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Population dynamics of marine benthic invertebrates in Antarctic and subantarctic environments: are there unique adaptations?

THOMAS BREY[1] and ANDREW CLARKE[2]

[1]*Alfred Wegener Institute for Polar and Marine Research, D-2850 Bremerhaven 1, Germany*
[2]*British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, UK*

Abstract: Data on the growth (20 species) and productivity (19 species) of Antarctic and subantarctic macrobenthos were compiled from published and unpublished sources. Differences in the production/ biomass (P/B) ratio between Antarctic, Arctic and non-polar populations were examined using a set of 363 data arrays (327 non-polar, 26 Antarctic, 10 Arctic). Each array contained annual P/B ratio, mean individual body mass, geographical latitude, water depth, bottom water temperature and the nominal variables TAXON (Mollusca, Crustacea, Polychaeta, Echinodermata) and REGION (Antarctic, Arctic, non-polar). The P/B ratio was found to vary with body mass, taxon, temperature and water depth. P/B ratios of Antarctic and Arctic populations were significantly lower than those of non-polar populations. For Antarctic populations this difference could be explained completely by the effects of temperature and water depth. The strikingly high biomass of many Antarctic benthic communities is probably related to adaptations to low and oscillating food levels, and particularly to the low maintenance energy requirement associated with the low ambient temperature.

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Introduction

The compilation of growth data by Everson (1977) was the first attempt to summarize knowledge of the population dynamics of Antarctic benthic invertebrates. His review could provide only limited insight into broader patterns of benthic invertebrate population dynamics in polar environments because of the small number of suitable autecological studies, and the dearth of data on parameters such as production. Since 1977, however, many new studies of high-latitude marine invertebrates have been published and there has been considerable development in techniques for the study of invertebrate population dynamics.

The purpose of this study was to undertake a thorough review of previous work on the biology of Antarctic benthic marine invertebrates, and in particular those aspects concerned with growth and production. Data were compiled from both published and unpublished studies (particularly those available only from internal reports of the British Antarctic Survey) available up to the end of 1991. When combined with a much larger data set on benthic marine invertebrate population dynamics from temperate and sub-tropical waters (Brey 1990, also updated to 1991), it was possible to assess if any features of the population dynamics of Antarctic benthic invertebrates differed from those elsewhere. The limited nature of much of the data means that this study must be restricted to a comparison of population (rather than individual) production/biomass ratios (P/B ratio). P/B ratio (also termed turnover rate) is a frequent measure of productivity in benthic populations, and this is the only measure for which enough data exist to allow for meaningful comparisons.

Polar marine invertebrates and fish tend to grow slowly (Everson 1977, Clarke 1983) and historically this has been explained either as a direct rate-limitation by temperature or because an elevated metabolic rate means that a lower proportion of ingested energy is available for growth (for a review of these ideas see Clarke 1991). More recently it has been proposed that overall growth rates in polar marine invertebrates and fish may be constrained by seasonal resource limitation rather than by temperature (Clarke 1988, 1991). This hypothesis has been tested with data for fish larvae by Clarke & North (1991) and although this analysis confirmed a strong relationship between growth and temperature the hypothesis of seasonal resource limitation could not be rejected. We have used the data compiled for marine invertebrates to test the hypothesis that population P/B ratios in polar benthic species are lower than in temperate and sub-tropical populations.

Methods

Data collection

For the purposes of this study the "Antarctic" was defined as those regions south of 55°S and with a mean annual bottom water temperature of $\leq 2°C$. The definition thus included South Georgia and some other subantarctic regions.

Data on the population dynamics of Antarctic benthic invertebrates were drawn from published papers, unpublished manuscripts, Ph.D. and M.Sc. theses, and unpublished internal reports of the British Antarctic Survey (BAS). We included all those sources which allowed quantitative assessment of growth, productivity and mortality. Data for Arctic marine benthic invertebrates were available from one area at the west coast of

Greenland and were included in the analysis of empirical relations by Brey (1990).

Growth

Growth data of the type size-at-age (S_t at age (time) t) were taken either from tabulated data, or reconstructed from figures showing the development of size with time. Three different growth models were fitted to the data by an iterative non-linear fitting algorithm (SIMPLEX, see Press *et al.* 1986). These were:

Linear: $S_t = d \bullet t + c$

von Bertalanffy: $S_t = S_\infty \bullet (1 - e^{-K \bullet (t - t_0)})$

Gompertz: $S_t = S_\infty \bullet e^{-e^{-K \bullet (t - t_0)}}$

The model resulting in the lowest residual sum of squares (RSS) was taken as the best fit.

Somatic Production

Somatic Production was computed by either the Mass (i.e. Weight) Specific Growth Rate Method (SGR), by means of an Average Growth Rate (AGR), or by the Increment Summation Method (ISM: Crisp 1984). For both SGR and AGR techniques the data required are (i) a growth function, (ii) a size-frequency distribution, and (iii) a regression of somatic mass on size. In most cases the size-frequency data had to be reconstructed from figures such as bar charts.

Mass specific growth rate G_i was calculated by:

Linear: $G_i = b \bullet d / S_i$ $[y^{-1}]$

von Bertalanffy: $G_i = b \bullet K \bullet (S_\infty - S_i) / S_i$ $[y^{-1}]$

Gompertz: $G_i = b \bullet K \bullet \ln(S_\infty / S_i)$ $[y^{-1}]$

where b = slope of the size-mass relation,

d, K, S_∞ = parameters of the growth functions and

S_i = mean size in size class i.

Annual production was calculated by:

$$P = \Sigma N_i \bullet M_i \bullet G_i$$

where N_i = number of animals in size class i,

M_i = mean individual body mass in size class i

and annual P/B ratio by:

$$P/B = P / \Sigma N_i \bullet W_i$$

In some cases G_i had to be estimated from a set of tagging-recapture data, (that is M_{t1} at time t1 and M_{t2} at time t2). Here mass specific growth rates were estimated by:

$$G = \ln(M_{t2}/M_{t1})/(t_2 - t_1)$$

for all specimens, and an empirical relationship between G_i and M_i was established. If this was not appropriate, for example because of too few data points, an average growth rate for the whole size range was calculated.

For the ISM (Increment Summation Method) the data required are (i) the abundance N_t of an age class at time t and (ii) the mean individual mass M_t in an age class at time t; where t = 1, 2,... n; and n = number of sampling dates. Production was calculated from growth increments by:

$$P_t = (N_t + N_{t+1})/2 \bullet (M_{t+1} - M_t)$$

as well as from mortality increments (elimination) by:

$$E_t = (M_t + M_{t+1})/2 \bullet (N_t - N_{t+1})$$

Total production during a longer period was calculated by summing up the values of P_t (E_t) of consecutive sampling intervals.

Gonad production

Calculations of gonad production were based either on the relation between individual gonad output and individual size (IGO) or on an estimate of average gonad output in the population (AGO). To calculate IGO the data required are (i) a size-frequency distribution, and (ii) a regression of individual gonad output (e.g. mass of eggs per female) on size. Gonad production was calculated by

$$PG = \Sigma N_i \bullet IGO_i$$

Some authors provided only information on the average annual change in gonad mass, the average gonad output, or the average change in a gonad index (gonad mass per body mass). For these cases gonad production was estimated from the data provided and population abundance or biomass data.

