Growth, reproduction and production of *Lissarca notorcadensis* (Bivalvia: Philobryidae) in the Weddell Sea, Antarctica*

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ABSTRACT: Growth, reproduction and production of the epizoic bivalve *Lissarca notorcadensis* were compared between 2 regions of the Weddell Sea, the South Orkney and South Shetland shelves (north of 63° S) and the southeastern continental shelf (south of 70° S). Growth lines on the shell surface were interpreted as annual growth marks. Von Bertalanffy growth functions were fitted to length-at-age data for the northern region (L_∞ = 12.140 mm, K = 0.085 yr^{-1}, t_0 = −1.477 yr) and for the southern region (L_∞ = 9.802 mm, K = 0.112 yr^{-1}, t_0 = −1.247 yr). Female gonad production was estimated from the number of embryos brooded per female, embryo mass at release and the fraction of females in the population. Somatic production was calculated from weight specific growth rates. Annual somatic and gonad production/biomass (P/B) ratios were 0.316 and 0.151 (north), and 0.305 and 0.132 (south), respectively. These values are lower than P/B ratios of boreal mollusc populations of comparable mean body mass.

INTRODUCTION

The bivalve *Lissarca notorcadensis* (Mevill & Standen, 1907), is endemic to the Antarctic and has a circum-Antarctic distribution in depths of 18 to 1120 m (Dell 1990). On the Weddell Sea shelf and slope it is the most abundant bivalve species present (Hain 1990). It is a suspension feeding species which attaches itself to sea urchin spines and bryozoan and hydrozoan colonies by byssus threads. Despite its widespread distribution and its frequency, little is known about the population dynamics of this species. The purpose of this paper is to compare growth, reproduction and production of *L. notorcadensis* in 2 regions of the Weddell Sea which are about 1500 km apart: the South Orkney & South Shetland shelves north of 63° S; and the southeastern shelf and slope south of 70° S.

METHODS

Specimens of *Lissarca notorcadensis* were collected from samples taken with RV 'Polarstern' between 1985 and 1990 in the Weddell Sea (see Table 1).

They were taken from 61 stations on the southeastern shelf and slope (80 to 1108 m water depth, mean = 417 m) and from 4 stations close to the South Orkney and South Shetland islands (176 to 414 m, mean = 319 m; Fig. 1). A modified Agassiz trawl (1 × 3 m mouth opening, 20 × 20 mm mesh size in the front parts, 10 × 10 mm in the medium parts and the cod end) was employed for collections (Voss 1988). Sea urchins, bryozoan colonies and hydrozoan colonies covered with *L. notorcadensis* were handpicked from the material collected and stored in 70 % ethanol.

In the laboratory, all specimens were removed from their substrate, counted, and measured by a Virtual Imaging System. Length was defined as the largest distance across the shell of the bivalves and measured to an accuracy of 0.023 mm. Mean individual ash-free dry mass (AFDM) per length class (range 1 to 7 mm, 0.25 mm class width) was determined by drying several pooled specimens at 80 °C for 24 h (DM) and subsequent ignition at
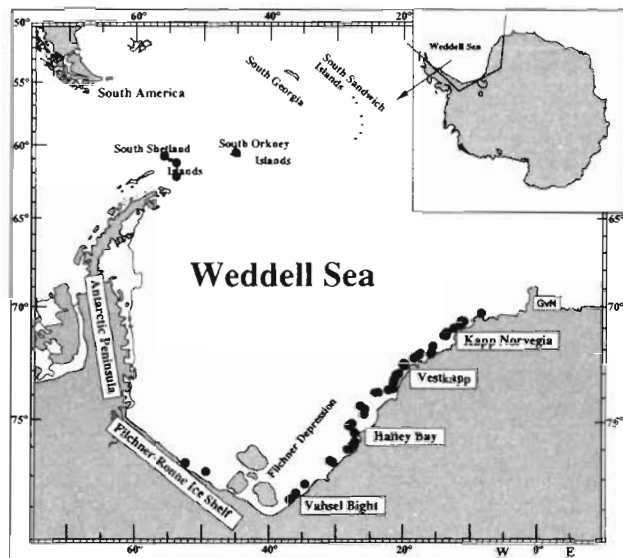
Fig. 1. Distribution of sampling stations in the Weddell Sea

