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Growth, development and productivity of *Chorismus antarcticus* (Pfeffer) (Crustacea: Decapoda: Natantia) in the eastern Weddell Sea, Antarctica

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Abstract: The Antarctic shrimp *Chorismus antarcticus* is the dominant benthic shrimp species in sponge communities of the Weddell Sea shelf. Growth, mortality and productivity were estimated from trawl samples and from laboratory observations. Growth (Von Bertalanffy function: $CL_{\infty} = 19.98$ mm, $K = 0.348$ yr⁻¹, $t = 0.643$ yr) was found to be slower and mortality ($Z = 0.731$ yr⁻¹) was found to be lower than in comparable boreal species. Somatic and gonad production-to-biomass ratios were estimated to be 0.587 yr⁻¹ and 0.021 yr⁻¹, respectively. Within sponge communities, annual production of *C. antarcticus* amounts to about 6 mg C_{org} · m⁻² · yr⁻¹.

Key words: Benthic invertebrate; Gonad production; Growth rate; Somatic production

INTRODUCTION

Decapod crustaceans play only a minor role in Antarctic benthic communities, although decapods contribute about one quarter to all known crustacean species on a world-wide scale (Barnes, 1987). Nine species of long tailed decapods (Natantia) but no short tailed decapod (Reptantia) are known to occur south of the Antarctic convergence (55°S) (Kirkwood, 1984). One of these is *Chorismus antarcticus* (Pfeffer 1887), a protandrous hermaphrodite (Yaldwyn, 1966) with circum-Antarctic distribution. *Chorismus antarcticus* is one of the most abundant benthic shrimp species of the eastern Weddell Sea and the Lazarev Sea, where it was found in trawl samples taken between 69°S and 78°S (Arntz & Gorny, 1991, Gorny, 1992). It is predominantly associated with sponge communities between 200 m and 500 m water depth where it was observed sitting on sponges and other epibenthic biogenic structures, but not on the sea floor (Arntz & Gorny, 1991; Gorny, 1992; Gutt et al., 1991). Adult *C. antarcticus* are purely carnivorous and may feed on a variety of motile prey organisms (Gorny, 1992). Hence *C. antarcticus* may be an important factor in the dynamics of Antarctic communities dominated by sponges.

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METHODS

INVESTIGATION AREA AND SAMPLING

Between 1984 and 1991, 136 trawl samples have been taken on the shelves and slopes of the eastern and southern Weddell Sea and of the Lazarev Sea from RV *Polarstern*. An Agassiz trawl (1 × 3 m mouth opening, 20 × 20 mm mesh size in the front parts, 10 × 10 mm in the medium parts and cod end, see Voß, 1988) and a 140 ft bottom trawl (see Ekau, 1988) were employed for collections. *C. antarcticus* was caught by Agassiz trawl at 51 stations and by bottom trawl at 22 stations situated between 123 and 782 m water depth (Fig. 1). Specimens of *C. antarcticus* were collected from the catch and stored in 4% buffered formalin.