Mortality

The fit of the single negative exponential mortality model

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

was tested either by a catch curve based on numbers per age class (ACC) or by one based on size-frequency data (SCC). This size-converted catch curve (Pauly 1984, Brey 1986) was calculated from a size frequency distribution and a growth curve,

$$(N_i/\Delta t) = N_0 \bullet e^{-Z \bullet t_i}$$

where Δt is the time required to growth through size class i. The instantaneous mortality rate Z was estimated from a linear regression of $\ln(N_t)$ or $\ln(N_i/\Delta t)$ on t.

Statistical analysis of P/B ratios

The rate of individual physiological processes (respiration, growth, turnover etc.) of ectothermal animals is known to vary with body mass (e.g. Calder 1985), taxon (e.g. Levinton 1983, Pauly 1981), temperature (e.g. Robinson *et al.* 1983, Taylor 1960) and food availability (e.g. Parry 1983). Since populations consist of individuals, overall population physiological parameters such as the P/B ratio can be assumed to be affected by the same factors.

Our aim was to test the alternate hypothesis (H_A) that P/B ratios of Antarctic and Arctic populations are different from those of non-polar populations against the null hypothesis (H_0) that there are no significant differences between polar and non-polar population P/B ratios.

The data set consisted of 363 data arrays referring to 150 different species; 327 were from non-polar environments and 36 from polar environments (see below). Each array contained the continuous variables annual P/B ratio (P/B [y^{-1}]), mean individual body mass (M [kJ]), geographical latitude (LAT), water depth (D, [m]), mean annual bottom water temperature (T, [K]) and the nominal variables TAXON (Mollusca, Crustacea, Polychaeta, Echinodermata) and REGION (Antarctic, Arctic, non-polar). These data have been extracted from the literature; for calculation procedures and most of the references see Brey (1990). The large differences between phyla in the proportion of inorganic skeletal material required body mass to be converted to kJ by factors given by the original authors or taken from Brey *et al.* (1988) and the references therein.

Metabolic processes usually exhibit a power or exponential relation to individual body mass, and so all production variables were transformed logarithmically ($\log_{10}$) to linearize the relationships. The best correlation between P/B ratio and the abiotic parameters was obtained with the transformations 1/T, log(D+1) and log(LAT).

There are too few polar data arrays for any effects of TAXON and REGION to be analysed simultaneously by a two-factor analysis of variance (ANOVA), therefore they had to be examined separately.

The complete data analysis protocol is shown in Fig. 1. The first step was to remove the effect of body mass on P/B ratio. Body mass is one of the most difficult confounding variables to allow for in ecological work. The frequent technique of simply dividing by body mass to calculate a mass-specific variable does not get around the problem and because the mass exponent for most ecological and physiological variables is not equal to unity (and is usually < 1) the mass-specific variable itself still varies with body mass. One useful technique is to calculate a least-squares regression of the variable of interest against body mass, and then use the residuals about the regression line as a replacement variable to remove the effect of body mass. The regression of log(P/B) against log(M) was calculated with all 363 data arrays and tested for effects of TAXON by analysis of covariance (ANCOVA). If these effects are non-significant then, the residuals (RESID 1) of the overall regression (*n*=363) can be used for further analysis. Otherwise the residuals of a multiple linear regression of log(P/B) against log(M) and dummy variables for taxa (see Draper & Smith 1981) can be used. The residuals RESID 1 may be tested for differences among Arctic, Antarctic and non-polar data (REGION) by ANOVA. Finally the effects of the abiotic parameters temperature, depth and latitude can be removed by a multiple linear regression of RESID 1 against the significant parameters, and the residuals (RESID 2) of the latter multiple linear regression used to test again for significant effects of REGION with ANOVA.

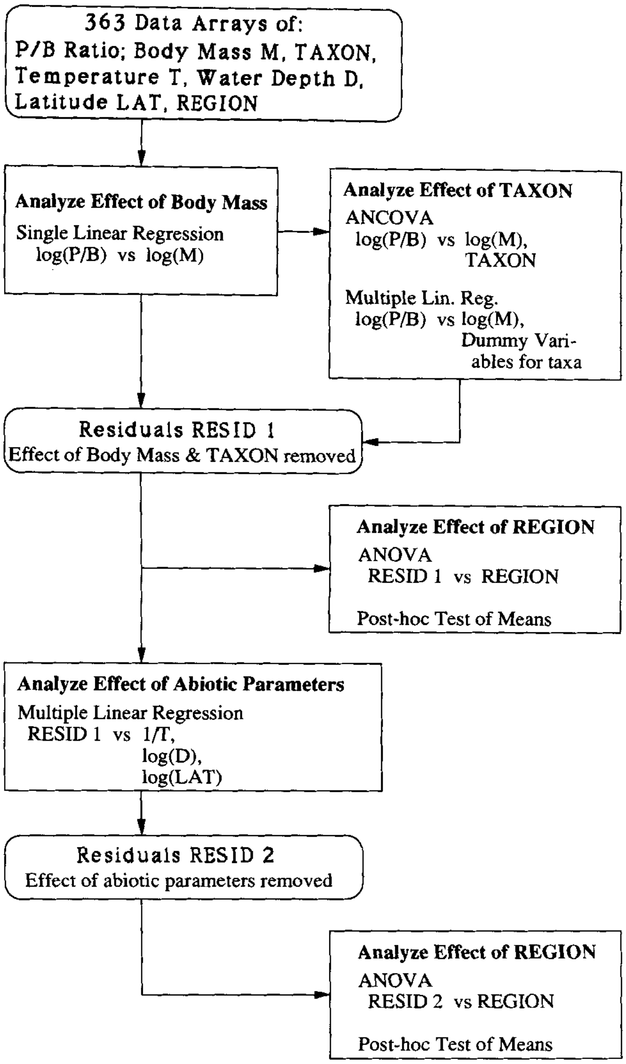

Fig. 1. Flow chart of way of data analysis ANOVA = Analysis of Variance ANCOVA = Analysis of Covariance.

Results

We obtained data for 23 Antarctic and subantarctic benthic marine invertebrate species: nine molluscs, seven crustaceans, two polychaetes and five echinoderms (Table I). The corresponding size-mass relations and the conversion factors for these taxa are shown in Table II. Although the two polychaete species *Amphicteis gunneri* and *Aglaophamus ornatus* are included in Tables I–IV, they were not classified as polar because of the high average water temperature at Iles Kerguelen (3.5°C).

Table I. Depth (m), average water temperature (°C) and latitude (°S) of Antarctic and subantarctic macrobenthic populations used in this study. The polychaetes *Amphicteis gunneri* and *Aglaophamus ornatus* are not included in the statitical analysis of Antarctic populations (see text). nd = no data.