500 °C for 24 h (ash). A length-mass relation of the form

$$M = a \times L^b \tag{1}$$

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

Specimens collected during spring/summer at depths between 200 and 350 m (northern region) and between 300 and 500 m (southern region) were used for growth analysis. The growth rings visible on the surface of the shells were assumed to be layed down annually as in other Antarctic and sub-Antarctic mollusc species (see e.g. Ralph & Maxwell 1977, Richardson 1979, Picken 1980). For growth ring analysis, shells were cleaned of organic matter using a 5 % solution of NaOCl, then washed in 96 % ethanol and dried at 60 °C. Growth rings were counted under a stereo microscope by submersing the shells in tert-butyl methyl ether. Von Bertalanffy growth curves

$$L_t = L_\infty \times \left(1 - e^{-K(t - t_0)}\right) \tag{2}$$

were fitted to length-at-age data sets by the SIMPLEX algorithm. The maximum growth rate (in mg AFDM yr^{-1}) attained during lifetime was used as a measure of overall growth performance:

$$\mathrm{Max} \frac{\mathrm{d}M}{\mathrm{d}t} = K \times M_\infty \times (1 - 1/b)^{b-1} \tag{3}$$

where K = growth constant of the von Bertalanffy function; M_∞ = asymptotic mass; and b = the exponent of the size-mass relation.

We determined the percentage of ovigerous females (i.e. specimens with developing eggs in the gonads

and/or with embryos in the mantle cavity) and the number of embryos per female from random subsamples of animals from both regions. Diameter of eggs and embryos was measured by a Virtual Imaging System to an accuracy of 0.004 mm, and AFDM of the embryos was determined as described above using pooled samples of about 100 specimens. The relation between the number of embryos and length, water depth and latitude was analyzed by linear regression.

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

$$P = \sum N_i \times M_i \times G_i \tag{4}$$

where P = production per total sample; N_i and M_i = no. of bivalves and mean individual somatic mass in size class i respectively; and G_i = weight-specific growth rate yr^{-1}, which is computed by:

$$G_i = b \times K \times (L_\infty - L_i) / L_i \tag{5}$$

where b = the exponent of the size-mass relation (Eq. 1); K and L_∞ = parameters of the von Bertalanffy function (Eq. 2); and L_i = mean length in class i.

Female gonad production (i.e. reproductive output *sensu* Clarke 1987) was computed from the number of embryos brooded in the mantle cavity and the embryo mass at release (i.e. embryo mass in October, see 'Results'):

$$PG = \sum N_{E,i} \times M_E \times N_i \times F_F \tag{6}$$

where $N_{E,i}$ = no. of embryos per female in length class i; M_E = average embryo mass at release; N_i = no. of individuals in length class i; and F_F = the fraction of brooding females in the population.

The annual P/B ratio was calculated using production (P), female gonad (PG) and biomass per total sample ($B = \sum N_i \times M_i$):

$$\begin{aligned} \text{Somatic } P/B \text{ ratio} &= P/B \\ \text{Gonad } P/B \text{ ratio} &= PG/B \\ \text{Total } P/B \text{ ratio} &= (P + PG)/B \end{aligned} \tag{7}$$

RESULTS

A total of 5057 specimens of *Lissarca notorcadensis* were counted and measured (Table 1). 97 % of these were sampled at stations between 170 and 500 m

Table 1 *Lissarca notorcadensis*. Number of stations and specimens (N) sampled in the Weddell Sea area during different years. Numbers in parentheses: samples from the northern region, <63° S

