

Patterns of life history and population dynamics of benthic invertebrates under the high Antarctic conditions of the Weddell Sea*

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Abstract

The paper summarizes data on the life history and population dynamics of benthic invertebrates (amphipods, decapod shrimps, molluscs, and echinoderms) from the high Antarctic region of the south-eastern Weddell Sea. These data were derived from the analysis of material collected during various cruises of R.V. *Polarstern* and from animals kept in aquaria during these cruises and in the laboratory.

All benthic species studied so far reveal an extremely slow life-history pattern with numerous, although differing, adaptations to the special ecological conditions of the high Antarctic marine ecosystem. These conditions, their implications for the macrozoobenthos of the southernmost part of the South Polar Sea, and the resultant faunal responses are discussed. It is concluded that certain latitudinal trends in life-history patterns, reproductive strategies, and population dynamics continue beyond the Antarctic Convergence into the high Antarctic areas of the Weddell Sea.

Keywords: Antarctic, macrobenthos, life history, reproduction, population dynamics.

Introduction

The South Polar Sea, especially the 'high Antarctic' area close to the continent, is a special marine ecosystem with a highly characteristic fauna presumably of old age (Clarke & Crame 1989). Up to a few years ago knowledge about this ecosystem was limited to the waters north of the Antarctic Convergence, around the Scotia Arc, and to a few locations close to the ice edge such as McMurdo Sound, Davis or Ellis Fjord. These areas all have shallow-water zones which in general are now less common around Antarctica compared with former geological periods (Clarke & Crame, loc. cit.). The SE Weddell Sea (Figure 1) differs from other Antarctic areas as it has no shallow areas. The ice edge usually prevents work in areas shallower than 200 m, and even in the inlets the sea-floor is usually several hundred metres deep.

The particular features of high Antarctic ecosystems have been detailed elsewhere (Hempel 1985, Schalk 1990). Except for a few polynyas, some of which seem to be lasting for longer periods according to satellite imagery, the major part of the inner Weddell Sea is covered by pack-ice most of the year. Water temperatures on the shelf do not show pronounced seasonal variation. Nevertheless, oscillations between about -1.8°C and $+0.4^{\circ}\text{C}$ are common in the bottom water at greater depths on the shelf (Figure 2). 'Deep warm water' from the Weddell Sea regularly advances into the shelf areas, causing these typical short-term temperature variations. In the upper part of the water column temperature oscillations were less distinct and highest (between -1.8°C and -1.2°C) in Austral summer, whereas relatively constant temperatures near -1.8°C occurred throughout the rest of the year. This is confirmed by further data obtained on cruise ANT VII/4 off Halley Bay (Arntz *et al.* 1990).

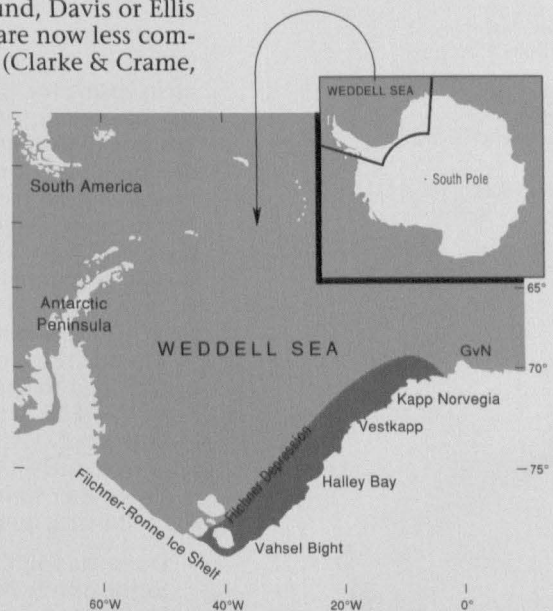


Figure 1. Map of the Weddell Sea showing the area of investigation shaded and its position in Antarctica in the inset.