Taxon		Species	Area [m]	Depth [°C]	Temp [°S]	Latitude	References
Mollusca	Bivalvia	*Adamussium colbecki* (Smith 1902)	McMurdo Sound	20	-1.8	77°35'	Stockton 1984 Berkman 1990
			Stonington Island	10	nd	68°11'	Ralph & Maxwell 1977
		Kidderia bicolor (Martens 1895)	South Georgia	0	1.5	54°17'	Ralph & Everson 1972
		Laternula elliptica (King & Broderip)	Signy Island	10	-0.8	60°43'	Ralph & Maxwell 1977
		Lissarca miliaris (Philippi 1845)	Signy Island	7	-0.8	60°43'	Richardson 1977, 1979
		Lissarca notorcadensis	Northern Weddell Sea Shelf	320	-1.0	61°	Brey & Hain 1992
		Meville & Standen 1907	Southern Weddell Sea Shelf	417	-1.0	74°	
		Yoldia eightsi (Couthouy)	Signy Island	12	-0.8	60°43'	Rabarts 1970a,b Nolan 1985, 1987, 1988
	Gastropoda	*Laevilacunaria antarctica* Martens 1895	Signy Island	6	-0.8	60°43'	Picken 1975, 1976, 1979, 1980b
		Nacella concinna	Signy Island	6	-0.8	60°43'	Picken 1980a, 1980b
		(Strebel 1908)		3			Nolan 1985, 1987, 1988, 1991
		Philine gibba Strebel 1908	South Georgia	10	1.5	54°17'	Seager 1974, 1975, 1978
Crustacea	Amphipoda	*Bovallia gigantea* Pfeffer 1888	Signy Island	5	-0.8	60°43'	Thurston 1968, 1970, Bone 1972
		Cheirimedon femoratus (Pfeffer 1888)	Signy Island	5	-0.8	60°43'	Bregazzi 1971, 1972
		Paramoera walkeri Stebbing 1906	Cape Bird	8	-1.6	77°13'	Sagar 1980
		Gondogeneia antarctica (Chevreux 1906)	Signy Island	6	-0.8	60°43'	Richardson 1977
	Decapoda	*Chorismus antarcticus* (Pfeffer 1887)	South Georgia	10	-0.8	60°43'	Maxwell 1972, 1976
	Isopoda	*Aega antarctica* Hodgson 1910	Weddell Sea Shelf	375	-1.0	75°	Wägele 1990
		Serolis polita Pfeffer 1888	Signy Island	14	-0.8	60°43'	Luxmoore 1978, 1981, 1982a,b, 1985
Polychaeta	Ampharetidae	*Amphicteis gunneri* Sars 1835	Kerguelen Island	50	3.5	49°20'	Desbruyeres 1977
	Nephtydae	*Aglaophamus ornatus* Hartman 1967	Kerguelen Island	50	3.5	49°20'	Desbruyeres 1977
Echinodermata	Echinoidea	*Sterechinus antarcticus* Koehler 1901	Southern Weddell Sea Shelf	500	-1.0	75°	Brey 1991
	Ophiuroidea	*Ophionotus hexactis* (Smith 1876)	South Georgia	5	1.5	54°17'	Morison 1976, 1979
	Asteroidea	*Acodontaster conspicuus* (Koehler 1912)	McMurdo Sound	45	-1.8	77°35'	Dayton *et al.* 1974
		Odontaster validus	McMurdo Sound	45	-1.8	77°35'	Dayton *et al.* 1974
		Koehler 1911		20	-1.8		McClintock *et al.* 1988
		Perknaster fuscus (Koehler 1906)	McMurdo Sound	45	-1.8	77°35'	Dayton *et al.* 1974

Growth of Antarctic macrobenthos

Individual growth curves were obtained for 20 species (Table III). For *Adamussium colbecki*, *Lissarca notorcadensis*, *Bovallia gigantea* and *Ophionotus hexactis*, two or three different curves, referring to different sites or years, are given. For four of the five amphipods, growth curves were computed separately for females and males. Additionally, the maximum growth rate during lifetime could be calculated for most of the data sets; this ranged from 0.3 (*Lissarca notorcadensis*) to 900 mg AFDW y^{-1} (*Adamussium colbecki)*, (Table III).

Table II. Size-mass relations and conversion factors.

Species	Size-mass relation	Reference	Conversion to AFDM	Conversion to kJ
Adamussium colbecki	log(g SFWM) = -4.733 + 3.283 * log (mm H)	Stockton 1984	0.150 * SFWM[1]	22.79/gAFDM[6]
Kidderia bicolor	-	-	-	-
Laternula elliptica	-	-	-	-
Lissarca miliaris	log(mg SFDM) = -1.739 + 2.985 * log(mm L)	Richardson 1979	0.831 * SFDM[1]	18.85/gSFDM[6]
Lissarca notorcadensis	mg AFDM = 0.018 * mm $L^{2.567}$	Brey & Hain 1992	-	22.79/gAFDM[6]
Laevilacunaria antarctica	-	-	0.837 * SFDM[1]	18.85/gSFDM[6]
Yoldia eightsi	log(mg AFDM) = -2.485 + 3.341 * log(mm L)	Nolan 1988	-	22.79/gAFDM[6]
Nacella concinna	log(mg SFDM) = -1.427 + 2.628 * log(mm L)	Picken 1980a	0.837 * SFDM[1]	18.85/gSFDM[6]
Philine gibba	log (mg AFDM) = -0.977 + 2.960 * log(mm L)	Seager 1978	-	20.73/gAFDM[7]
Bovallia gigantea	log(mg DM) = -2.393 + 3.178 * log(mm L)	Bone (unpubl. data)	0.720 * DM[1]	15.31/gDM[6]
Cheirimedon femoratus	-	-	-	-
Paramoera walkeri		Sagar 1980	0.720 * DM[1]	15.31/gDM[6]
females	log(mg DM) = -2.121 + 2.414 * log(mm L)			
males	log(mg DM) = -2.175 + 2.375 * log(mm L)			
Gondogeneia antarctica	-	-	-	-
Chorismus antarcticus	log (mg AFDM) = -0.946 + 2.730 * log(mm L)	Maxwell 1976	0.19 * WM[1,2]	15.31/gDM[6]
Aega antarctica	log (mg WM) = -1.748 + 3.378 * log(mm L)	Wägele 1990	0.15 * WM[1]	22.74/gAFDM[6]
Serolis polita		Luxmoore 1982b	0.580 * DM[3]	11.99/gDM[6]
females	ln(mg DM) = -2.906 + 2.750 * ln(mm W)			
males	ln(mg DM) = -2.658 + 2.608 * ln(mm W)			
Amphicteis gunneri	"Length" = $WM^{1/3}$	Desbruyeres 1977	0.11 * WM1[1,4]	23.33/gAFDM[6]
Aglaophamus ornatus	"Length" = $WM^{1/3}$	Desbruyeres 1977	0.11 * WM[1,4]	23.33/gAFDM[6]
Sterechinus antarcticus	log (mg AFDM) = -1.444 + 2.420 * log(mm D)	Brey 1991	-	-
Ophionotus hexactis	mg AFDM = 0.044 * $D^{2.840}$	Dahm 1991	-	-
Acodontaster conspicuus	DM = 0.225 * $WM^{0.944}$	Dayton *et al.* 1974	0.718 * DM[5]	28.02[5]
Odontaster validus	DM = 0.444 * $WM^{0.718}$	Dayton *et al.* 1974	0.499 * DM[5]	22.61[5]
Perknaster fuscus	DM = 0.398 * $WM^{0.737}$	Dayton *et al.* 1974	0.354 * DM[5]	23.74[5]

WM = Wet mass; DM = Dry mass; SF = Shell free; AF = Ash free; D = Diameter; H = Height; L = Length; W = Width. 1) Rumohr *et al.* (1987); 2) Maxwell (1976); 3) Luxmoore (1982b); 4) Desbruyeres (1977); 5) Dayton *et al.* (1974); 6) Brey *et al.* (1988); 7) Seager (1978).