Year	Winter/Spring							Spring/Summer				Total	
	October		November		December		January		February				
	Stn	N	Stn	N	Stn	N	Stn	N	Stn	N	Stn	N
1985	0	–	0	–	0	–	5 (3)	103 (270)	8	444	16	817
1986	9	337	14	701	0	–	0	–	0		23	1038
1987	0	–	0	–	0	–	3	172	2	235	5	407
1988	0	–	0	–	0	–	4	79	4	9	8	88
1989	0	–	0	–	1	100	0 (1)	– (1679)	1	305	3	2084
1990	0	–	0	–	0	–	6	319	4	304	10	623
Total	9	337	14	701	1	100	22	2622	19	1297	65	5057

water depth. Mean bivalve length per station was correlated neither with water depth (p = 0.60) nor with latitude (p = 0.80), but there were geographical and seasonal differences between the pooled size-frequency distributions of the northern and southern stations for January-February (spring/summer) and October-December (winter/spring) (Fig. 2). The spring/summer distributions of the northern and southern regions as well as the spring/summer and the winter/spring distribution of the southern region were significantly different (Brandt-Snedecor test; p < 0.05). These differences were mainly due to the different size of the first peak of the distributions between 1 and 2 mm length. There were no significant differences in the length-mass relationship between northern and southern stations (p = 0.18); the relation for the combined data is:

$$M = 0.018 \times L^{2.567} \text{ (mg AFDM-mm)}$$

for 26 length classes and 232 specimens.

Growth

The residuals of a von Bertalanffy growth function fitted to the combined length-at-age data from both the northern and southern region were significantly different between regions (Table 2). Within the 2 regions no significant effects of latitude or depth were detectable. Growth was similar in both regions during the first 6 to 8 yr, but older specimens were distinctly larger in the north (Fig. 3): north: L_∞ = 12.140 mm, K = 0.085 yr^{-1}, t_0 = −1.477 yr; south: L_∞ = 9.802 mm, K = 0.112 yr^{-1}, t_0 = −1.247 yr. The maximum growth rate of *Lissarca notorcadensis* was 0.429 mg AFDM yr^{-1} in the northern region and 0.326 mg AFDM yr^{-1} in the southern region.

Reproduction and recruitment

No ovigerous females smaller than 3.8 mm length were found. The percentage of ovigerous females was
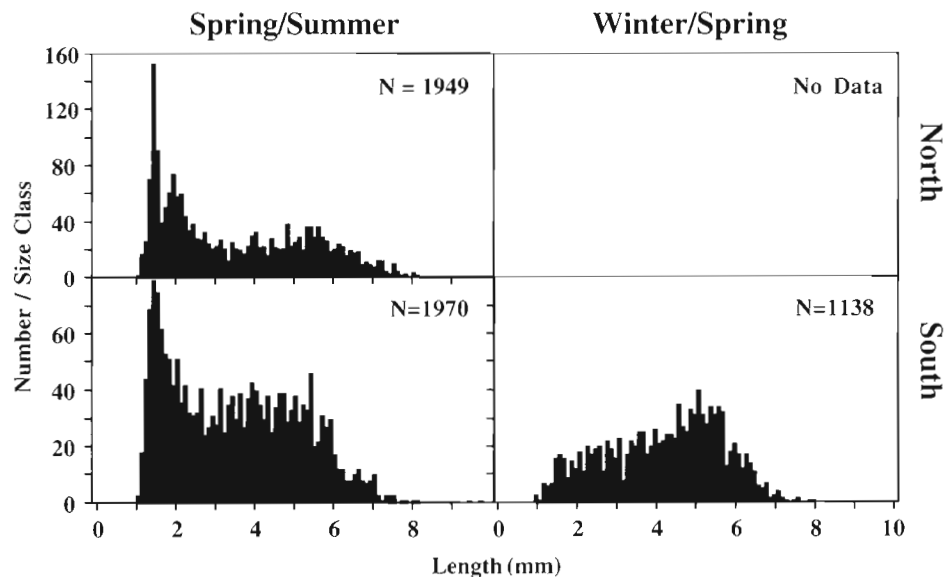

Fig. 2. *Lissarca notorcadensis*. Length-frequency distributions of pooled samples from the northern region and the southern region in spring/summer and winter/spring