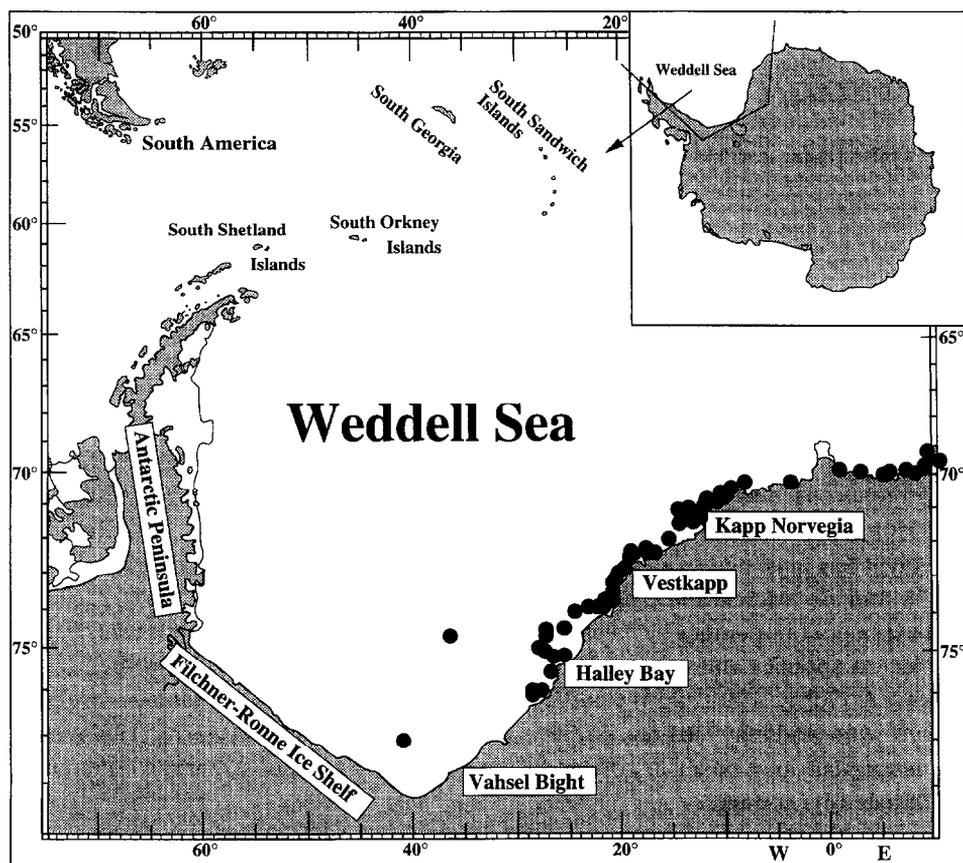


Fig. 1. Location of trawl stations in the Weddell Sea.

SIZE-MASS RELATIONS

Carapace length (CL, from eyestalk base to central dorsal carapace edge) was used as standard size measurement. Dry mass was measured after drying at 60 °C for 48 h. Relations between somatic dry mass, female gonad dry mass, egg dry mass and CL were established by linear regression of the \log_{10} -transformed data:

$$\log(\text{Mass}) = a + b \cdot \log(\text{CL})$$

DEVELOPMENT AND GROWTH

Developmental stages (juvenile, male, transitional stages, female) were identified by the structure of the "appendix masculina" at the endopodite of the second pleopod (Rasmussen, 1953; Allen, 1959; Gorny, 1989) and by the state of gonad development. Data from all years were lumped assuming interannual variations to be negligible, and the total catch was divided into three subsamples, i.e. spring (samples from October 22 to November 26, mean date November 2), summer (samples from January 9 to February 27, mean date February 3) and autumn (samples from April 7 to April 21, mean date April 14), and mean CL per developmental stage and season was calculated. From this information a series of size-at-age data was constructed.

Von Bertalanffy growth curves:

$$L_t = L_\infty \cdot [1 - e^{-K \cdot (t - t_0)}]$$

and Gompertz growth curves:

$$L_t = L_\infty \cdot [e^{-e^{-K \cdot (t - t_0)}}]$$

were fitted to the size-at-age data by the iterative non-linear fitting algorithm SIMPLEX (see Press et al., 1986) of the SYSTAT[®] statistical package (Wilkinson, 1989).

MORTALITY

The mortality rate Z of the single negative exponential mortality model:

$$N_t = N_0 \cdot e^{-Z \cdot t}$$

was estimated by a size-converted catch curve (see Pauly, 1984; Brey et al., 1988; Brey, 1991). This curve was calculated from the size-frequency distribution of the total catch and the Von Bertalanffy growth function:

$$(N_i / \Delta t) = N'_0 \cdot e^{-Z \cdot t_i}$$

N_i is the number of animals in size class i , Δt is the time required to grow through this size class and t_i is the relative age of the mid-size of class i . If the plot of $\ln(N_i / \Delta t)$ versus

t_i shows a straight descending right arm, total mortality Z can be computed by the linear regression:

$$\log_e(N_i/\Delta t) = a + b \cdot t_i; \quad Z = -b$$

PRODUCTIVITY

Annual somatic production was calculated by the mass-specific growth rate method (see Crisp, 1984) from (i) the pooled size-frequency samples, (ii) the Von Bertalanffy growth function and (iii) the size-mass relation:

$$P = \sum N_i \cdot M_i \cdot G_i \quad (\text{Production per total sample})$$

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

$$G_i = b \cdot K \cdot (L_\infty - L_i) / L_i \quad [\text{yr}^{-1}]$$

where b is the exponent of the size-mass relation, K , L_∞ are parameters of the Von Bertalanffy function, and L_i is the mean size in class i .