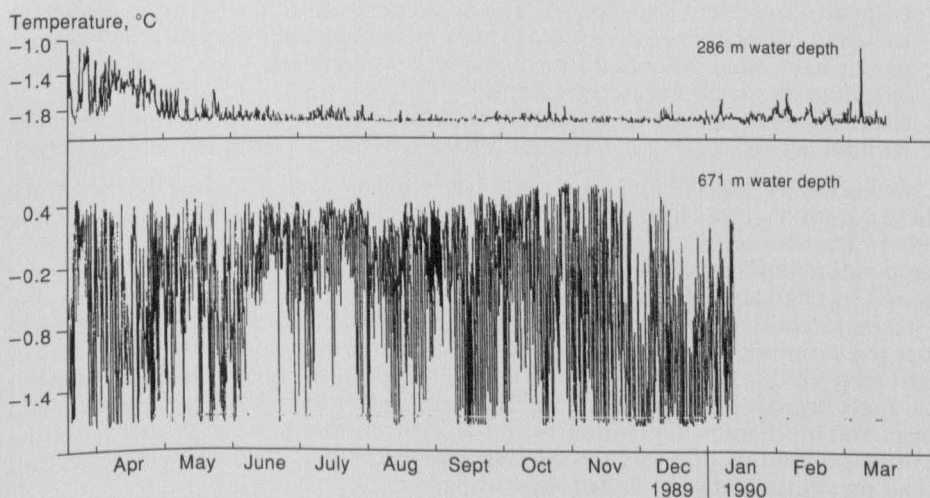


Figure 2. Temperature plots of the current meter data from a station off Kapp Norvegia ($71^{\circ}02,0'S$; $11^{\circ}44,6'W$) in 286 m and 671 m water depth.

Another factor of disturbance in this area is iceberg scouring. Melting icebergs move along the coast according to the prevailing winds and currents and may influence all bottoms above 400 m depth.

Most biological activity in the water column is restricted to a short period in spring and summer which starts with the melting of the pack-ice. Related sedimentation of organic matter to the sea-floor reflects this situation. The only sedimentation data available (Figure 3) indicate a strong vertical flux after the primary production phase. Due to oscillations in the hydrographic regime, especially in current speed and direction, sedimentation takes place over a much longer period of the year than the plankton bloom itself. In winter, primary production is low and the pelagic community splits into two parts, an impoverished community subsisting on the algae production at the underside of the ice cover and a deep-living system, consisting of hibernating stocks and their predators.

The benthic system in the south-eastern Weddell Sea, predominantly a deep-water system close to the edge of the continental shelf ice, depends almost entirely upon the short spring/summer pulse in the sedimentation of organic matter produced in the pelagic zone. Despite this, the epifauna (mostly suspension feeders such as sponges and bryozoans with a variety of motile elements such as amphipods, isopods, shrimps and echinoderms) is surprisingly rich and diverse in most shelf and slope

areas; however, densities are rather patchy. The benthic infauna generally plays a minor part in the high Antarctic system as compared to Antarctic areas of lower latitudes (Mühlenhardt-Siegel 1988, Gallardo 1987), but patches of high biomass of sipunculids and echiurids occur on soft bottoms.

Reviews on particular features of the Antarctic benthic fauna (Dell 1972, Picken 1984, White 1984, Clarke 1983) agree that they 'grow slowly, reproduce slowly, and have only very low rates of metabolism' (Clarke 1983). Longevity is common and usually accompanied by a long period of growth to first maturity. However, growth in many cases is slow only if averaged over the entire year; seasonal growth following sedimentation of a plankton bloom can be quite rapid (Clarke 1988).

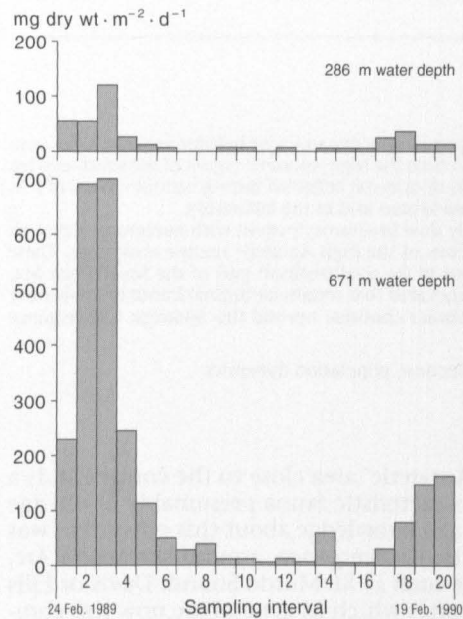
Most of these characteristics of Antarctic benthos were confined to waters north of 60°S and to shallow water whereas our study area is south of 70°S and relatively deep. Even McMurdo Sound where much benthic research has been done (see e.g. Dayton *et al.* 1974, Dayton 1989), and where high Antarctic conditions prevail, is predominantly a shallow water area.