Table 2. Analysis of variance of the residuals of the von Bertalanffy growth function fitted to the combined length-at-age data from both the northern and southern region. L_∞ = 10.533 mm; K = 0.103 yr^{-1}; t_0 = –1.284 yr; N = 112; residual sum of squares = 32.910. Dependent variable: residuals of growth function; independent variable: region (North/South)

Source	df	Sum of squares	Mean square	F	p
Region	1	1.875	1.875	6.645	0.0113
Residual	110	31.031	0.282		

46 % in the portion of the population above 3.8 mm length in the north as well as in the south. Mature females simultaneously carry eggs in the ovaries and embryos in the mantle cavity. Size measurements of eggs and embryos in January and October revealed differences between regions as well as seasons (Fig. 4). In January, the diameter of eggs was slightly but not significantly different between the 2 regions (north: mean = 0.241 mm, SD = 0.035; south: mean = 0.254 mm, SD = 0.057; p = 0.08). Embryo diameter, however, was significantly smaller (p < 0.001) in the north (mean = 0.543 mm, SD = 0.060) than in the south (mean = 0.581 mm, SD = 0.064). In October (southern region only) eggs (mean = 0.513 mm, SD = 0.074) as well as embryos (mean = 1.248 mm, SD = 0.042) were significantly (p < 0.001) larger than in January. The average embryo mass in January was 0.014 mg AFDM in the north and 0.016 mg AFDM in the south, and in October 0.031 mg AFDM (southern region).

Table 3. Analysis of covariance of the factors affecting the no. of embryos per female. Dependent variable: no. of embryos per female; independent variables: female body mass (mg AFDM), depth (m), region (North/South); interaction term (Depth × Region)

Source	df	Sum of squares	Mean square	F	p
Female body mass	1	3918.453	3918.453	124.142	0.0001
Depth	1	1032.964	1032.964	32.726	0.0001
Region	1	482.304	482.304	15.280	0.0001
Depth × Region	1	578.232	578.232	18.319	0.0001
Residual	127	4008.677	31.564		

The number of embryos brooded per female depends on female body mass, water depth and region, but there were strong intercorrelations between depth and region (Table 3). The slope of the single linear regression between the number of embryos per female (N_E) and body mass (M) was significantly higher in the northern than in the southern region (p < 0.05). The functional regressions (Fig. 5; and see Ricker 1973) were used for production calculations (see below):

North: $N_E = -8.414 + 17.655\ M$;   r = 0.687, N = 38
South: $N_E = -2.923 + 12.477\ M$;   r = 0.682, N = 94

Production

All production calculations refer to the pooled samples from the northern and southern region, respectively. Individual somatic production increased with length up to 7.5 mm (north) and 6 mm (south) and decreased again (Fig. 6). Female gonad production increased with length above 4 mm. In both populations, individual gonad production exceeded individual somatic production above 5 mm length. In the north the annual production/biomass ratios amounted to 0.316 (somatic production), 0.151 (female gonad production) and 0.467 (both), and for the south 0.305 (somatic), 0.132 (female gonad), and 0.437 (both).