Annual female gonad production was computed from (i) the relation between size and gonad mass per female and (ii) the size-frequency distribution of females in the total catch:

$$\text{PG} = (\sum \text{NF}_i \cdot M_{G,i}) / 2$$

NF_i and $M_{G,i}$ are the number of females and the gonad mass per female in size class i , respectively. The division by 2 refers to the fact that one gonad cycle takes 2 yr (see below).

The annual P/B ratio was calculated from production P and PG and biomass per total catch B :

$$B = (\sum N_i \cdot M_i) + (\sum \text{NT}_i \cdot M_{G,i}) + (\sum \text{NF}_i \cdot M_{G,i})$$

$$\text{P/B ratio} = P/B$$

NT_i is the number of transitional stages in class i .

Biomass and production per m^2 were estimated from abundance values ($N \cdot \text{m}^{-2}$) based on underwater photo counts (Gutt et al., 1991, 1993; Gorny, 1992).

RESULTS

SIZE-MASS RELATIONS

Table I shows the relations between individual CL and somatic dry mass, gonad dry mass, and number of eggs carried per female. Female gonad development starts at about 11 mm length and eggs are carried by females above 13 mm length.

TABLE I

Relations between carapace length (mm) and somatic dry mass, gonad dry mass and number of eggs per female in *C. antarcticus*, $\log_{10}(Y) = a + b \cdot \log_{10}(CL)$.

Dependent variable Y	Intercept a	Slope b	N	r^2
Dry body mass, mg	-0.201	2.402	31	0.463
Dry gonad mass*, mg	-6.770	7.179	15	0.679
Number of eggs/female	-3.140	4.390	47	0.521

* Females with headroe (eggs under the carapace) only.

DEVELOPMENT AND GROWTH

The total catch consisted of 2230 specimens of *C. antarcticus*. The distribution into juveniles and males, transitional stages and females and the development of the appendix masculina are shown in Fig. 2. Table II shows the changes in mean CL with developmental stage and season. The larvae hatch in spring (2.1 mm CL) and have

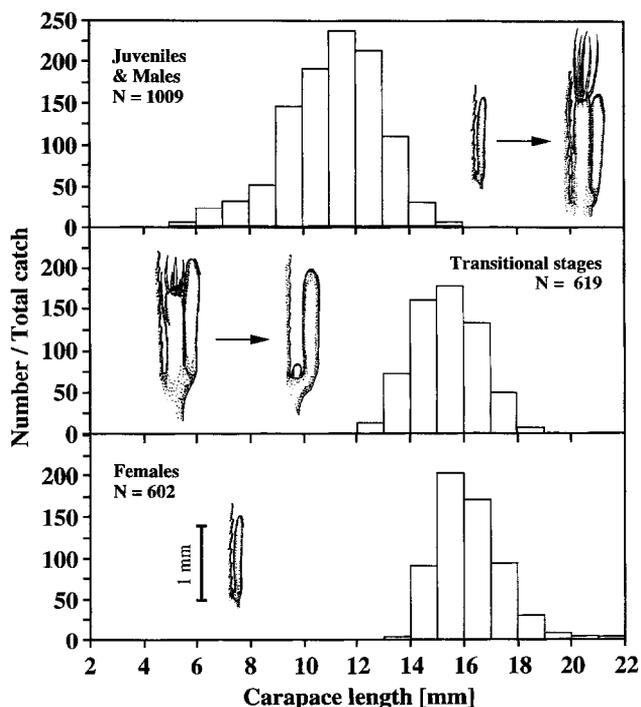


Fig. 2. Size-frequency distributions of males, transitional stages and females of *C. antarcticus* in the total catch. The superimposed drawings show the development of the appendix masculina at the endopodite of the second pleopod.

