Age and productivity of the Antarctic scallop, *Adamussium colbecki*, in Terra Nova Bay (Ross Sea, Antarctica)

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Abstract

Body size, geographical distribution, and biomass make *Adamussium colbecki* (Smith, 1902) one of the most conspicuous bivalve species in the Antarctic. Based on samples collected in austral summer 1999/2000 in Terra Nova Bay, the annual formation of shell growth bands visible on X-ray photographs was verified by stable isotope analysis. A general von Bertalanffy growth function was fitted to size-at-age data of 25 individuals ($H_\infty = 108.86$ mm, $K = 0.114$ year^{-1}, $t_0 = -0.367$, $D = 1.284$). Somatic production calculated from mass-specific growth rates was 234.6 kJ m^{-2} year^{-1}. Gonadal productivity amounted to 70.92 kJ m^{-2} year^{-1}. Annual somatic and gonad production-to-biomass ratios (P/B) were 0.199 and 0.052, respectively. According to its consumption and production, *A. colbecki* is likely to play a significant role in the trophic web of Terra Nova Bay.
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1. Introduction

In contrast to temperate benthic environments (e.g. Loo and Rosenberg, 1989; Wildish and Kristmanson, 1997; Mistri et al., 2001), molluscs contribute little to the often

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extraordinarily high benthic standing stock in Antarctic waters (Arntz et al., 1994; Brey and Gerdes, 1997) and are generally thought to play a minor role regarding energy flow (Jarre-Teichmann et al., 1997). Locally, however, some populations may reach considerable abundances and may play a significant role in nutrient cycling and benthic–pelagic coupling.

In nearshore waters of the Ross Sea, the endemic scallop *Adamussium colbecki* (Smith, 1902) is the most abundant bivalve down to 100-m depth (Chiantore et al., 2001). *A. colbecki* 'banks' play an important role in the coastal food web as they process up to 14% of the total carbon flux (Chiantore et al., 1998) and represent an important food source for higher tropic levels, e.g. fish (*Trematomus bernacchii* Boulenger) and invertebrates such as *Neobuccinum eatoni* (Smith, 1875) and *Paraborlasia corrugata* (McIntosh, 1876) (Vacchi et al., 2000). Despite its widespread distribution and assumed significance for the system's energy flow (e.g. Stockton, 1984; Berkman, 1990; Albertelli et al., 1998; Chiantore et al., 1998, 2001), little is known about the population dynamics and production of this species.

This study presents the first reliable age determination of *A. colbecki* from Terra Nova Bay as confirmed by stable isotope analysis. Based on these data, production and productivity values are calculated in order to evaluate the significance of *A. colbecki* in the trophic web and energy flow of the coastal Ross Sea ecosystem.

2. Materials and methods

2.1. Sampling and processing of samples

Specimens were collected in Terra Nova Bay ('Road Cove', 74°41.9′S, 164°07.5′E) in austral summer 1999/2000 at 30- to 76-m depth by Charcot-Picard and naturalist dredge. Shell height (defined as the maximum distance between the dorsal hinge and ventral margin) of a representative subsample of 895 individuals was measured to the nearest 0.1 mm using vernier callipers. A size frequency distribution (SFD) was obtained by pooling individuals using class intervals of 2-mm size. Additional size frequency data from the same site, obtained with the same gear, have been provided by Chiantore et al. (2000), Cattaneo-Vietti et al. (1997), and references therein. To remove the fluctuations between years and obtain a more representative long-term 'average' population, a multiyear size frequency distribution was constructed by pooling data taken from the years 1989/1990 to 1999/2000. Prior to pooling, each sample was converted into percentage values to give the same weight to each sample.

Size–mass relationships were modeled by linear regression of:

$$\log(M) = \log(a) + b\log(\mathrm{SH}) \tag{1}$$

where M is the soft tissue mass (g) at shell height SH (mm). Gonad colouring was used to determine sex of the individuals (Chiantore et al., 2002). Soft tissue dry masses (DM) were determined by oven drying of tissues at 60 °C for 24 h.

2.2. Age and growth

Traditional methods of ageing *A. colbecki* such as counting bands on the shell surface (e.g. Stockton, 1984; Berkman, 1990) or on X-ray photographs (Ralph and Maxwell, 1977; Cattaneo-Vietti et al., 1997) are not reliable without validation of annual formation of those bands, as shown for scallops in general by Krantz et al. (1984) and Dare and Deith (1990). We identified and verified annual growth bands in *A. colbecki* shells in a three-step procedure: (i) external growth band identification, (ii) comparison with internal growth band pattern, and (iii) validation of annual formation by stable isotope analysis.