DISCUSSION

Geographical intraspecific variations in growth, reproduction and productivity are mainly related to 2 factors, temperature and food supply. In boreal benthic species, some investigations stress the importance of temperature only (see e.g Taylor 1960, Bachelet 1980, Beukema & Meehan 1985), whereas others suggest food supply plays a more important role (see e.g.
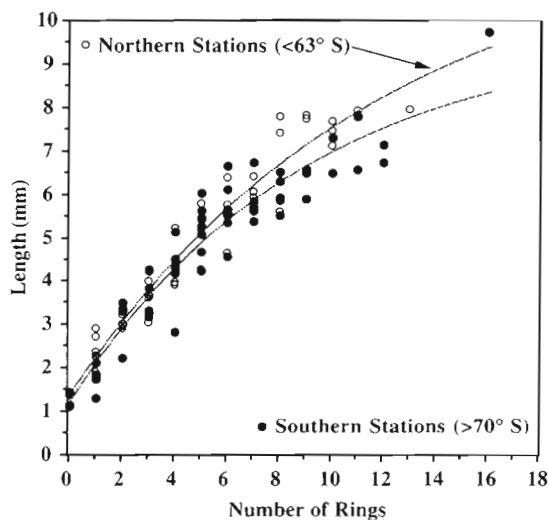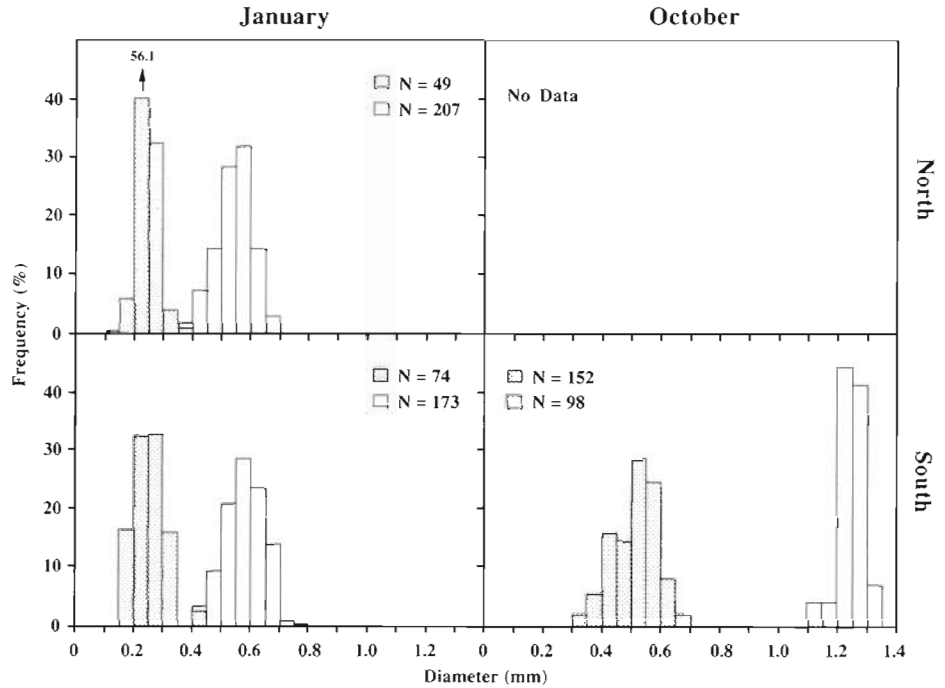

Fig. 3 *Lissarca notorcadensis*. Von Bertalanffy growth curves fitted to length-at-age data. Growth rings are assumed to be formed annually. North: L_∞ = 12.140 mm, K = 0.085 yr^{-1}, t_0 = –1.477 yr, N = 40, residual sum of squares = 10.783; south: L_∞ = 9.802 mm, K = 0.112 yr^{-1}, t_0 = –1.247 yr, N = 72, residual sum of squares = 19.448

Fig. 4. *Lissarca notorcadensis.* Size-frequency distributions of eggs in the ovary (shaded bars) and of embryos brooded in the mantle cavity (white bars) in January and in October (pooled material from several females). Egg and embryo counts are normalized separately to 100%

Dehnel 1956, Frank 1975, MacDonald & Bourne 1987, MacDonald & Thompson 1988). In the Antarctic, the low water temperatures have been suggested to be the main limiting factor for metabolic processes and population dynamics. However, there is evidence for a greater significance of food supply, which becomes increasingly scarce and oscillating towards the south (see e.g. Hedgepeth 1977, Clarke 1988, Arntz et al. in press).