This paper summarizes the preliminary results obtained – mainly with respect to the following questions:

- Does the high Antarctic Weddell Sea shelf environment differ from other areas in the South Polar Sea; if so, in which respect?
- Has the invertebrate benthic fauna in this area developed particular features compared to present knowledge of the Antarctic benthos? For example, do certain trends in life-history patterns, reproduction strategies and population dynamics which have been described for the tropical – temperate – polar seas gradient continue into high Antarctic regions?
- How can methodological difficulties such as interpreting population dynamics without access to data on continuous time series be overcome in the Antarctic?

Evolutionary aspects and metabolic activities are not discussed further since these questions have recently been discussed by Clarke (1990) and Clarke & Crame (1989). The Southern Ocean is characterized by a combination of very low, but stable, temperatures and a clear seasonality of primary production. However, the latter is caused by changes in light rather than variations in temperature, making possible a separation of the effects of temperature and food availability. These make it likely that the properties of the fauna reflect food limitation rather than the effects of extremely cold temperatures (Clarke 1988). This paper concentrates on whether the high Antarctic environment (with, compared to low Antarctic regions, even lower and more stable temperatures and an even shorter pulse of primary production) has caused adaptations in the life style of the benthic fauna which are beyond those previously detected in Antarctic waters.

Figure 3.
Mass flux rates at 286 m and 671 m water depth off Kapp Norvegia determined by sediment traps. The much higher flux rates at 671 m are most likely due to re-suspension.



Material and methods

Work on the benthic community structure based on trawl catch composition (Voss 1988) and on still-photo transects and video sequences (Gutt 1988, Gutt & Vogel 1988) provide background information. In addition, several invertebrate groups were sampled during *Polarstern* cruises ANT III, V, VI, and VII (1985-1989). The trawling gear used between 180 and 2000 m depth included bottom-, semi-pelagic and Agassiz trawls with 10 mm mesh size in the cod-ends; amphipods were also caught using baited traps. Part of the material was preserved in 5% buffered formalin, organisms with calcareous hard parts were transferred to 70% alcohol. Live specimens of molluscs, amphipods, caridean shrimps, and echinoderms were kept at $-1 \pm 0.5^\circ\text{C}$ in 25- and 30-l aquaria in containers on board and later on in the Institute's cool-rooms to produce information on reproduction, growth, and general biology, e.g. feeding and swimming behaviour (Klages & Gutt 1990). In a few cases, eggs, larvae and juveniles of benthic invertebrates were obtained from plankton catches, from egg capsules found in demersal hauls, or from animals spawning in the aquarium.

Preserved females of different groups were analysed for the development of their ovaries, oostegites (amphipods) and pleopods (shrimps). Egg diameters were measured using a computer-assisted image analysing system. Further details on methodology have been published by Hain (1989).

Sedimentation and temperature data were obtained from a mooring which was deployed at $71^\circ 02.0'S$ and $11^\circ 44.6'W$ in 676 m water-depth. The multi-sample sediment traps (Salzgitter Elektronik, FRG) with 20 cups and 0.5 m^2 collection area were attached in 286 and 671 metres water depth. The trap was programmed to collect samples in intervals of 18 days from 24th February 1989 to 19th February 1990. Two Aanderaa current meters and temperature and conductivity sensors registered hydrographic data.

Results

The four macrobenthic groups referred to above are dealt with separately below. In each case, a short summary of background data and results obtained in other South Polar areas is given in order to better distinguish special features of the south-eastern Weddell Sea fauna. Results are presented on selected high Antarctic species which have been studied recently in the laboratory.