Productivity and mortality

P/B ratio and/or mortality could be computed for 19 Antarctic species (Table IV). Two or more estimates, referring to different sites or years could be made for seven species - *Adamussium colbecki, Lissarca notorcadensis, Yoldia eightsi, Laevilacunaria antarctica, Bovallia gigantea, Ophionotus hexactis* and *Odontaster validus*. A total of 27 estimates of annual somatic P/B ratio, 15 estimates of annual gonad P/B ratio and 18 estimates of annual mortality rate were calculated. P/B ratio and mortality rate values (which are equivalent under certain circumstances, see Allen 1971) ranged from 0.07 y^{-1} (*Sterechinus antarcticus*) to 1.85 y^{-1} (*Laevilacunaria antarctica*).

Data were available for five species of Arctic marine invertebrates, all from one area on the west coast of Greenland at 69°N. These included the bivalves *Hiatella byssifera, Macoma calcarea, Mya truncata* and *Serripes groenlandicus*, and the polychaete *Terebellides stroemi*. In these populations, annual P/B rations ranged from 0.10 y^{-1} (*Serripes groenlandicus*) to 0.34 y^{-1} (*Mya truncata*), (Table V).

Comparison of Antarctic, Arctic and non-polar populations

The analysis was based on 363 productivity data sets: 36 from polar populations (26 Antarctic, 10 Arctic) and 327 from non-polar populations. The distribution of these data with respect to body mass (M), temperature (T), depth (D) and latitude (LAT) is shown in Fig. 2.

As indicated by the correlation matrix (Table VI), log(P/B) is correlated most strongly with log(M), followed by 1/T and log(LAT). However, there are also many intercorrelations between log(M), 1/T, log(1+D) and log(LAT).

When all data are pooled there is a strong negative relationship between population P/B ratio and mean individual body mass (Fig. 3). This relation is highly significant ($r = -0.667$, $P \leq 0.0001$; Table VIIa). However, there is a significant effect of TAXON on the slope of the regression line (ANCOVA, $P = 0.0018$, Table VIIb).

The residuals from the initial pooled regression show significant differences ($P \leq 0.0001$) between Echinodermata ($\bar{x} = -0.219$) and Polychaeta ($\bar{x} = 0.081$) as well as Crustacea

Table III. *Growth in Antarctic and subantarctic macrobenthic invertebrate populations.*

Species	Area	Growth function1)	Method2)	Parameters K [y^{-1}]	 S$_\infty$[mm]3)	 t$_o$ [y]	Number of data	Residual Sum of	Max.growth rate dM/dt 4) [mgAFDM y^{-1}]
Adamussium colbecki	McMurdo Sound								
	Stockton 1984	B	W	0.120	105.00 (H)	-	-	-	627.57
	Berkman 1990	B	W	0.090	128.00 (H)	-0.765	-	-	901.83
	Stonington Island	B	S*	0.252	89.06 (H)	0.203	7	7.211	767.58
Kidderia bicolor	South Georgia								
		G	S*	0.345	6.79 (L)	2.013	436	106.770	nd
Laternula elliptica	Signy Island								
		B	S*	0.156	105.61 (L)	-0.620	13	6.254	nd
Lissarca miliaris	Signy Island								
		G	S*	0.322	6.63 (L)	2.354	67	2.591	0.50
Lissarca notorcadensis	Weddell Sea								
	Northern Shelf	B	S	0.085	12.14 (L)	-1.477	40	10.783	0.43
	Southern Shelf	B	S	0.112	9.80 (L)	-1.247	72	19.448	0.33
Yoldia eightsi	Signy Island								
	Nolan 1988	B	W	0.062	34.09 (L)	-	-	-	11.65
Laevilacunaria antarctica	Signy Island								
		G	S*	1.137	6.56 (L)	1.290	25	2.418	4.57
Nacella concinna	Signy Island								
		B	S*	0.051	67.51 (L)	0.332	10	0.844	47.02
Philine gibba	South Georgia								
		G	S*	0.707	14.55 (L)	1.821	5	0.567	75.78
Bovallia gigantea	Signy Island								
females	Thurston 1968, 1970	B	S*	0.268	65.75 (L)	-0.142	35	29.684	205.28
	Bone 1972	B	S*	0.154	81.23 (L)	-0.330	42	40.142	230.97
males & juv.	Thurston 1968, 1970	B	S*	0.377	42.72 (L)	-0.235	30	16.102	73.35
	Bone 1972	B	S*	0.396	38.66 (L)	-0.261	30	17.672	56.10
Cheirimedon fem.	Signy Island								
females		G	S*	0.455	20.44 (L)	1.676	49	14.910	nd
males		G	S*	0.559	13.84 (L)	0.906	39	7.822	nd
Paramoera walk.	Cape Bird								
females		B	S*	0.420	26.51 (L)	0.572	23	21.086	2.93
males		B	S*	0.367	25.19 (L)	0.537	24	11.116	1.77
Gondogeneia ant.	Signy Island								
females		G	S*	1.740	16.48 (L)	1.187	31	11.673	nd
males		G	S*	1.123	16.85 (L)	1.385	24	9.969	nd
Chorismus ant.	South Georgia	L							
females				d=0.599	c=10.25	-	7	0.037	-
Aega antarctica	Weddell Sea								
		B	W	0.120	26.20 (L)	-	-	-	8.35
Serolis polita	Signy Island								
		B	S*	0.366	18.69 (W)	-0.406	14	5.421	16.54
Amphicteis gunneri	Kerguelen Island								
		G	S*	0.681	4.74 (M)	0.143	17	1.003	nd
Aglaophamus ornatus	Kerguelen Island								
		G	S*	0.165	27.95 (M)	5.117	29	34.665	198.87
Sterechinus antarcticus	Southern Weddell Sea Shelf	B	S	0.017	82.40 (D)	1.633	217	2181.8	12.42
Ophionotus hexactis	South Georgia								
	Site A	B	S*	0.083	41.52 (D)	-2.493	232	216.601	64.80
	Site B	B	S*	0.160	27.58 (D)	-1.647	102	206.580	38.96
	Sites A&B	B	S*	0.079	43.81 (D)	-2.195	334	474.147	71.83

1) L = Linear: $S_t = d * t + c$. B = Von Bertalanffy: $S_t = S_\infty * (1 - e^{-K*(t-t_o)})$. G = Gompertz: $S_t = S_\infty * e^{-e^{-K*(t-t_o)}}$. 2) W = Walford Plot; S = Nonlinear fit by SIMPLEX Algorithm; * = recalculated by this study. 3) D = Diameter; L = Length; M = WM$^{1/3}$; W = Width. 4) Von Bertalanffy: Max. dM/dt = $K * M_\infty * (1-1/b)^{b-1}$. Gompertz: Max. dM/dt = $K * M_\infty / e$.