Both the northern and the southern investigation areas are situated in the region of the cold 'Antarctic winter water' in 100 to 500 m depth (-1.8 to -1.2 °C at 276 m on the continental shelf; Arntz et al. in press), so temperature differences are negligible (Hellmer & Bersch 1985). In areas above 100 m temperatures are
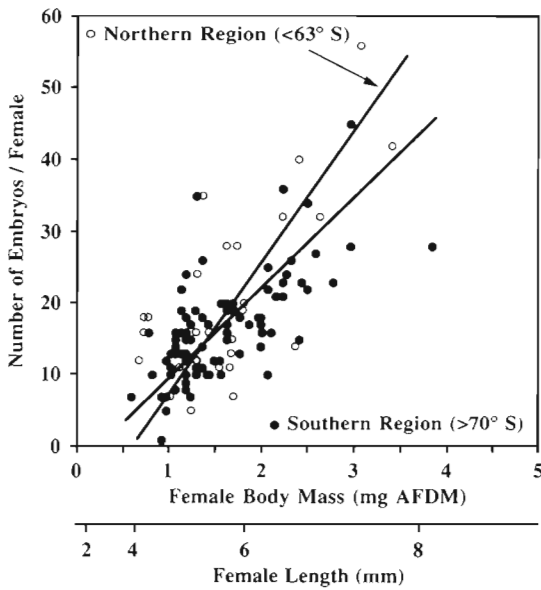

Fig. 5. Relation between no. of embryos brooded in the mantle cavity (N_E) and female body mass (M). Functional regression (geometric mean model) according to Ricker (1973). North: $N_E = -8.414 + 17.655\,M$, r = 0.687, N = 38; south: $N_E = -2.923 + 12.477\,M$, r = 0.682, N = 94
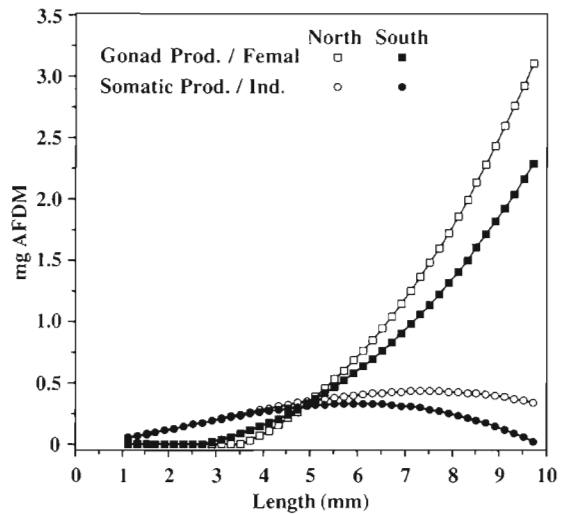

Fig. 6. *Lissarca notorcadensis.* Relation between length and individual somatic and female gonadal production in the northern and southern region

higher during summer (annual average in shallow waters around Signy Island about −1.8 to + 0.8 °C; Clarke 1988, Clarke et al. 1988). Below 500 m in the 'warm deep water' layer temperatures are higher too (−1.8 to −0.4 °C at 607 m on the continental shelf; Arntz et al. in press).

The food supply of benthic suspension feeders such as *Lissarca notorcadensis* depends on sedimenting matter from the pelagic zone and hence on the amount of pelagic primary production and on water depth. Primary production is much higher in the north close to the Weddell Sea islands (up to 3 g C d⁻¹ near Signy and Deception islands; Mandelli & Burkholder 1966, Horne et al. 1969) than in the south (about 0.6 g C d⁻¹; El Sayed 1971, El Sayed & Taguchi 1981, Bröckel 1985). Moreover, the period of high primary production and sedimentation in austral summer lasts for 8 to 10 wk in the northern region (Clarke 1988, Clarke et al. 1988) but only for about 4 to 6 wk in the southern region (Bodungen et al. 1988, Bathmann et al. 1991).

Therefore it is likely that differences in growth, reproduction and production of *Lissarca notorcadensis* between the northern and southern regions are mainly related to differences in food supply.

Growth

Growth performance (= maximum growth rate) of *Lissarca notorcadensis* on the shelf decreased from north (0.429 mg AFDM yr⁻¹) to south (0.326 mg AFDM yr⁻¹). This decrease may be related either to geographical latitude or to water depth, because the specimens included in the growth analysis were from different depth ranges (north: 200 to 350 m, south: 300 to 500 m). The closely related species *L. miliaris* inhabits shallow waters above 10 m at Signy Island (60°43' S). Its maximum growth rate, 0.532 mg AFDM yr⁻¹ (calculated from Richardson 1979), is higher than in *L. notorcadensis* which indicates a decrease in growth performance from shallow to deeper waters.