TABLE II

Mean carapace length (CL, mm) of the subsequent development stages of *C. antarcticus* in spring, summer and autumn.

Developmental stage	Spring (Nov. 2)		Summer (Feb. 3)		Autumn (April 14)		Assumed year of life
	N	CL	N	CL	N	CL	
Hatching larvae*	23	2.1	–	–	–	–	1
Juveniles	3	6.5	42	7.5	0	–	2
Males	92	9.5	765	11.5	84	12.5	3
Transitionals	32	13.5	194	14.5	111	15.5	4
Females	139	15.5	232	14.5	67	15.5	5
Breeding females	23	17.5	146	16.5	19	16.5	6+

* Hatching date (November 23) and size at hatching derived from laboratory observations.

developed into juveniles (6.5 mm) one year later. In the third year of life, males mature (about 11 mm), and during the next year the transition to females takes place. Mature females (about 14 mm) with visible eggs under the carapace (headroe) are found in the 5th year of life. After spawning, females brood the eggs attached to the pleopods during their sixth year of life. Since breeding takes about 11 months and the development of new eggs takes about 1 yr (Gorny, 1992), each female reproduces every second year only. Consequently, the largest breeding females (21.5 mm) were at least 7 yr old. For further details of the developmental cycle see Arntz et al. (1992), Bruns (1992) and Gorny et al. (1992).

The Von Bertalanffy growth curve:

$$CL_t = 19.98 \cdot [1 - e^{-0.348 \cdot (t - 0.643)}], \quad R^2 = 0.981$$

and the Gompertz growth curve:

$$CL_t = 17.55 \cdot [e^{-e^{-0.721 \cdot (t - 1.903)}}], \quad R^2 = 0.987$$

fitted the data equally well, both functions estimate *C. antarcticus* to attain a maximum age of about 7 yr (Fig. 3). The Von Bertalanffy curve was used for further calculations since the higher CL_∞ allowed for the inclusion of two additional size classes (17.5 and 18.5 mm) in the production and mortality computations.

MORTALITY

The size converted catch curve:

$$\log_e(N/\Delta t) = 9.290 - 0.731 \cdot t, \quad r^2 = 0.935$$

estimated the mortality rate in *C. antarcticus* to be 0.731 yr^{-1} . As indicated by Fig. 4, only specimens older than 3 yr (> 11 mm CL) are fully sampled by the gears used.

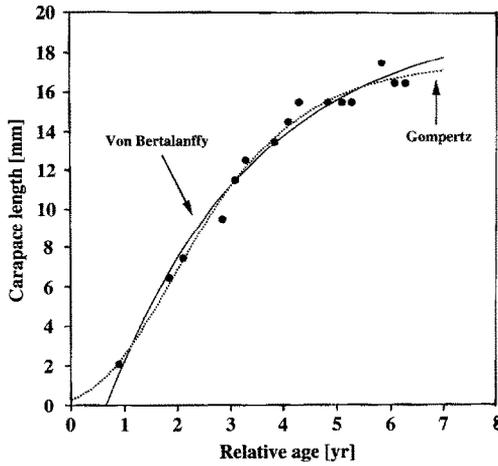


Fig. 3. Size-at-age data of *C. antarcticus* and superimposed Von Bertalanffy ($CL_t = 19.98 \cdot [1 - e^{-0.348 \cdot (t - 0.643)}]$) and Gompertz ($CL_t = 17.55 \cdot [e^{-e^{-0.721 \cdot (t - 1.903)}]}$) growth curves.

PRODUCTIVITY

Figure 5 shows the change in individual somatic production and female gonad production with increasing size. Somatic production increases up to a maximum at