In this study, only undamaged upper (left) shell valves free of epibionts were used for growth analysis. Prior to analysis, shells were cleaned of organic matter with warm 5% NaOCl solution, washed with 96% ethanol, rinsed with water, and dried at 60 °C for 12 h. External, macroscopically visible shell surface growth bands were identified following the method described by Merrill et al. (1965). This visual growth band pattern was compared with the pattern of conspicuous rings of higher density detected on X-ray photographs of the same shells. X-rays were taken by a Hewlett Packard Faxitron 43855 mammograph with fixed anode, using an AGFA-Strukturix D4 FW film and the following parameters settings: focal film distances 45 cm, voltage 30 to 45 kV, exposure times 35 to 80 s. To test whether or not identified growth bands are formed annually, we analyzed stable isotopes of shell carbonate (for review, see Richardson, 2001). This approach has recently been applied successfully to identify annual growth patterns of Antarctic invertebrates (e.g. Marshall et al., 1996; Brey and Mackensen, 1997) and of various scallops (e.g. Krantz et al., 1984; Tan et al., 1988; Dare and Deith, 1990; Lasta et al., 2001). Stable oxygen ratios ($\delta^{18}O$) are inversely related to temperature (Epstein et al., 1953), hence lower $\delta^{18}O$ characterises shell parts deposited during spring/summer, whereas higher values correspond to parts formed during autumn/winter. Isotope analyses were performed on five representative specimens (largest individual: 87-mm shell height). Calcium carbonate powder was sampled from the outer shell layer in equally spaced ($\sim$ 1 mm) dorso-ventral series using a small dental drill (bit size: 0.5 mm). $\delta^{18}O$ were determined with a Finnigan MAT251 mass spectrometer coupled to an automatic carbonate preparation device. The results were reported in mil (‰) deviations related to the Pee Dee belemnite (PDB) standard through repeated analyses of National Bureau of Standard (NBS) isotopic reference material 19 (Hut, 1987). The precision of measurements was better than ± 0.08‰, based on routine measurements of a laboratory-working standard.

On confirmation of annual formation of X-ray visible growth bands, shells of 25 individuals of *A. colbecki* (15 males, 10 females) were X-ray photographed. Number (i.e. age) and corresponding SH of each detectable X-ray growth band in each shell were recorded. A generalized von Bertalanffy growth model (gVBGF) was fitted to the resulting 185 size-at-age data pairs by an iterative nonlinear least-square method (Newton algorithm, see Brey, 2001 for details):

$$H_t = H_\infty \left(1 - e^{-K(t-t_0)}\right)^D \tag{2}$$

where H_t is shell height at time t, H_∞ is mean asymptotic shell height, K is the Brody growth coefficient, D determines the shape of the curve (inflection point if $D>1$), and t_0 is the age when shell height equals zero.

2.3. Production

Somatic production of soft tissue (P_S) was calculated by the mass-specific growth rate method according to Crisp (1984) and Brey (2001) from the SFD, the VBGF parameters, and the appropriate size–mass relation:

$$P_S = \sum N_i M_i G_i \tag{3}$$

where N_i and M_i are the number of bivalves and mean individual somatic mass in size class i, respectively, and G_i is the annual mass-specific growth rate which is computed by

$$G_i = bK(H_\infty - H_i)/H_i \tag{4}$$

where b is the exponent of the size–mass relation (Eq. (1)), K and H_∞ are parameters of the von Bertalanffy function (Eq. (2)), and H_i is the mean height in size class i.

Since *A. colbecki* has a discrete reproductive cycle and spawns only once a year (Berkman et al., 1991), gonad production per total sample (P_G) was estimated by the decline of gonad mass before (summer) and after spawning (winter):

$$P_G = \sum N_i (M_{\text{gonad (summer)}} - M_{\text{gonad (winter)}}) \tag{5}$$

where N_i is the number of bivalves in size class i and $M_{\text{gonad (summer)}}$ is the mean individual gonad mass in summer in size class i. $M_{\text{gonad (winter)}}$ values in this study were obtained from a linear regression calculated from measurements of some individuals maintained under simulated winter conditions in aquaria at the AWI (Germany, Bremerhaven):

$$\log M_{\text{gonad (winter)}} (\text{g DM}) = -6.342 + 2.52 \log SH \ (\text{mm}) \tag{6}$$

Annual production/biomass ratios were calculated from somatic production (P_S), gonad production (P_G), and biomass per total sample ($B_S = \Sigma N_i M_i$). Annual production of *A. colbecki* per square metre was calculated by multiplying the production-to-biomass (P/B) ratios with an estimate of average biomass derived from mean body mass per total sample and mean abundance at the sampling site (60 individuals m^{-2}; Cattaneo-Vietti et al., 1997).

The following conversion factors were used:

1 g somatic DM = 20.22 kJ (Brey et al., 1988).
1 g gamete DM = 23.4 kJ (average according to MacDonald and Thompson, 1985).
1 g C_{org} = 45.7 kJ (Brey, 2001).