Table IV. Productivity and mortality in Antarctic and subantarctic macrobenthic populations. Units of body mass: g ash free dry mass (AFDM).

Species	Area/Remarks	Biomass	Somatic production			Gonad production			Total production		Mortality	
		$[\mathrm{g\,m^{-2}}]$	Method1)	P_S $[\mathrm{g\,m^{-2}\,y^{-1}}]$	P_S/B $[\mathrm{y^{-1}}]$	Method2)	P_G $[\mathrm{g\,m^{-2}\,y^{-1}}]$	P_G/B $[\mathrm{y^{-1}}]$	P_{Total} $[\mathrm{g\,m^{-2}\,y^{-1}}]$	P_T/B $[\mathrm{y^{-1}}]$	Method3)	Z $[\mathrm{y^{-1}}]$
Adamussium colbecki	McMurdo Sound											
	Stockton 1984	59.250	SGR	10.073	0.170	-	-	-	-	-	SCC	nf
	Berkman 1990	66.000	SGR	13.09	0.198	-	-	-	-	-	SCC	nf
Kidderia bicolor	South Georgia	-	-	-	-	-	-	-	-	-	SCC	0.299
Lissarca miliaris	Signy Island	-	SGR	-	0.664	IGO	-	0.114	-	0.778	SCC	0.600
Lissarca notorcadensis	Weddell Sea											
	Northern Shelf	-	SGR	-	0.316	IGO	-	0.128	-	0.444	SCC	0.316
	Southern Shelf	-	SGR	-	0.305	IGO	-	0.115	-	0.420	SCC	0.297
Yoldia eightsi	Signy Island											
	Rabarts 1970b	69.011	SGR	8.046	0.117	-	-	-	-	-	SCC	0.114
	Nolan 1988	-	SGR	-	0.162	-	-	-	-	-	SCC	0.130
Laevilacunaria antarctica	Signy Island 1975–76	0.039	SGR	0.067	1.706	-	-	-	-	-	SCC	1.832
	1976–77	0.299	SGR	0.472	1.577	-	-	-	-	-	SCC	1.647
	1976–77	0.299	ISM	0.553	1.849	-	-					
Nacella concinna	Signy Island											
	Picken 1980a	11.570	SGR	2.854	0.247	AGO	0.921	0.080	3.775	0.326	SCC	nf
	Nolan 1987	-	SGR	-	0.203	AGO	-	0.093	-	0.296	SCC	nf
Philine gibba	South Georgia	10.314	SGR	4.218	0.409	IGO	4.754	0.461	8.972	0.870	ACC	nf
Bovallia gigantea	Signy Island											
females	Thurston 1968, 1970	-	SGR	-	0.775	-	-	-	-	-	SCC	0.729
	Bone 1972	-	SGR	-	0.905	-	-	-	-	-	SCC	0.889
males & juv.	Thurston 1968, 1970	-	SGR	-	0.856	-	-	-	-	-	SCC	0.802
	Bone 1972	-	SGR	-	1.206	-	-	-	-	-	SCC	1.385
Cheirimedon femoratus	Signy Island	-	-	-	-	-	-	-	-	-	SCC	0.803
Chorismus antarcticus females	Signy Island	-	SGR	-	0.142	IGO	-	0.257	-	0.397	SCC	nf
Aega antarctica	Weddell Sea	-	SGR	-	0.096	-	-	-	-	-	SCC	0.130
Serolis polita	Signy Island	5.467	SGR	4.117	0.753	IGO	0.224	0.041	4.341	0.794	SCC	0.626
Amphicteis gunneri	Kerguelen Island	1.665	SGR	1.402	0.845	-	-	-	-	-	SCC	1.083
Sterechinus antarcticus	Southern Weddell Sea Shelf	0.005	SGR	0.00032	0.065	AGO	0.00025	0.05	0.00058	0.116	SCC	0.070
Ophionotus hexactis	South Georgia											
	Site A	7.226	SGR	2.196	0.304	AGO	0.419	0.058	2.615	0.362	SCC	nf
	Site B	8.117	SGR	4.775	0.588	IGO	1.420	0.174	6.195	0.763	SCC	0.597
	Sites A&B	7.672	SGR	3.486	0.454	both	0.920	0.120	4.406	0.574	SCC	nf
Acodontaster conspicuus	McMurdo	2.709	AGR	0.187	0.069	AGO	0.411	0.152	0.598	0.221	-	-
Odontaster validus	McMurdo											
	Dayton *et al.* 1974	2.305	SGR	0.104	0.045	AGO	0.338	0.147	0.442	0.192	-	
	McClintock *et al.* 1988	18.463	AGR	0.665	0.036	AGO	1.848	0.100	2.511	0.136	-	
Perknaster fuscus	McMurdo	0.168	AGR	0.023	0.135	AGO	0.040	0.241	0.063	0.376	-	-

1) ISM = Increment Summation Method; SGR = Weight Specifc Growth Rate Method; AGR = Average Growth Rate Method. 2) IGO = Calculated by Individual Gonad Output ; AGO = Calculated by Average Gonad Output . 3) ACC = Calculated by Age class based Catch Curve; SCC = Calculated by Size class-based Catch Curve. nf = Single negative exponential mortality model does not fit the data

($\bar{x} = 0.081$), whereas Mollusca ($\bar{x} = -0.046$) do not differ significantly from the other taxa. The residuals of a multiple linear regression (RESID 1, Table VIIc) involving dummy variables for TAXON were therefore used for further analysis.

A one-factor ANOVA (independent variable = REGION) on these residuals RESID 1 (Fig. 4a) showed significant differences between geographic regions (Table VIII). Antarctic ($P \leq 0.0001$) as well as Arctic ($P \leq 0.0001$) values are below the non-polar values, whereas Arctic and Antarctic values do not differ significantly ($P = 0.0620$).

The multiple linear regression of RESID 1 against abiotic parameters showed negative relations between RESID 1 and 1/T as well as log(D+1); latitude had no significant effect (Table IX).

The final one-factor ANOVA on the residuals RESID 2 of the multiple linear regression showed that there are significant differences between Arctic and non-polar regions ($P = 0.0010$) as well as between Arctic and Antarctic regions ($P = 0.0074$), but there are no differences between Antarctic and non-polar regions ($P = 0.5348$), (Table X & Fig. 4b).

These results indicate that the null hypothesis H_0 (that the P/B ratio of polar benthic macroinvertebrate populations do not differ from those of non-polar populations) must be rejected in favour of the alternate hypothesis H_A. The differences between the P/B-ratios of Antarctic and non-polar populations can be explained entirely by factors operating in all benthic environments, namely temperature and water depth. It is notable however that Arctic populations are significantly different from Antarctic and non-polar populations if temperature and depth are taken into account.