However, the maximum short term growth rate of *Lissarca notorcadensis* may be much higher than indicated by the curve based on annual growth band readings (Fig. 3). If growth of benthic suspension feeders is closely linked to the period of primary production and sedimentation, then total annual growth may take place only during a small fraction of the year. This has been observed in other Antarctic and sub-Antarctic benthic invertebrates such as the gastropod *Laevilacunaria antarctica* at Signy Island (Picken 1979), the amphipod *Paramoera walkeri* at Cape Bird (Sagar 1980), or the polychaete *Amphicteis gunneri* at the Kerguelen Islands (Desbruyeres 1977).

Reproduction

Lissarca notorcadensis has an annual reproductive cycle, but egg and embryonic development takes 2 yr. There are 2 overlapping generations of developing young in 1 female, the embryos in the mantle cavity and the eggs in the ovary (Fig. 4). The negligible difference between the average size of the embryos in October (1.25 mm; Fig. 5) and the juveniles of the population (about 1.3 mm, first peak of the spring/summer size frequency distributions in Fig. 2) indicates that these embryos should be released soon. This is in agreement with the clear difference between the size-frequency distributions of spring/summer and winter/spring (Fig. 2) and with the increase of the fraction of juveniles in the samples from < 10 % in October to values > 20 % between late November and February (Fig. 7).

Our results show distinct differences in the reproduction of *Lissarca notorcadensis* between the northern and southern region. In the south, the number of embryos per female is lower (above 5.5 mm female length; Fig. 5), but they are larger (Fig. 4; January). Similar intraspecific latitudinal trends in clutch size and egg size were found in several benthic taxa in the Antarctic such as serolid isopods (Wägele 1987) and caridean shrimps (Gorny et al. in press). The number of offspring per female tends to decrease the further south one samples but size of eggs and of hatching juveniles increases. However, our data are not sufficient to decide whether the observed differences in *L. notorcadensis* are mainly related to latitude or to water depth (see Table 3).
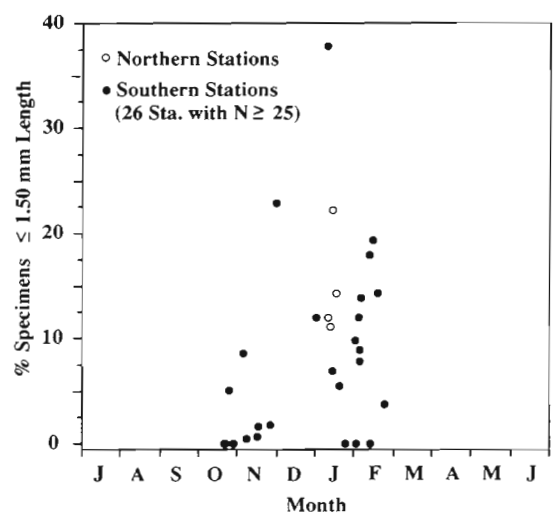

Fig. 7 *Lissarca notorcadensis*. Annual variation in the percentage of newly recruited specimens (≤ 1.5 mm length). All stations where a total of ≥ 25 specimens were collected are shown

Most Philobryidae investigated so far exhibit brood protection (Dell 1972). However, those 3 species investigated in more detail show different levels of parental care. In *Philobrya munita* living on macroalgae at the coast of New Zealand, eggs are retained in the mantle cavity past metamorphosis and the developing young '...attach themselves to the byssus of the parent both within and external to the mantle cavity' (Morton 1978, p. 176). In the sub-Antarctic shallow water species *Lissarca miliaris*, 2 clusters of embryos develop within the anterior mantle cavity, and fully developed juveniles (mean size = 0.73 mm) are released (Richardson 1979). In the Antarctic shelf species *L. notorcadensis* the number of embryos is much lower than in *L. miliaris* ($N_E = -160.17 + 53.69\ L$; Richardson 1979), but the juveniles released are larger (mean size = 1.25 mm in the southern region). These trends within the genus *Lissarca* give evidence that increasing parental care is related to geographical latitude and to increasing water depth, which can be interpreted as a strategy to counteract the negative effects of increasingly scarce food supply on individual survival of the offspring (see e.g. Christiansen & Fenchel 1979).