3. Results

3.1. Morphometrics

Size frequency distribution for several austral summers (Fig. 1a–g) showed a high persistency of large individuals (>60 mm), with large oscillations in the smaller size
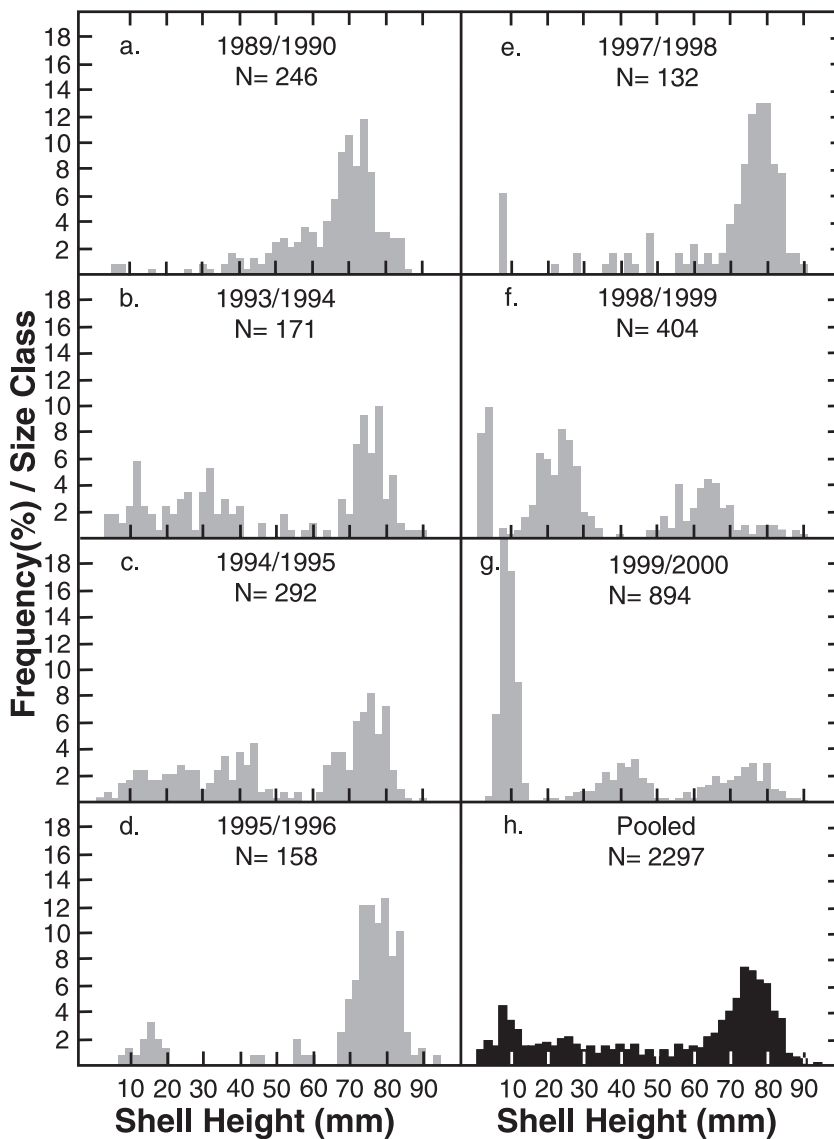
Fig. 1. *A. colbecki*. Size frequency distribution in Terra Nova Bay ('Road Cove') using class intervals of 2 mm: (a and b) in austral summer 1989/1990, 1993/1994 (redrawn from Cattaneo-Vietti et al., 1997), (c and d) in austral summer 1994/1995, 1995/1996 (redrawn from Chiantore et al., 2000), (e) in austral summer 1997/1998 (Chiantore and Cattaneo-Vietti, unpublished data), (f) in austral summer 1998/1999 (redrawn from Chiantore et al., 2001), (g) in January 2000, and (h) pooled samples (1989/1990 to 1999/2000).

classes (<30 mm). The multiyear size frequency distribution (Fig. 1h) was polymodal and dominated (>50%) by large animals (>66 mm).

Mean soft tissue DM was 1.35 g (SD=1.4 g) with a range from 0.12 to 5.2 g. A slight but significant difference (ANCOVA: $P=0.011$, $N=165$) in size–soft tissue DM relation was found between males (log (g DM)=2.882 log (mm SH) − 4.832) and females (log (g DM)=2.882 log (mm SH) − 4.836). As the sex ratio was nearly 1:1, we did not differentiate between sexes and used the overall equation log (g DM)=2.882 log (mm SH) − 4.837 for all subsequent calculations. The relation between gonad dry mass and shell height was not significantly different between male and female animals (ANOVA of log-transformed data, $P>0.5$) and can be described by the overall equation:

$$\log M_{\text{gonad (summer)}}(\text{g DM}) = -8238 + 4.058 \log (\text{mm SH})$$
$$N = 69; \quad R^2 = 0.89; \quad P < 0.01$$

3.2. Age and growth

X-ray bands could clearly be distinguished up to 80-mm shell height; further growth bands closer to the shell edge could not be resolved accurately and were hence not included in the analysis. A comparison of external vs. X-ray bands showed a high degree of consistency (89.4%) in total number of growth bands, whereas the position of external and X-ray band differed quite often (up to 2/3 of all bands in one shell).

Fig. 2 shows X-ray photographs and corresponding $\delta^{18}O$ profiles of two representative A. colbecki shells from Terra Nova Bay. $\delta^{18}O$ values ranged from 3.04‰ to 3.88‰ (Fig. 2b) and 3.13‰ to 3.92‰ (Fig. 2d) over the scallops lifetime, showing a cyclical pattern with a slight trend towards lower values with increasing height. Eighty-five percent of all X-ray growth bands coincide spatially with a local $\delta^{18}O$ peak (Fig. 2a and b), indicating that these bands were formed at times of lowest temperature. The 185 size-at-age data pairs obtained from X-rays were fitted best by a general von Bertalanffy equation (Fig. 3)

$$H_t = 108.86 \text{ mm} \left(1 - e^{-0.114 \, (t+0.367)}\right)^{1.284} \qquad R^2 = 0.983.$$

The analysis of the residuals of this model showed no significant differences in growth between males and females. The oldest individual found was estimated to be 18 years old (91.8-mm height), but maximum age is likely to be higher.