Table V. Biomass and somatic production (P_S) of Arctic benthic invertebrate populations from the Disko Bugt area, West Greenland (69°N). Units of mass: g ash free dry mass (AFDM). Bivalve data from Petersen (1978), polychaete data from Curtis (1977).

Species	Depth, temperature	Biomass [g m^{-2}]	P_S [g m^{-2} y^{-1}]	P_S/B Ratio [y^{-1}]
Hiatella byssifera	8 m, 2.0 °C	5.364	0.803	0.150
Macoma calcarea	8 m, 2.0 °C	3.764	0.720	0.191
	10 m, 2.0 °C	0.193	0.064	0.333
	94 m, 0 °C	0.079	0.013	0.166
Mya truncata	8 m, 2.0 °C	18.019	2.608	0.145
	10 m, 2.0 °C	5.011	1.696	0.338
	37 m, 0 °C	0.900	0.154	0.171
Serripes groenlandicus	8 m, 2.0 °C	16.060	2.120	0.132
	37 m, 0 °C	4.754	0.482	0.101
Terebellides stroemi	37 m, 0 °C	2.610	2.720	1.042

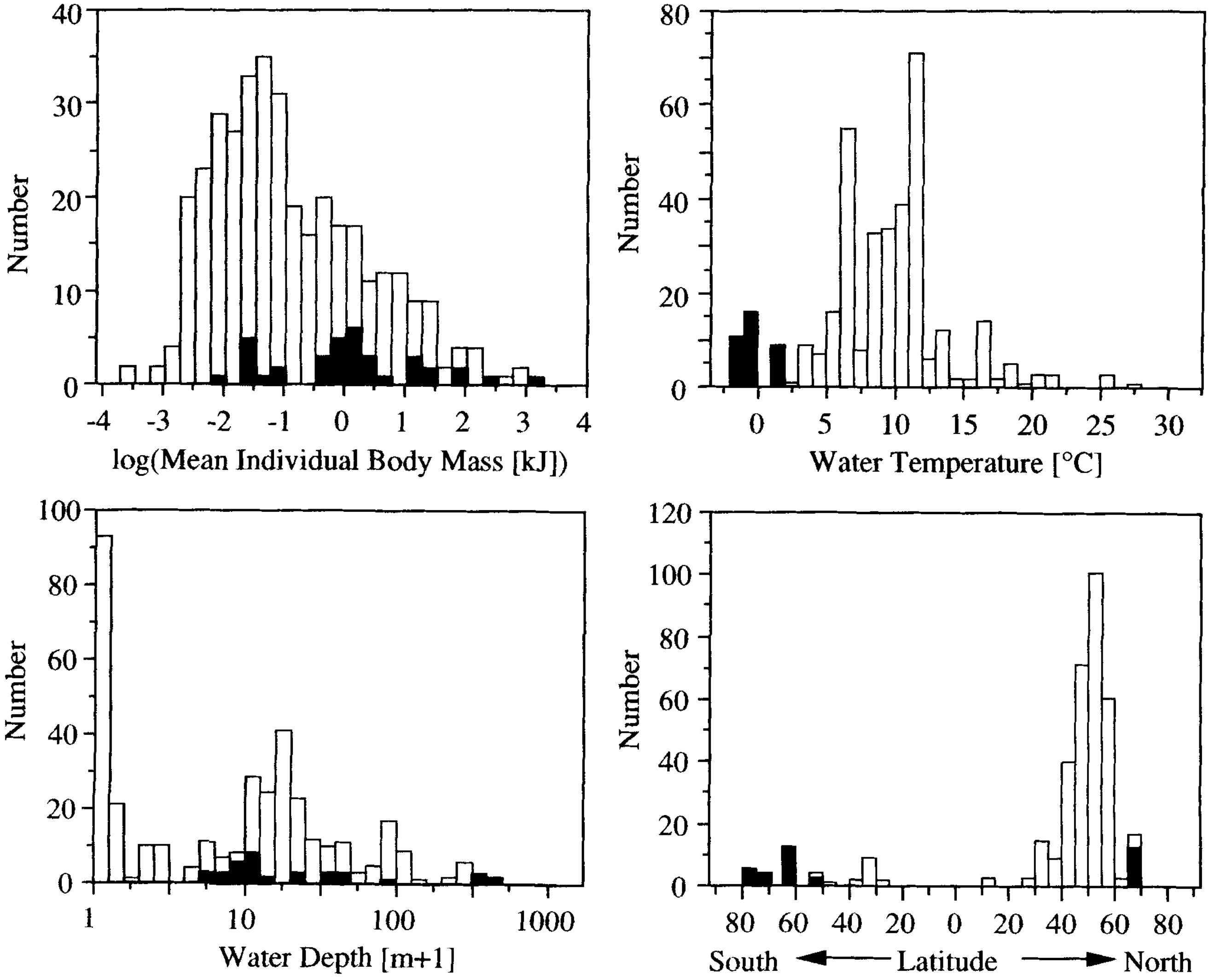

Fig. 2. Distribution of the 363 data arrays included with respect to mean individual body mass, water temperature, water depth and geographical latitude. Polar data are indicated by black bars.

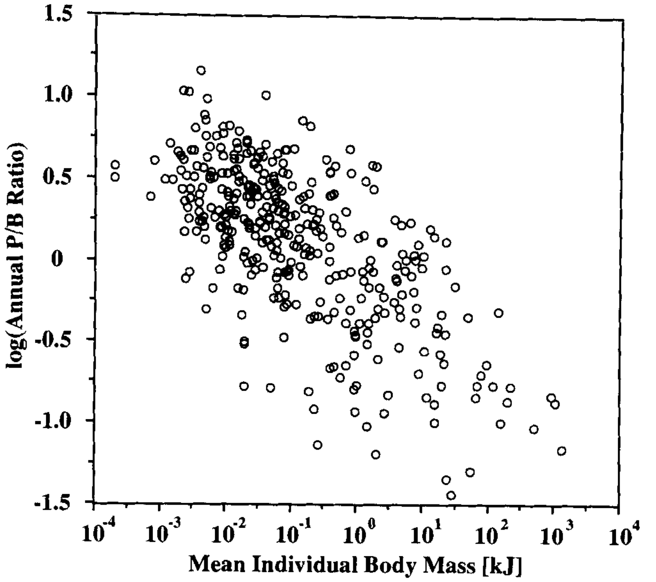

Fig. 3. Plot of log(P/B) against log(Body Mass). (Regression: log(P/B) = -0.124 - 0.252 * log(M); r = 0.667, n = 363.

Discussion

Relations between P/B ratio and biotic parameters

The slope of the common regression of log(P/B) against log(M), -0.219 (Table VIIc), is well within the range of mass exponents found for the relation between various physiological variables and body mass, and resembles closely the generally expected value of -0.25 (Calder 1985, Feldman & McMahon 1983, Platt & Silvert 1981). The differences in P/B ratio between the four taxa, with crustaceans and polychaetes showing the highest rates and echinoderms the lowest ones, are likely to be related to the general differences in the life history patterns of the four taxa. Most crustaceans and polychaetes are motile, agile species and hence presumably have higher metabolic requirements than slowly moving or sedentary living echinoderms and molluscs. Although these higher requirements might suggest a lower P/B ratio because of less energy being available for production, it is possible that a greater mobility allows for more efficient food capture. Clearly a fuller examination of the data, including additional parameters such as mobility type and feeding type, would be required for a better understanding. At present this information is lacking.