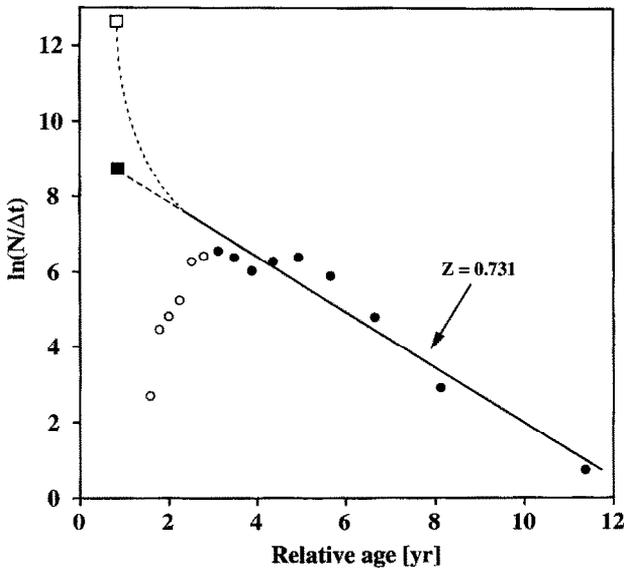


Fig. 4. Size-converted catch curve of *C. antarcticus* calculated from the size-frequency distribution and the Von Bertalanffy growth curve. ●, data points not included in the regression $\log_e(N/\Delta t) = 9.290 - 0.731 \cdot t$, $r^2 = 0.935$. ■, Number of eggs (1 mm size) extrapolated from the catch curve (920/total catch); □, true number of eggs found in the population (46400/total catch).

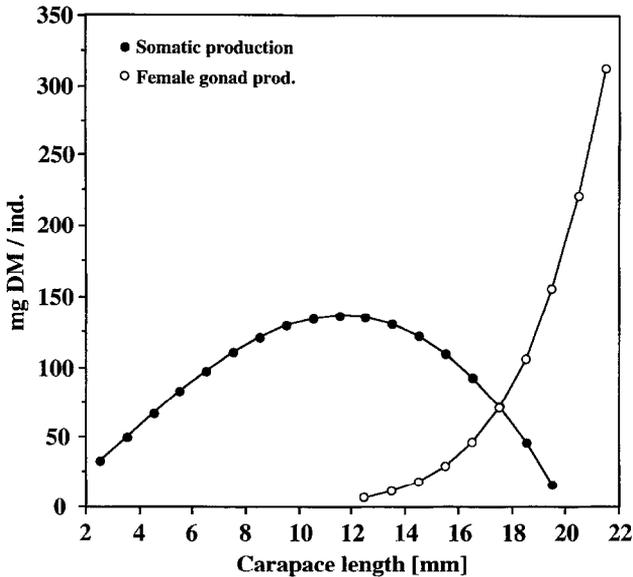


Fig. 5. Size specific distribution of somatic production and female gonad production in single individuals of *C. antarcticus*. Somatic production was calculated by the mass specific growth rate method, gonad production from the size-gonad mass relation. DM = dry mass

11.5 mm CL and decreases again with increasing length. Gonad production is zero below 12 mm CL and increases exponentially from 12 mm up to the highest length classes.

Annual somatic production and female gonad production were calculated to be 258.1 g DW/total catch and 28.2 g DW/total catch, respectively. Regarding the total biomass of 803.0 g DW/total catch, these figures are equivalent to population P/B ratios of 0.288 yr^{-1} (somatic) and 0.031 yr^{-1} (gonad).

DISCUSSION

GROWTH

According to our results, *C. antarcticus* reaches an age of at least 7, but most likely up to 10 yr on the south-eastern Weddell Sea shelf (Fig. 3). Although the data of Maxwell (1977) and Gorny et al. (1992) indicate differences in egg size and size at maturity between the Weddell Sea population and a population at South Georgia, the lack of data does not allow for intra-specific comparisons of growth at different latitudes.

Clarke & Lakhani (1979) found inter-specific differences in early growth between several boreal caridean shrimps and *C. antarcticus* living at South Georgia. Growth of the Antarctic shrimp was distinctly slower during the first 15 months of post-larval life.