3.3. Production and productivity

Total annual production for the season 1999/2000 amounted to 14.63 g DM m^{-2} year^{-1} (305.51 kJ m^{-2} year^{-1}), corresponding to an annual P_{tot}/B ratio of 0.251 (0.199 for soma and 0.052 for gonads). Individuals >60 mm contributed most to somatic as well as gonad production of the population (Fig. 4b). Mean annual
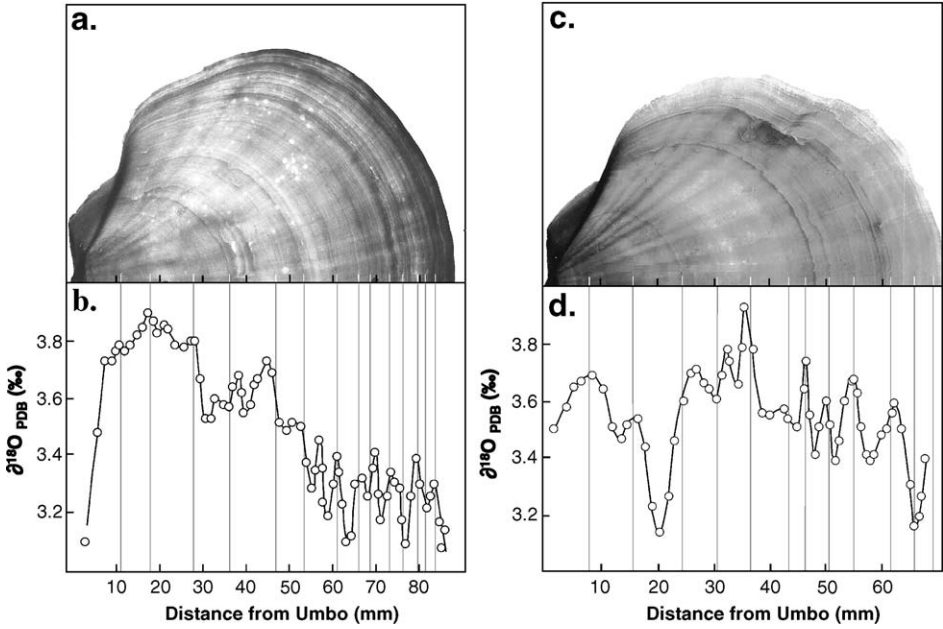
Fig. 2. *A. colbecki*. X-ray photographs ((a) 87.1 mm SH, (c) 72.1 mm SH) and corresponding stable oxygen isotope ratio profiles ((b) 74 samples, (d) 62 samples) of two specimen. Grey bars indicate internal growth bands. $\delta^{18}O$ is plotted as weighed moving average ($(x_1 + 2x_2 + x_3)/4$).
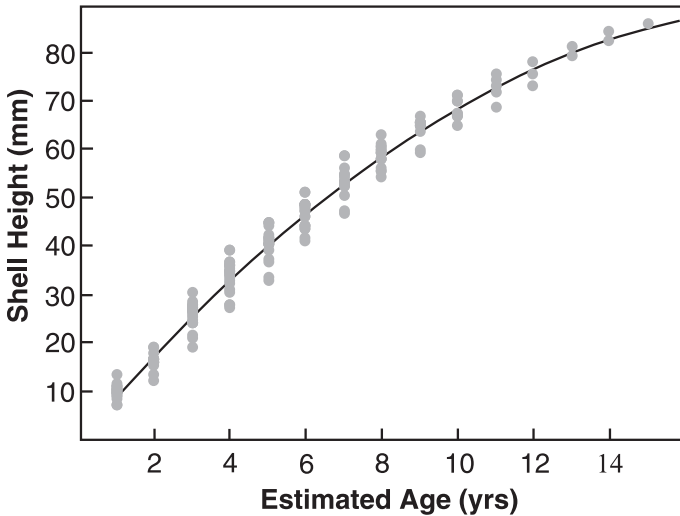

Fig. 3. *A. colbecki*. General von Bertalanffy growth function fitted to size-at-age data obtained from 25 X-ray photographed shells. Growth function parameters are $H_\infty = 108.86$ mm, $K = 0.114$, $D = 1.284$, and $t_0 = -0.367$ ($N = 185$, $R^2 = 0.983$).