Relations between P/B ratio and abiotic parameters

P/B ratio was found to decrease with decreasing temperature and with increasing water depth (Table IX). The inter-correlations between the independent variables (see Table VI) will distort the effects of these parameters on the P/B ratio to a certain extent in the multiple linear model, (Edwards 1979). The application of the composite variables such as log(1+D) * 1/T in place of the highly correlated log(1+D) and 1/T did not

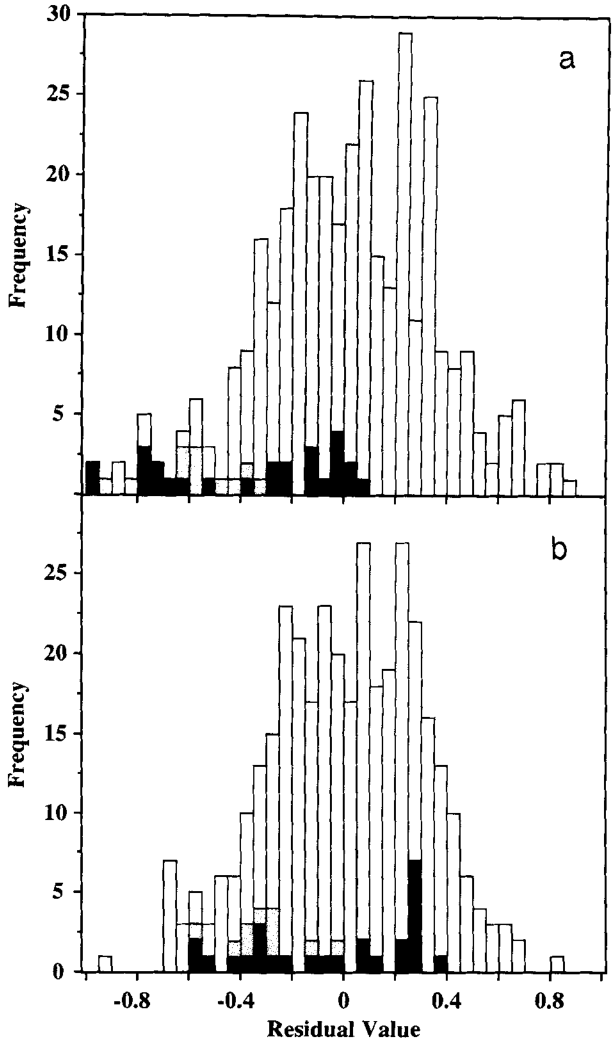

Fig. 4. Frequency distribution of residuals. White bars: Non-polar data; black bars: Antarctic data (≥ 55°S); stippled bars: Arctic data (≥ 69°N). **a.** Distribution of the residuals RESID 1 of the multiple regression of log(P/B) against log(M) and dummy variables for taxa (Table VIIc). **b.** Distribution of the residuals RESID 2 of the multiple regression of RESID 1 against 1/T and log(1+D) (Table IX).

Table VI. Correlation matrix for annual P/B ratio (y^{-1}), mean individual body mass M (kJ), bottom water temperature (K), water depth (m), and geographical latitude (0–90°). All variables entered in their most appropriate transformations. Bold figures indicate significance at the 5% level ($P <= 0.05$).

	log(P/B)	log(M)	1/T	log(1+D)	log(LAT)
log(P/B)	1				
log(M)	**-0.667**	1			
1/T	**-0.287**	-0.053	1		
log(1+D)	-0.088	**-0.271**	**0.416**	1	
log(LAT)	**-0.246**	-0.033	**0.757**	**0.244**	1

Table VII. Analysis of the effect of body mass and taxon on P/B ratio by linear regression.

a) Single linear regression: log(P/B) = a + b * log(M).

Intercept a	Slope b	No. of data	Correlation Coefficient	F	*P*
-0.124	-0.252	363	-0.667	289.938	**0.0001**

b) ANCOVA test on different slopes of the regression among the four taxa

Source	Degrees of freedom	Sum of squares	Mean square	F	*P*
log(M)	1	10.985	10.985	92.360	**0.0001**
TAXON	3	3.115	1.038	8.730	**0.0001**
log(M) * TAXON	3	1.829	0.610	5.126	**0.0018**
Residual	355	42.220	0.113		

c) Multiple Linear Regression with dummy variables for taxa

Dummy	D1	D2	D3
Mollusca	1	0	0
Polychaeta	0	1	0
Crustacea	0	0	1
Echinodermata	0	0	0

	Coefficient	s.e	t	*P*
Intercept a	-0.359			
log(M)	-0.219	0.016	13.612	**0.0001**
Dummy D1	0.206	0.093	2.225	**0.0267**
Dummy D2	0.355	0.100	3.545	**0.0004**
Dummy D3	0.372	0.103	3.606	**0.0004**

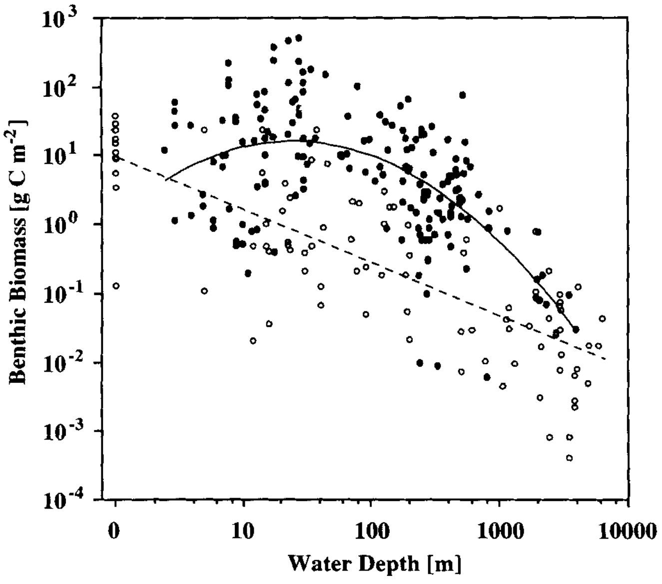

Fig. 5. Distribution of macrobenthic community biomass (B) with depth (D) in Antarctic (dots) as well as boreal & subtropic regions (circles). Zero depth indicates intertidal data. (References see Appendix - Biomass Data Sources) Antarctic: $\log(B) = 0.112 + 1.583 \bullet \log(D) - 0.568 \bullet (\log(D))^2$ $r = 0.582$, $n = 175$ Boreal & Subtropic: $\log(B) = 0.986 - 0.903 \bullet \log(D)$ $r = 0.763$, $n = 94$

Table VIII. First analysis of the effect of geographic regions on P/B ratio. Dependent variable: RESID1, residuals of the multiple regression of log (P/B) against log(M) and taxon dummies (see TableVIIc). Independent variable: REGION (Arctic - Antarctic - Non-Polar)

1-Factor ANOVA

Source	Degrees of freedom	Sum of squares	Mean square	F	*P*
Region	2	6.978	3.489	33.876	**0.0001**
Residual	360	37.078	0.103		

Bonferroni/Dunn post-hoc test of differences between means

		Data set		Test versus	
REGION	N	mean	s.e.	Non-Polar	Antarctic
Arctic	10	-0.544	0.053	P = **0.0001**	P = 0.0620
Antarctic	26	-0.359	0.068	P = **0.0001**	-
Non-Polar	327	0.045	0.018	-	-

change the results significantly. The missing significant effect of latitude on P/B ratio may be explained by the strong correlation between latitude and temperature (Table VI).