Productivity

The small difference in the *P/B* ratio of *Lissarca notorcadensis* between the northern (0.467 yr^{-1}) and southern region (0.437 yr^{-1}) may be due to the same factors as discussed above, i.e. mainly the lower food supply in the south. However, the *P/B* ratio in the north can be slightly over-estimated due to sampling during the recruitment period only (January, see Table 1).

The *P/B* ratios presented here are the first calculated for a bivalve inhabiting the Antarctic shelf. A comparison with other Antarctic macrobenthic species is not very useful at this time, because data are still scarce. However, compared with boreal mollusc populations of similar mean individual body mass the *P/B* ratio of *Lissarca notorcadensis* is low (Fig. 8), indicating a comparatively low weight specific metabolic rate in this Antarctic bivalve.

Successful adaptation of *Lissarca notorcadensis*

With respect to growth, reproduction and productivity, *L. notorcadensis* corresponds well to our present knowledge of adaptations to the particular conditions of the Antarctic shelf environment (see discussion in Clarke 1988, 1991). Growth and reproductive output (*sensu* Clarke 1987) seem to be lower than in closely related shallow water species and decrease further towards south, whereas parental care shows the opposite trend. The annual *P/B* ratio is very low compared to boreal populations (Fig. 8). Nevertheless, *L. notorcadensis* must be considered as a successful
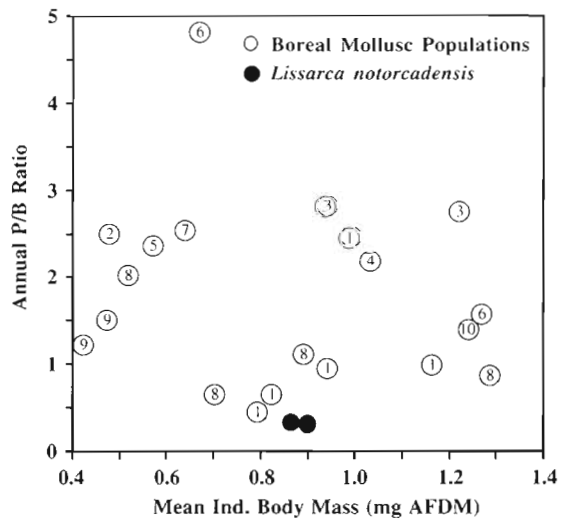

Fig. 8. Annual somatic *P/B* ratio of *Lissarca notorcadensis* (●) compared to 10 temperate mollusc species of similar mean individual body mass (data based on a literature survey, references see Brey 1990). ① *Abra nitida*; ② *A. ovata*; ③ *A. prismatica*; ④ *Hydrobia* sp.; ⑤ *Littorina saxatilis*; ⑥ *Spisula solidissima*; ⑦ *Tellina agilis*; ⑧ *T. fabula*; ⑨ *Thyasira flexuosa*; ⑩ *Venus ovata*

species: the frequency of occurrence is high, and abundance, biomass and production are likely to be higher than in any other mollusc species in the Weddell Sea. The intense brood protection may be one of the most important factors responsible for the ecological success of this species on the Antarctic shelf.

Our results indicate that besides the well-known north-south gradient in various biological parameters of Antarctic benthic species there may be a second, equally important, shallow-deep water gradient. We still cannot prove whether temperature or food supply is the major environmental force that causes the observed adaptations in Antarctic benthic invertebrates. However, future investigations in the region of the 'warm deep water' layer (500 to 1500 m depth) of the Weddell Sea may give better evidence of the adaptations of benthic animals to a regime of very low food supply but comparatively higher temperature.

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