biomass of *A. colbecki* was estimated to be about 58.34 g DM m^{-2} (1179.64 kJ m^{-2}). From the multiyear size frequency distribution (1989–2000), average biomass, somatic tissue, and gonad production were calculated to be 134.46 g DM m^{-2} (2718.78 kJ m^{-2}), 21.57 g DM m^{-2} year^{-1} (432.81 kJ m^{-2} year^{-1}), and 7.54 g DM m^{-2} year^{-1} (176.47 kJ m^{-2} year^{-1}), respectively. Annual P_{tot}/B ratio amounted to 0.215.
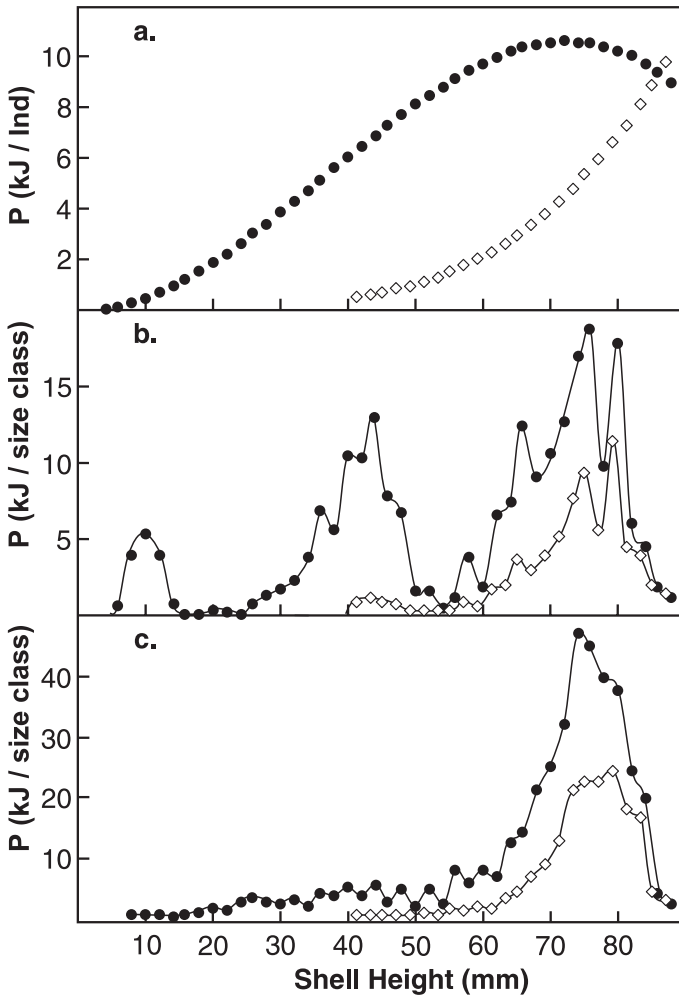

Fig. 4. *A. colbecki*. (a) Individual production of somatic tissues and individual gonad production for different size classes. (b) Size-specific distribution of annual somatic tissues and gonad production at the population level, based on SFD from austral summer 1999/2000. (c) As in (b) but based on the multiyear SFD 1989–2000.

4. Discussion

4.1. Age determination

The general correlation between changes in seawater temperature and changes in shell $\delta^{18}O$ has already been demonstrated for molluscs living at temperatures close to 0 °C (Marshall et al., 1993; Simstich et al., 2001), as well as for *A. colbecki* in particular (Barrera et al., 1990; Lohmann et al., 2001). Maximum $\delta^{18}O$ amplitudes in the scallops investigated here correspond to an annual temperature range of about 2.6 °C (Craig palaeotemperature equation, cf. Marshall et al., 1993), which is in good agreement with the observed seawater temperature range of -1.8 to $+0.75$ °C in the Ross Sea (Picco et al., 2000; Povero and Petrillo, 2000). The slight overall trend to lower $\delta^{18}O$ values with increasing size and shell height up to 50 mm (Fig. 2b and d) is not uncommon in molluscs (e.g. Krantz et al., 1987; Weidman et al., 1994; McConnaughey et al., 1997). Such trends may be related to a continuous change in the relation of somatic to gonad production with age (Calow, 1983) and/or to metabolic changes at onset of sexual maturity (Chiantore et al., 2000).

A mark-recapture study recently conducted in Terra Nova Bay and in the aquaria of the Alfred Wegener Institute in Bremerhaven (Chiantore et al., in press) indicates that annual growth increments in *A. colbecki* are ≥ 1 mm up to about 75-mm shell height and 15 years of age. Therefore, the 1-mm spatial resolution of our isotope shell transects seems to be sufficient to resolve intra-annual $\delta^{18}O$ oscillations within this size and age range.

The annual water temperature cycle is assumed to be the major determinant of shell $\delta^{18}O$. Salinity fluctuations can change water $\delta^{18}O$ and hence may also affect shell $\delta^{18}O$, but this effect is of minor significance (Tan et al., 1988). Moreover, salinity fluctuations caused by ice formation and melting affect $\delta^{18}O$ in the same directions as temperature (Barrera et al., 1990) and hence will enhance the isotope signal. The annual water temperature cycle at Terra Nova has one peak in summer and one trough in winter. Therefore, we conclude that one X-ray growth band is formed every winter in *A. colbecki*, as already shown for many other scallop species (e.g. Tan et al., 1988; Schick et al., 1988; Dare and Deith, 1990; Lasta et al., 2001). In our example shells (Fig. 2), there are some $\delta^{18}O$ peaks without corresponding X-ray growth bands, i.e. in some winters, no distinguishable band may be formed. This may cause underestimation of true age, but the large number of shells ($N=25$) used here compensates this potential bias.