Caridean shrimps

There are few decapod crustacean species in the South Polar Sea. In the high Antarctic waters of the Weddell Sea eight species of caridean shrimps are the only representatives; no reptant crustaceans have been found. On the shelf and continental slope *Chorismus antarcticus* Pfeffer, 1887 (a protandrous hermaphrodite), *Notocrangon antarcticus* Pfeffer, 1887 and *Nematocarcinus lanceopes* Bate, 1888 are the most abundant species (Arntz & Gorny 1991). Within the area of investigation between Atka Bay (70°S) and Gould Bay (78°S), *C. antarcticus* has a depth range mainly between 200 and 500 m, and *N. antarcticus* between 300 and 600 m. These benthic shrimps are also the most commonly encountered circumpolar species (Kirkwood 1984). *N. lanceopes* occurs between 595 and 2031 m. This species has not been recorded south of 75°S (Arntz & Gorny, loc. cit.).

Length-frequency distributions alone of the three common shrimp species do not reveal annual cohorts or rate of growth. Combining the development of morphological characters, the growth of female ovaries and aquarium observations (Figure 4), however, it is possible to follow the life cycle of *Chorismus antarcticus*.

From aquarium observations, the size of larvae is known, and the smallest juvenile shrimps caught are assumed to appear one year after hatching. The appendix masculina, the male copulatory organ, starts developing after another year, and the animals mature as males in their second year. With at least four stages of development *C. antarcticus* then reduces the appendix masculina in shape and

Figure 4.

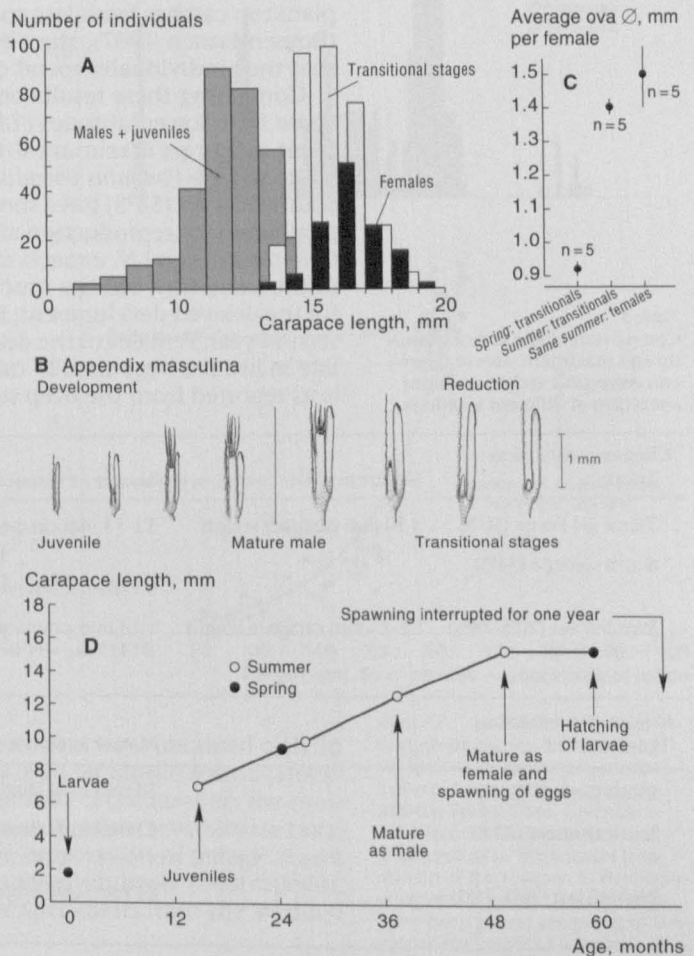
Chorismus antarcticus.

A: Length-frequency distribution during cruise ANT VII/4 (total investigation area, all depths). Most shrimps pass the transitional stage between 13 and 17 mm carapace length (c.l.), but in some animals this stage may last until they reach 19 mm c.l.

B: Development and reduction of the appendix masculina.

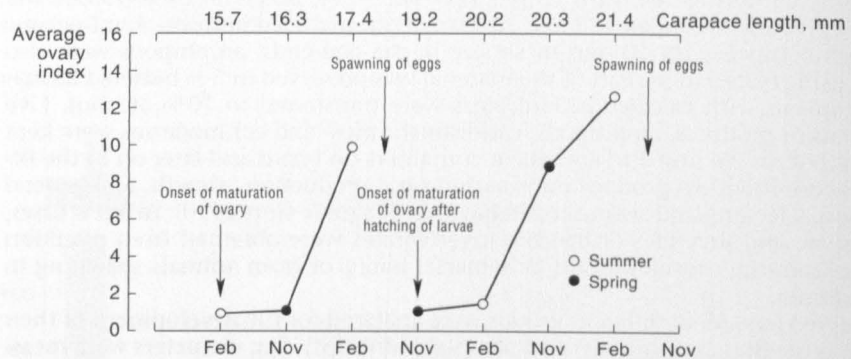
C: Size increase of ova within the ovaries during Antarctic spring and summer. Ovary development starts during the transitional stage and ends with spawning of eggs into the brood pouch in the following summer. Transitional and spawning females are of the same size, about 16 mm c.l.