Biology and ecology of the deep water prawn *Pandalus borealis* (Krøyer) are comparable to *C. antarcticus*. This protandrous hermaphrodite prawn is an ecologically and commercially important component of the soft bottom fauna of northern boreal areas (see Shumway et al., 1985). Von Bertalanffy growth parameters of this species are available from Spitsbergen (78°N), Barents Sea (75°N), Balsfjord (69°N), Oslofjord (59°N) and Gullmarsfjord (58°N), see Bergström (1992), Hopkins & Nilssen (1990) and references therein. CL_{∞} is generally higher in *P. borealis* than in *C. antarcticus*, 25.6 to 31.4 mm, and K ranges between 0.2 and 0.7 yr⁻¹. Since non-linear functions with more than one parameter are difficult to compare, the index of overall growth performance Φ' (Munro & Pauly, 1983, Pauly & Munro, 1984) was applied:

$$\Phi' = \log(K) + 2 \cdot \log(CL_{\infty})$$

The Φ' values of *P. borealis* range between 2.31 (Barents Sea) and 2.65 (Oslofjord), whereas the value for *C. antarcticus* is 2.14, indicating a lower growth performance of the Antarctic species.

MORTALITY

A mortality rate of $Z = 0.731 \text{ yr}^{-1}$ was calculated from the size-converted catch curve (SCCC, Fig. 4). The good fit of the catch curve ($r^2 = 0.823$) indicates the negative exponential model to be appropriate to describe mortality in that part of the population above 3 yr of age. The validity of the model for younger animals can be tested by comparing the number of eggs brooded by the population with the number of eggs estimated by the SCCC, assuming the population to be in a steady state. The number of eggs brooded per year is 46400/total catch, calculated from the egg-size relation (Table I) and the size-frequency distribution of the females (Fig. 2). Larvae at hatching are 2 mm long, so if we assume 1 mm to be the average length of embryos, the number of eggs is estimated to be 920/total catch by the SCCC. Although this figure is only a rough estimate, the observed discrepancy indicates clearly that mortality must be much higher than 0.731 yr^{-1} somewhere between the egg stage and the age of three years. We assume mortality to be highest during larval development, as found in other benthic invertebrates, too (see e.g. Thorson, 1966; Mileikovsky, 1971). Later it may level out at the value computed by the SCCC, as indicated by the stippled line in Fig. 4. The assumed high larval mortality is likely to be due mainly to predation. However, the current regime on the Weddell Sea shelf may also play a significant role. Near bottom currents can be sufficiently strong ($\geq 30 \text{ cm} \cdot \text{s}^{-1}$, see Arntz et al., 1992) to carry away settling larvae. Laboratory observations showed that *C. antarcticus* larvae switching to a benthic habit (during the 4th larval stage, Bruns, 1992) try to hold on to bottom structures, which may be an attempt to counteract the effects of currents.

A mortality rate of 0.731 yr^{-1} is in the upper range of observations in Antarctic benthic invertebrate populations (see Brey & Clarke, 1993), but much lower than in the boreal shrimp *P. borealis*. Hopkins & Nilssen (1990) computed mortality rates ranging between 1.89 yr^{-1} and 2.12 yr^{-1} for a population of this species in Balsfjord. These rates include natural mortality " M " as well as fishing mortality " F " due to commercial exploitation ($Z = M + F$). However, if we assume these stocks to be in the range of optimum exploitation, i.e. $M = F$ (Gulland, 1971), natural mortality is about 1.0 yr^{-1} and hence much closer to the figure of 0.731 yr^{-1} estimated for *C. antarcticus*.

PRODUCTIVITY

Productivity of *C. antarcticus* was estimated to 0.288 yr^{-1} (somatic) and 0.031 yr^{-1} (gonad) by the mass specific growth rate method. However, Allen (1971) showed that in a steady state population the somatic P/B ratio is equal to the mortality rate Z , if mortality can be described by the single negative model and if individual growth follows a Von Bertalanffy function. Hence, the difference between Z (0.731 yr^{-1}) and P/B (0.288 yr^{-1}) indicates that the P/B ratio of *C. antarcticus* has been under-estimated by