The P/B ratio of a steady-state population is directly proportional to the individual growth rates of the specimens forming the population (Allen 1971), and the individual growth rate (i.e. individual P/B ratio) is positively related to individual metabolic rate (Banse 1982, Humphreys 1979, Parry 1983). Hence factors influencing individual metabolic rate affect population P/B ratio in the same way. The most important factors influencing the metabolic rate of ectotherms are body mass, temperature and food (Precht *et al.* 1973, Robinson *et al.* 1983, Parry 1983, Calder 1985, Alongi 1990).

Exposing an individual ectothermic organism to a lower temperature will almost always result in a lower metabolic rate, at least initially, for purely thermodynamic reasons. It has also long been established that in ectotherms living at different habitat temperatures there is a positive relationship between temperature and metabolic rate (for marine examples see Ikeda 1985, Ivleva 1980, Maxwell & Ralph 1985). Although this pattern is similar to the thermodynamic response of a typical individual ectotherm to a change in temperature, the relationship between metabolic rate and habitat temperature established for polar, temperate and tropical ectotherms (Alongi 1990) is not necessarily a direct causal relationship. It is likely that the relationship is related to the costs of protein turnover, osmotic work, etc. and is dictated by how these processes are themselves related to temperature (Clarke 1993). Since it has been clearly established that some enzymes from organisms living at different temperatures differ in activation parameters and stability (Johnston & Walesby 1977, Dittrich in press), the precise form of the relationship between metabolic activity and temperature will not be simple to predict. Nevertheless all investigations to date have indicated a monotonic positive relationship between metabolic rate and mean habitat temperature in marine ectotherms (Clarke 1991). Hence we can expect a general positive correlation between population P/B ratio and temperature, as shown in Tables VI & IX. Population biomass must necessarily decrease

Table IX. Analysis of the effect of abiotic parameters on the P/B ratio. Dependent variable: RESID1, residuals of the multiple regression of log (P/B) against log(M) and taxon dummies (see Table VIIc). Independent variables: Water temperature (K), water depth (m). Latitude shows no significant effect ($P > 0.05$).

Multiple Linear Regression with significant independent variables

	Coefficient	s.e.	t	*P*
Intercept a	7.186			
1/T	-2005.802	284.674	7.047	**0.0001**
log(1+D)	-0.094	0.025	3.816	**0.0002**

with increasing temperature, if the food level and conversion efficiencies do not change.

Food appears to be the limiting resource in many benthic environments (Levinton 1982). Under these conditions, there will always be a balance between biomass and metabolic costs. Species with high food requirements, either because of high maintenance costs or rapid growth rates, would be expected to have low biomass, but species with low metabolic rates could maintain a higher biomass. Different species within a community may well emphasize either aspect of the balance between metabolic costs and biomass, but there is evidence for a general trend towards lower metabolic rates via reduced growth rates if food is scarce (Parry 1983). This trend may cause the negative relationship between water depth and P/B ratio (Table IX), since there is a strong negative correlation between depth and sedimentary input to the benthos (Rowe 1971, Suess 1980).

Adaptations of the Antarctic benthos

The main purpose of this study was to examine available data for population dynamic parameters of Antarctic benthic macroinvertebrates which might be interpreted as adaptations to the particular environmental conditions of the Antarctic. Although the recent studies have failed to confirm earlier concepts such as "Metabolic Cold Adaptation" (Clarke 1980, 1983), there still exists a widespread belief that Antarctic invertebrates have to cope with extremely harsh environmental conditions which may have led to unique evolutionary adaptations. Our results show no evidence of any unique characteristic of Antarctic benthos with respect to population dynamics. The P/B ratios of Antarctic benthic populations do not differ from those of temperate populations, once the effects of body mass, taxon, temperature and water depth have been eliminated (Fig. 4b, Table X). The distinctly lower P/B ratios of the few Arctic species included in this analysis should be interpreted with care because all of these populations came from a limited geographical area.

Table X. Second analysis of the effect of geographic regions on P/B ratio. Dependent variable: RESID2, residuals of the multiple linear regression of RESID2 against 1/T and log(1+D) (see Table IX). Independent variable: REGION (Arctic - Antarctic - Non-Polar)

1-Factor ANOVA

Source	Degrees of freedom	Sum of squares	Mean square	F	*P*
REGION	2	0.983	0.492	5.340	**0.0052**
Residual	360	33.150	0.092		

Bonferroni/Dunn post-hoc test of differences between means

	Data set			Test versus	
Region	N	Mean	s.e.	Non-Polar	Antarctic
Arctic	10	-0.296	0.047	*P* = **0.0010**	*P* = **0.0074**
Antarctic	26	-0.045	0.060	*P* = 0.5348	-
Non-Polar	327	0.013	0.017	-	-

Recent discussions of adaptations in Antarctic marine invertebrates focus on the importance of temperature and food and their seasonal oscillations for metabolism and growth rates in ectotherms. Clarke (1988, 1991), Clarke & North (1991) and others have stressed the significance of food supply as an important limiting factor in the growth of Antarctic animals. They argue that the observed changes in growth rates of several Antarctic species during the short summer period of high primary production (Bregazzi 1972, Picken 1979, Richardson 1979, Seager 1978, Sagar 1980) cannot be explained by the increase in temperature alone, but must be due to the increase in food supply. Therefore the slow annual growth rates observed in Antarctic ectotherms could be mainly caused by seasonal resource limitation and not by rate-limiting effects of low temperature. Hence, our conclusions based on the dependence of P/B ratio on food supply (see above) resemble the hypothesis of Clarke (1988, 1991) and Clarke & North (1991). Adaptions to permanent or intermittent low food supply, however, are not specific to the Antarctic, but may occur in any environment with low food levels.

The particular features of the Antarctic benthic environment are the unique combination of extremely low temperature and long periods without food. Our results indicate that depth-related low food input and low temperature are responsible for the differences between the P/B ratios of Antarctic and non-polar populations; if their effects are removed, the differences vanish (Tables VIII & X). The combined effects of seasonally oscillating food input and low temperature may also explain the most striking feature of many Antarctic benthic communities, the extraordinary high biomass compared to boreal and subtropical areas (Fig. 5). The very low temperatures cause a shift towards low basic metabolic rates, and a comparatively larger proportion of the available energy is used for building up and maintaining standing stocks which are thus much larger than in warmer areas of comparable food input. The strong seasonal oscillation in food supply may have enhanced the competitive development of large standing stock too, since a high biomass seems to be the best way to maximize a population's share of the limited food input under the low temperature regime of the Antarctic.

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