D: Assumed growth curve derived from approaches A-C and events of the life cycle during the first five years.



size, and oocytes are produced. During their fourth year, most of the shrimps change sex and mature again as females (Gorny 1989). *Notocrangon antarcticus* females seem to mature at an age of 4-5 years, *Nematocarcinus lanceopes* at an age of at least 5-6 years in the Weddell Sea. Large females of *N. lanceopes*, with a total length of 160 mm, may reach an age of 9-10 years.

Figure 5.
Model of the ovary development of *Notocrangon antarcticus*: changes of the ovary index ($100 \times$ wet weight ovary/(wet weight female - (wet weight ovary))) indicate a seasonal increase of ovary development during Antarctic spring (November) and summer (February).



The three common species have patterns of seasonal reproduction. As an illustration, a model for *Notocrangon antarcticus* is shown (Figure 5). During Antarctic spring and summer, ova growth starts and the size of the ovaries increases. Then, at the end of summer (January, February), the females spawn their eggs and become 'berried'. The eggs (mean length 1.6 mm) are attached to the pleopods and breeding continues over a period of ten months until the larvae hatch during Antarctic spring (October, November). The size of first-time spawners was 17 mm carapace length. Spawning is repeated several times in the life cycle. The oocyte sizes of berried females with eggs in an advanced stage (prior to the hatching of the larvae) indicate that *N. antarcticus* spawns only every second year. The same phenomenon was observed with berried females of *Chorismus antarcticus* where the first time spawners measured 14 mm carapace length, and *Nematocarcinus lanceopes* females, spawning for the first time at 27 mm carapace length.

Pelagic larvae are known only of *Chorismus antarcticus* and *Notocrangon antarcticus*. *Nematocarcinus lanceopes* larvae are not known to be pelagic as they were absent in the plankton catches. Although larvae of the two former species were found in plankton catches from late spring (November) until the end of summer (February) (Boysen-Ennen 1987), the advanced stage at hatching in the aquarium indicates that they individually spend only a short time in the pelagic zone.

Comparing these results on *Chorismus antarcticus* and *Notocrangon antarcticus* to those from lower latitudes (Table 1), there is a similar gradient of delayed development and larger maximum sizes towards the polar regions as reported for the boreo-arctic shrimp *Pandalus borealis* (Allen 1959). Lipid investigations of *C. antarcticus* at South Georgia (54°S) have shown that food during the spring-summer period is directly used for reproduction and somatic growth (Clarke 1982). In the Weddell Sea, *C. antarcticus* and *N. antarcticus* seem to use this time of higher primary production in the same way, but the much shorter productive period here may be responsible for the delayed development; furthermore it allows the females to spawn only every second year. Females of the deep-living shrimp *Nematocarcinus lanceopes* spawn very late in life at a large size (27 mm carapace length), however the size at first maturity is as reported from the deep sea off South Africa (Barnard 1950).

Table 1.
Comparison of size at first maturity and maximum sizes of *Chorismus antarcticus* and *Notocrangon antarcticus* at different locations.

<i>Chorismus antarcticus</i>				
Location	Mature as male	Mature as female	Maximum length	Author
Tierra del Fuego (50°S)	≤ 10 mm carapace length	12-13 mm carapace length	14.5 mm carapace length	Yaldwyn 1966
South Georgia (54°S)		≥ 1200 mg wet weight	14.6 mm carapace length	Maxwell 1977 Clarke 1979
Weddell Sea (70°S-78°S)	12-13 mm carapace length	≥ 14 mm carapace length; ≥ 1410 mg wet weight	21.5 mm carapace length	Arntz & Gorny 1991 Gorny, unpubl.
<i>Notocrangon antarcticus</i>				
Location		Mature as female	Maximum length	Author
South Georgia (54°S)		58 mm total length	68 mm total length	Makarov 1970
South Orkneys (62°S)		62 mm total length	84 mm total length 23.2 mm carapace length	Makarov 1970 Maxwell 1977
Weddell Sea (70°S-78°S)		84 mm total length	117 mm total length 27.1 mm carapace length	Arntz & Gorny 1991