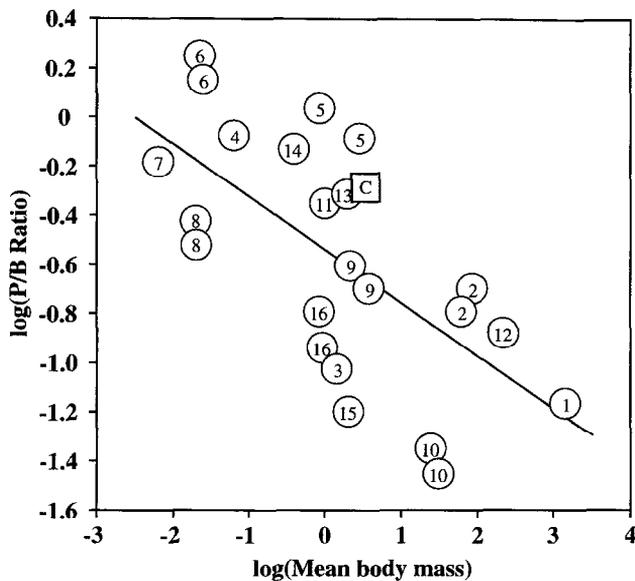


Fig. 6. The somatic P/B ratio of *C. antarcticus* (C) compared with populations of other Antarctic benthic invertebrates. Body mass has been converted to kJ (see Brey & Clarke, 1993). The relation between P/B ratio and body mass M is described by the linear regression $\log_{10}(\text{P/B}) = -0.522 - 0.224 \cdot \log_{10}(M)$, $r^2 = 0.419$, $N = 24$. 1 *Acodontaster conspicuus*, 2 *Adamussium colbecki*, 3 *Aega antarctica*, 4 *Amphiteis gunneri*, 5 *Bovallia gigantea*, 6 *Laevilacunaria antarctica*, 7 *Lissarca miliaris*, 8 *L. notorcadensis*, 9 *Nacella concinna*, 10 *Odontaster validus*, 11 *Ophionotus hexactis*, 12 *Perknaster fuscus*, 13 *Philine gibba*, 14 *Serolis polita*, 15 *Sterechinus antarcticus*, 16 *Yoldia eightsi* (data from Brey & Clarke, 1993 and references therein).

the mass specific growth rate method. This is due to size specific gear selectivity that led to a biased size frequency distribution, wherein the smaller, more productive specimens are under-represented (Figs. 2 and 4).

Assuming Z to be constant in the post-larval population of *C. antarcticus*, the size-frequency distribution (≥ 5.5 mm CL) was corrected for gear selection and the corrected annual P/B ratio was calculated to be 0.587 yr^{-1} (somatic) and 0.021 yr^{-1} (gonad), respectively. Figure 6 indicates that – taking into account the effects of body mass – somatic P/B ratio of *C. antarcticus* is in the upper range of other Antarctic benthic invertebrate species, i.e. *C. antarcticus* seems to be a comparatively highly productive species.

Brey & Clarke (1993) calculated the productivity of breeding females of *C. antarcticus* at South Georgia based on data of Maxwell (1972). Somatic P/B ratios of breeding females are similar at South Georgia, 0.188 yr^{-1} , and in the Weddell Sea, 0.142 yr^{-1} , but gonad P/B ratio is distinctly higher at South Georgia, 0.257 yr^{-1} , than in the Weddell Sea, 0.092 yr^{-1} . This discrepancy is related to differences in the individual female reproductive cycle at the two sites. At South Georgia, each female reproduces every year, whereas in the Weddell Sea one cycle takes 2 years of life (Gorny 1992; Gorny et al., 1992). This difference could be due to seasonal resource limitation. In the Weddell Sea the amount of food (e.g. juveniles of seasonally recruiting benthic species) provided during one austral summer may not be sufficient for the complete development of eggs in *C. antarcticus*, although crustaceans are able to invest assimilated matter directly into gonad development (Harrison 1990).

PRODUCTION AND ECOLOGICAL SIGNIFICANCE

The discussion above showed that *C. antarcticus* in the Weddell Sea exhibits relatively slow growth, low mortality rate and low somatic production rate compared with similar boreal shrimp species. These findings confirm the conclusion of Maxwell & Ralph (1985) who found that the metabolic rate of *C. antarcticus* is low compared to temperate invertebrate species. Gonad production rate and maybe also somatic production rate are even lower than in *C. antarcticus* inhabiting areas further to the north. The reason for this is taken to be the combined effects of extremely low temperature and strongly seasonally-oscillating food input in the Weddell Sea, which will also affect predatory species (see Clarke 1988; Brey & Clarke, 1993). However, frequency of occurrence and abundance of *C. antarcticus* demonstrate a successful adaptation to these conditions.