4.2. Growth of A. colbecki

Previously published estimates of VBGF growth parameter values in *A. colbecki* are not directly comparable to our data because those studies (e.g. Ralph and Maxwell, 1977; Stockton, 1984; Berkman, 1990; Pranovi et al., 1994) (i) applied the specialized VBGF only, where the ''shape'' parameter D is set equal to 1, or (ii) were obtained from size-increment data (Chiantore et al., in press) (for a detailed discussion, see Francis, 1988). A common plot (Fig. 5), however, shows that all these growth models form a rather dense
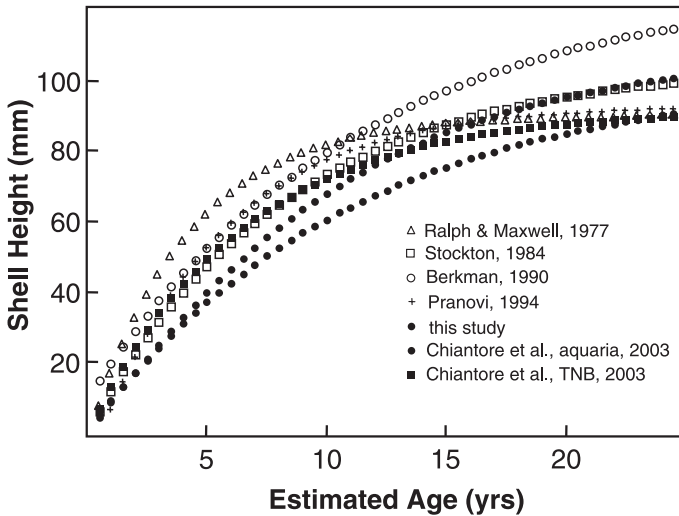
Fig. 5. Von Bertalanffy growth functions of *A. colbecki* populations published by various authors. VBGF parameters: Ralph and Maxwell (1977), $H_\infty = 90$ mm, $K = 0.24$, D set to 1; Stockton (1984), $H_\infty = 105$ mm, $K = 0.12$, D set to 1; Berkman (1990), $H_\infty = 128$ mm, $K = 0.09$, D set to 1; Pranovi et al. (1994), $H_\infty = 93$ mm, $K = 0.19$, D set to 1; Chiantore et al. (in press, TNB), $H_\infty = 92$ mm, $K = 0.154$, D set to 1; Chiantore et al. (in press, aquaria), $H_\infty = 101$ mm, $K = 0.09$, D set to 1; this study, $H_\infty = 108.86$ mm, $K = 0.114$, $D = 1.284$.

cluster of quite similar curves. Obvious differences may be caused partially by the application of the less reliable visual shell growth band analysis (Stockton, 1984), partially by differences in population age structure, and partially by differences in environmental conditions between sites.

The index $P = \log(KM_\infty)$, where K is the growth rate constant K of the VBGF and M_∞ is inferred from H_∞, can be used to compare overall growth performance of different populations or species (Moreau et al., 1986). According to this measure, growth performance of scallops decreases with increasing latitude, and *A. colbecki* shows the lowest growth performance of all scallops investigated so far (Fig. 6a). In comparison to other Antarctic invertebrates, however, growth performance of *A. colbecki* appears rather high (Fig. 6b). Actually, besides the bivalve *Laternula elliptica* (King and Broderip, 1831) (Ralph and Maxwell, 1977; Urban and Mercuri, 1998), *A. colbecki* shows the highest values of all Antarctic species investigated to date.