Hatching of larvae during times of higher primary production with a short pelagic phase, coupled with *K*-strategic behaviour such as slow growth, deferred maturity and low fecundity, may allow caridean shrimps to live under the conditions of the constantly icy waters of the Weddell Sea.

Amphipods

Gammaridean amphipods are the most abundant and diverse malacostracan crustacean group in the Antarctic benthos with about 600 species belonging to approximately 200 genera and 40 families. However, information about reproduction and growth of Antarctic gammaridean amphipods is available only for five species. The literature reveals that the duration of embryonic development increases exponentially with decreasing habitat temperature (Figure 6).

Embryonic development in the Scotia Arc area mostly lasts between five and eight months (Bregazzi 1973). There are other latitudinal trends similar to those of shrimps, such as increased egg size, lower egg number, smaller number of broods per year, slower growth and delayed age at first maturity in Antarctic species compared with their relatives at lower latitudes (Bone 1972, Bregazzi 1973).

The giant predatory amphipod *Eusirus perdentatus* Chreux, 1912 was found to be a common epibenthic species of the south-eastern Weddell Sea. Females of this species attain approximately 10 cm length and carry very large eggs of a mean size of 2.7 mm diameter in their brood-pouch when they reach a body size of 58 mm. All females between 58 and 66 mm caught during Austral summer carried either eggs of similar developmental stage or fairly well developed embryos or juveniles. Oostegites increase in size with female length and change their morphology. If the length-frequency distribution (Figure 7) represents age classes, an assumption supported by oostegite development, eggs are spawned after 3.5 years. Eggs are assumed to be spawned during the Austral summer, which is supported by observations of females with large oocytes of 1.2 mm in length apparently ready for spawning at the end of February. The embryonic development lasts for a minimum period of 14 months (hatching of juveniles has been observed in late April in the laboratory). After hatching of the juveniles the females either die or moult again, which leads to a decrease in oostegite shape and a loss of setae. However, at a size of 78 mm very few females ($n = 11$) which again bore large setae oostegites were found in the samples suggesting a second breeding period in a small number of females. So far only one female of *Eusirus perdentatus* of 82 mm body length has been found with large yolky eggs of a mean egg diameter of 2.4 mm.

Most females, however, carry only one brood during their life, and according to the length-frequency distribution they may become nearly six years old. The few which carry a second brood probably become eight years old. The males of *Eusirus perdentatus* never grow larger than 65 mm and they die at a size at which the females carry their first brood. A male life-span of approximately 5.5 years is considered a valid estimate.

Molluscs

Data on life history and population dynamics are scarce and were obtained only in shallow water areas around Signy Island (Picken 1980) or in McMurdo Sound (Stockton 1984). A review of the literature and the investigations carried out on the molluscs of the eastern Weddell Sea reveals similar trends as in other invertebrate taxa: long lecithotrophic development, large egg sizes, and suppression of pelagic stages either by brooding (Bivalvia) or by intra-capsular metamorphosis (Gastropoda). However, observations on preserved material and live specimens from the Weddell Sea revealed some new information.

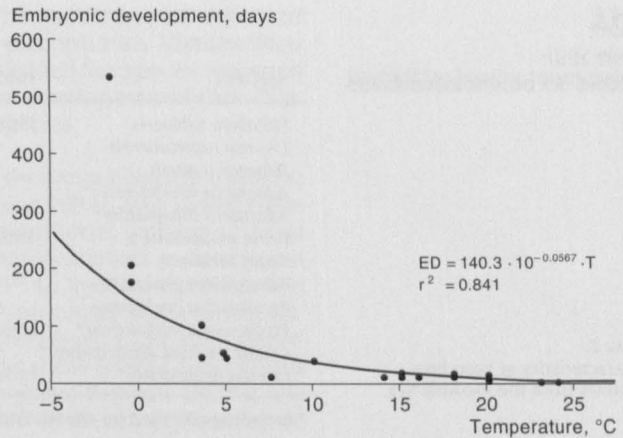


Figure 6. The duration of embryonic development in gammaridean amphipods at different temperatures. Data derived from the literature (Bregazzi 1972, Thurston 1970) and own unpublished results.