Production (in terms of mass per area and time) may indicate the ecological significance of *C. antarcticus* in the investigation area. Average abundance of *C. antarcticus* on the Weddell Sea shelf and slope (100–1250 m water depth) was estimated to be $0.02 \text{ ind.} \cdot \text{m}^{-2}$ (Gutt et al., 1991; Gutt et al., 1993). Within areas inhabited by sponge communities in 100–600 m water depth average abundance was about $0.07 \text{ ind.} \cdot \text{m}^{-2}$ (up to $0.47 \text{ ind.} \cdot \text{m}^{-2}$, Gutt et al., 1991; Gutt et al., 1993). Mean individual body mass

is 141 mg C_{org} (1 mg DM = 0.353 mg C_{org} , computed from Salonen et al., 1976 and Rumohr et al., 1987) in the total trawl catch, hence average biomass of *C. antarcticus* is estimated to be 10 mg $C_{org} \cdot m^{-2}$ within sponge communities, but it may reach values up to 70 mg $C_{org} \cdot m^{-2}$. This represents only a minor fraction of total community biomass (including sponges), which is several thousand mg $\cdot m^{-2}$ on average and may reach values above 70 000 mg $C_{org} \cdot m^{-2}$ (Gerdes et al., 1992 recalculated in Brey & Clarke, 1993).

With the total P/B ratio of 0.608 yr^{-1} (0.587 + 0.021) annual production of *C. antarcticus* is estimated to 6 mg $C_{org} \cdot m^{-2} \cdot yr^{-1}$ (up to 40 mg $C_{org} \cdot m^{-2} \cdot yr^{-1}$) in sponge communities. Assuming a growth efficiency (100 \cdot production/consumption) of roughly 23% (mean of estimates for various carnivorous crustaceans published by Johnson, 1976; Klein Breteler, 1976; Strong & Daborn, 1979; Shafir & Field, 1980; Pihl & Rosenberg, 1984; Pihl, 1985), the annual food demand is ≤ 30 mg $C_{org} \cdot m^{-2} \cdot yr^{-1}$. The large epibenthic suspension feeders of the sponge communities such as sponges, bryozoans and hydrozoans are colonized by a diverse and numerous fauna of small motile animals such as amphipods (Arndt, 1933; Kunzmann, 1992), on which *C. antarcticus* was observed to prey in experiments (Gorny, 1992). Nothing is known about the productivity of this fauna, but it is likely to be a sufficient food source for the shrimp.

On the other hand, 6 mg $C_{org} \cdot m^{-2} \cdot yr^{-1}$ of shrimp production are available to the next trophic level. In Antarctic shallow water areas such as McMurdo Sound, shrimps are heavily preyed on by penguins and seals (Dearborn, 1965; Green & Burton, 1987), whereas on the deeper Weddell Sea shelf benthic shrimps contribute virtually nothing to the diet of these predators (Plötz et al., 1991). Here, finfishes and cephalopods could play a significant role, such as actively hunting species of the finfish genus *Trematomus* (Schwarzbach, 1988). Observations during the deployment of a video-equipped box corer (pers. obs.) gave further evidence for the significance of epibenthic swimming predators, since *C. antarcticus* showed strong and fast escape reactions to the shock wave in front of the corer.

Annual production and consumption figures of *C. antarcticus* seem to be low compared with figures referring to various benthic crustaceans from temperate regions (see e.g. Shafir & Field, 1980; Kemp et al., 1985; Peer et al., 1986; Willows 1987; Dauvin, 1989). However, *C. antarcticus* is only one invertebrate predator in a highly diverse benthic system which consists of several hundred species (Arntz et al., 1993). Little is known about the interaction web, the food web and the energetic links among the various species. However, due to its carnivorous habit and its food demand, *C. antarcticus* is likely to be an important key species in this particular benthic community.

Due to the slow growth, the low mortality rate and the low average abundance compared to exploited boreal shrimp populations, *C. antarcticus* has little potential for commercial exploitation. Commercial bottom trawling would not only quite over-exploit the stock, but also destroy its habitat, the fragile sponge communities.

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