4.3. Production and productivity

Size frequency distributions of the *A. colbecki* population from Terra Nova Bay show distinct annual differences (Fig. 1). This seems to be caused by extreme year-to-year variability in recruitment success (Chiantore et al., 2001, 2002). Insufficient nutrition of adults and of larvae during summer may be the major reason for recruitment failures (Cattaneo-Vietti et al., 1999). Hence, production data referring to a single season such as 1999/2000 (Fig. 1g, $P_{tot} = 305.51$ kJ m^{-2} year^{-1}, $P_{tot}/B = 0.251$ year^{-1}) are poor
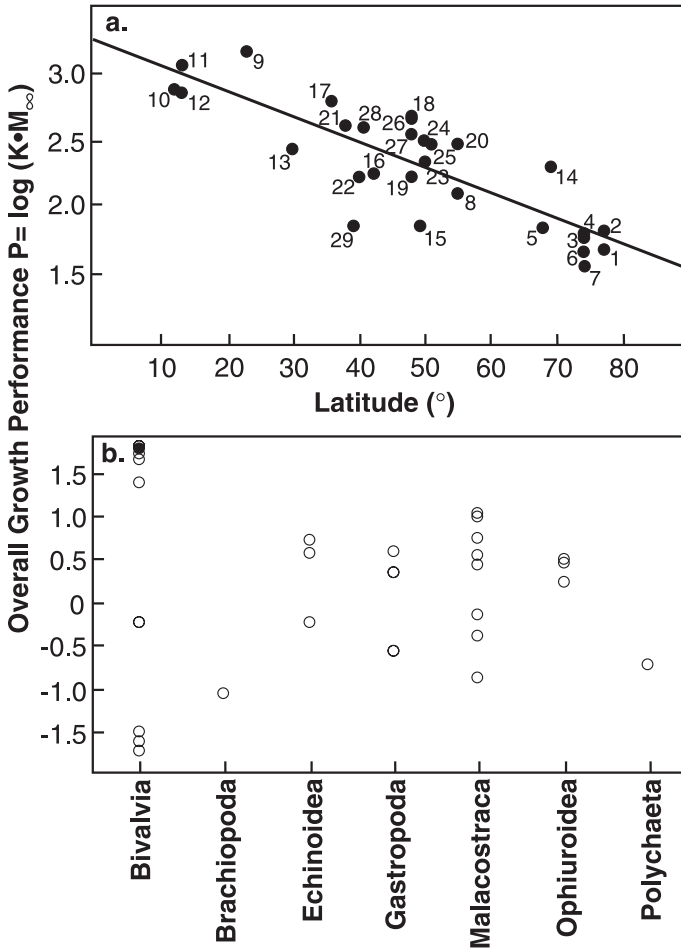
Fig. 6. Overall growth performance ($P = \log(KM_\infty)$) in (a) scallop populations worldwide and (b) Antarctic invertebrates of different taxons compared with *A. colbecki* from this study (filled dot). Data sources. (a) 1–5: *A. colbecki* (1: Stockton, 1984; 2: Berkman, 1990; 3: this study; 4: Pranovi et al., 1994; 5: Ralph and Maxwell, 1977; 6: Chiantore et al., in press, wild population 7: Chiantore et al., in press, aquaria), 8: *Aequipecten opercularis* (Allison, 1994), 9: *Amusium japonicum* (Williams and Dredge, 1981), 10: *Amusium pleuronectes* (Nugranad, 1988, fidem Vakily, 1992), 11–13: *Argopecten purpuratus* (11: Yamashiro and Mendo, 1988; 12: Mendo and Jurado, 1993; 13: Tomicic and Kong, 1978, in Wolff, 1994), 14–15: *Chlamys islandica* (14: Vahl, 1981; 15: Naidu et al., 1982, in Orensanz et al., 1990), 16: *Chlamys techuela* (Orensanz, 1986), 17: *Mizuhopecten yessoensis* (Yoo et al., 1981), 18–20: *Patinopecten caurinus* (18: Haynes and Hitz, 1971, 19: MacDonald and Bourne, 1987; 20: Ignell and Haynes, 2000), 21: *Pecten alba* (Gwyther and McShane, 1988), 22: *Pecten fumata* (Fairbridge, 1953), 23–25: *Pecten maximus* (23: Dare and Deith, 1990; 24: Dare, 1991; 25: Allison, 1994), 26–28: *Placopecten magellanicus* (26–27 MacDonald and Thompson, 1985, 1986; 28: Thouzeau et al., 1991), 29: *Zygochlamys patagonica* (Lasta et al., 2001). Regression line: $P = 3.257 - 0.019 \cdot \text{latitude}$ (°); $N = 29$; $R^2 = 0.686$. (b) Brey and Clarke (1993), Brey (1999), and references therein.

representatives of the population steady-state, whereas estimates derived from a multiyear size frequency distribution (Fig. 1h, $P_{tot} = 609.28$ kJ m^{-2} year^{-1}, $P_{tot}/B = 0.215$ year^{-1}) are more representative from a long-term point of view (Allen, 1971). The strongly left-skewed multiyear distribution (Fig. 1h) is typical of slow growing, long-lived species and populations with irregular recruitment events (e.g. Brey et al., 1990, 1995b; Arntz et al., 1992).

So far, this study presents the first attempt to estimate the gonad productivity of *A. colbecki* which is based on differences between gonadal mass before and after spawning. This approach assumes that all materials stored during the mass increase in summer are devoted to reproduction, which may not be true. Precise spawning times are unknown. Berkman et al. (1991) presume spawning in McMurdo Sound during austral spring, while Cattaneo-Vietti et al. (1997) suggest that gonad maturation takes place in late summer. P_S/B as well as P_{tot}/B of *A. colbecki* are at the lower end of the range reported for scallops, even when the scaling effect of average individual body mass is taken into account (Fig. 7). This coincides well with the comparatively low overall growth performance (Fig. 6) and indicates that the temperature-induced low metabolism of individual *A. colbecki* (Heilmayer et al., 2002) is reflected at the level of population turnover, as also found in other Antarctic invertebrates (Brey and Clarke, 1993; Brey et al., 1995a,b; Urban and Mercuri, 1998).
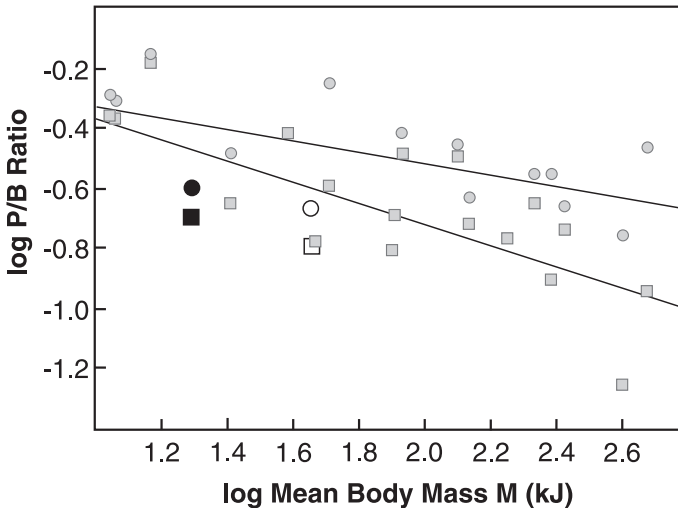

