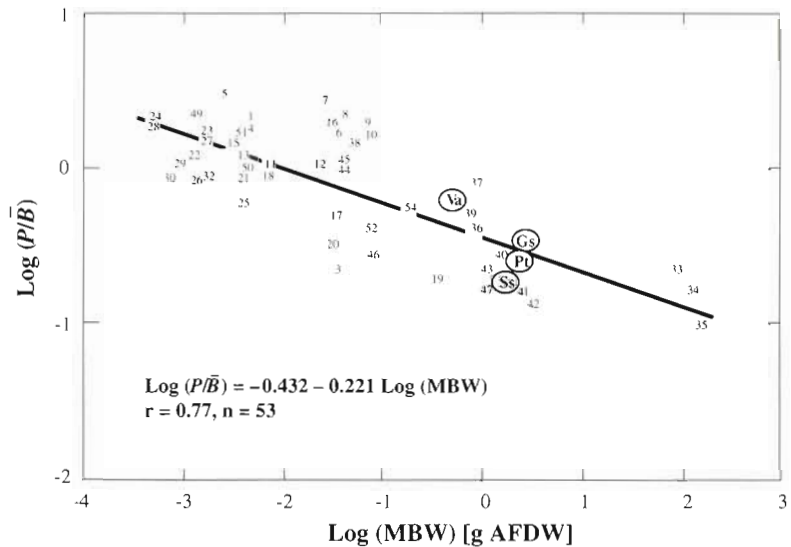
gia, USA (Walker & Tenore 1984)
44–46: *Venerupis aurea*, Southampton, UK (Hibbert 1976)
47: *Venerupis pullastra*, North Sea, Norway (Johannessen 1973)
49–51: *Venus ovata*, English Channel, France (Dauvin 1985)
52: *Venus striatula*, South Wales, UK (Warwick et al. 1978)
54: *Pharus legumen*, South Wales, UK (Warwick et al. 1978)

individuals with low somatic production. Accordingly, the $P/\bar{B}$ ratio of *Venus antiqua* from Chiloe in Fig. 7, a population of younger individuals with high somatic production, is located more towards the upper $P/\bar{B}$ and the lower mean body range.

The different findings on somatic production in Dichato and Chiloe could be caused by different exploitation rates in the fisheries. Hall et al. (1970) showed that after fish predation in a freshwater pond increased, only benthic production increased while its biomass remained constant. Fish consumed only the large individuals from the benthic population and consequently the $P/\bar{B}$ ratio increased. In the case of the clam fisheries the situation is similar: mainly clams with a certain minimum (marketable) size are collected for consumption. Clasing et al. (1994) reported a high fishing pressure for the *Venus antiqua* population from Chiloe, which altered the size structure towards younger individuals with high somatic production and $P/\bar{B}$ ratio.

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