Fig. 7. Annual P_S/B ratio (circles) and P_{tot}/B ratio (squares) versus mean body mass (kJ) in scallop populations. Data sources: *A. colbecki* (Stockton, 1984; Berkman, 1990), *C. islandica* (Vahl, 1981), *Comptopallium radula* (Lefort, 1994), *Crassadoma gigantea* (MacDonald et al., 1991), *Mimachlamys gloriosa* (Lefort, 1994), *Mimachlamys varia* (Shafee and Conan, 1984), *Mizuhopecten yessoensis* (Goliko and Scarlato, 1970), *Patinopecten caurinus* (MacDonald and Bourne, 1987), *Placopecten magellanicus* (MacDonald and Thompson, 1985, 1986; Claereboudt and Himmelman, 1996), *Zygochlamys patagonica* (Lasta et al., 2001). Black symbols: *A. colbecki*, this study—season 1999/2000, open symbols: this study—based on multiyear SFD. Regression lines: (dots) log(P_S/B) = $-0.024 - 0.345\log(M)$; $N = 20$; $R^2 = 0.536$; $P < 0.01$: (squares) log(P_{tot}/B) = $-0.146 - 0.186\log(M)$; $N = 15$; $R^2 = 0.383$; $P < 0.05$.

4.4. Ecological significance

The ecological significance of *A. colbecki* in the Terra Nova Bay ecosystem is defined by its position in the food web and by the amount of energy flowing through the population. As *A. colbecki* is a suspension feeder, it represents a direct link between pelagic primary production and benthic or demersal higher level predators. Known predators of *A. colbecki* are *T. bernacchii* and invertebrates such as *N. eatoni* and *Odontaster validus* (Vacchi et al., 2000). According to our results, about 433 kJ m^{-2} year^{-1} (ca. 9.5 g C m^{-2} year^{-1}) are transferred from the scallop to its predators.

The question how much *A. colbecki* in Terra Nova Bay consumes and whether this dense population living in the euphotic zone may be able to control primary production as already observed in populations from temperate waters (see Smaal and Prins, 1993; Dolmer, 2000) is more difficult to answer. Of the simple energy budget (see Crisp, 1984):

$$\text{Consumption} = \text{Production} + \text{Respiration} + \text{Egestion} + \text{Excretion}$$

total production, 609 kJ m^{-2} year^{-1}, and respiration, 1558 kJ m^{-2} year^{-1} (whole year average, calculated from measurements of summer and winter metabolism, Heilmayer et al., 2002), are known, i.e. annual assimilation amounts to 2167 kJ m^{-2} year^{-1} (all estimates referring to the long-term average population structure, Fig. 1h). Chiantore et al. (1998) found the assimilation efficiency (100 × Assimilation/Consumption) of *A. colbecki* to be about 36%; hence, the annual consumption of the Terra Nova Bay population is about 6000 kJ m^{-2} year^{-1} (ca. 131 g C m^{-2} year^{-1}). Using Albertelli et al.'s (1998) estimate of daily sedimentation rate in Terra Nova Bay, 0.36 g C m^{-2} day^{-1}, and assuming a productive phase of about 60 days per year (Albertelli et al., 1998), the annual input to the benthos is about 1000 kJ m^{-2} year^{-1} (22 g C m^{-2} year^{-1}), i.e. about 17% of the food required by the *A. colbecki* population. Even if we allow for distinct interannual variability of production and duration of productive phase, this is far too low to maintain the *A. colbecki* population investigated. Potential additional food sources may be (i) ice algae, (ii) macroalgal detritus, or (iii) lateral advection of organic matter from the open Ross Sea. Ice algae can contribute significantly to total primary production (Spindler and Dieckmann, 1991; Melnikov, 1998), but their production in Terra Nova Bay has not yet been determined. The same is true for macroalgal detritus, which is known to be produced in large quantities on littoral rocky shores (Berkman et al., 1986; Albertelli et al., 1998). Lateral advection of organic matter is supposed to play a significant role in Antarctic coastal and shelf systems (Dayton, 1990; Brey et al., 1993, 1995a; Arntz et al., 1994), and the open Ross Sea is a potential source of matter laterally advected to Terra Nova Bay. With primary production rates up to 180 g C m^{-2} year^{-1} (~ 8200 kJ m^{-2} year^{-1}) and average sedimentation rates of 97% (Fabiano et al., 1997; Saggiomo et al., 2000), the Ross Sea is considered to be the most productive system in the Southern Ocean (Smith et al., 1996).

Further quantitative and qualitative studies of whole year sedimentation in TNB will answer open questions and may be the key to explain the interannual variability in *A. colbecki* recruitment and population structure.

Acknowledgements

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