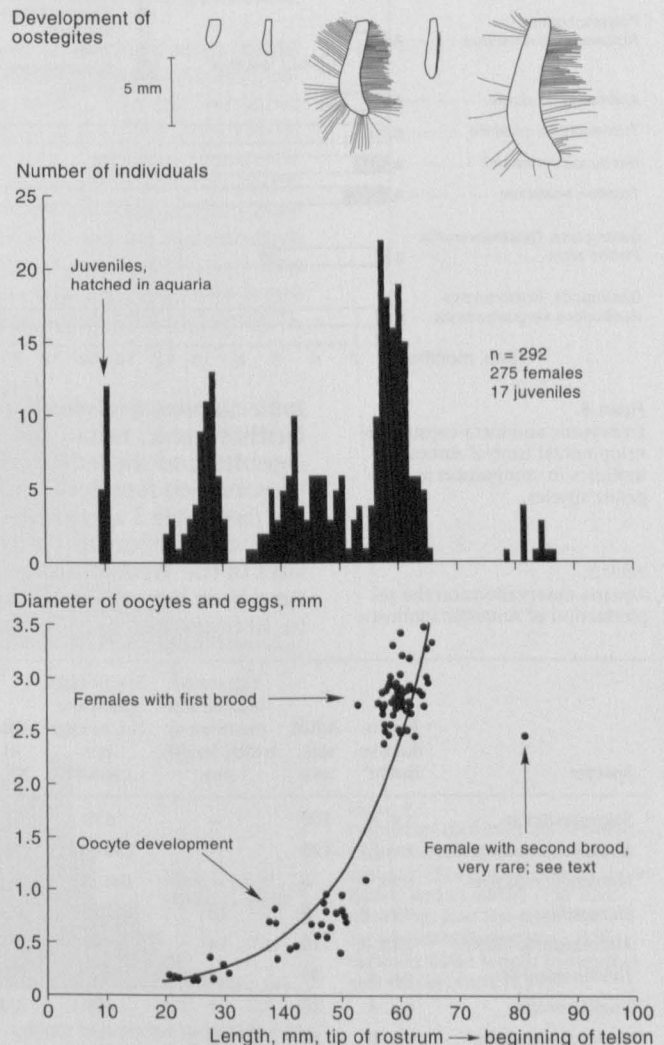


Figure 7. Length-frequency distribution of all females of *Eusirus perdentatus* collected during cruises into the eastern Weddell Sea. Juveniles were hatched in laboratory and measured as in the females from the tip of the rostrum to the beginning of the telson. The oostegites have been placed according to the respective length of females.

Table 2.
Characteristics of brooding
bivalves from the Weddell Sea.

Species	Family	Max. adult shell diameter, mm	Max. no. of shelled juveniles per female	Max. juvenile shell diameter, μ m
<i>Philobrya sublaevis</i>	Philobryidae	15	590	820
<i>Lissarca notorcadensis</i>	"	8	47	540
<i>Adacnarca nitens</i>	"	8	55	900
<i>Adacnarca wandelensis</i> *	"	5	14	540
<i>Adacnarca limopsoides</i> *	"	4	36	700
<i>Kellia nimrodiana</i> *	Kellidae	5	35	580
<i>Kellia simulans</i>	"	9	72	700
<i>Pseudokellya gradata</i> *	"	5	7	660
<i>Pseudokellya cardiformis</i>	"	8	5	740
<i>Ptychocardia vanhoeffeni</i> *	Cyamiidae	10	22	660
<i>Cyamiocardium denticulatum</i> *	"	5	14	740
<i>Lyonsia arcaeformis</i> *	Lyonsiidae	27	301	860

* brooding observed for the first time.

Brooding (*Bivalvia*). Brooding is generally assumed to be a common feature of Antarctic bivalves although this had been proven only for four high Antarctic species (Dell 1972). Table 2 summarizes the results obtained on the Weddell Sea bivalves (ca. 50 species of 16 families).

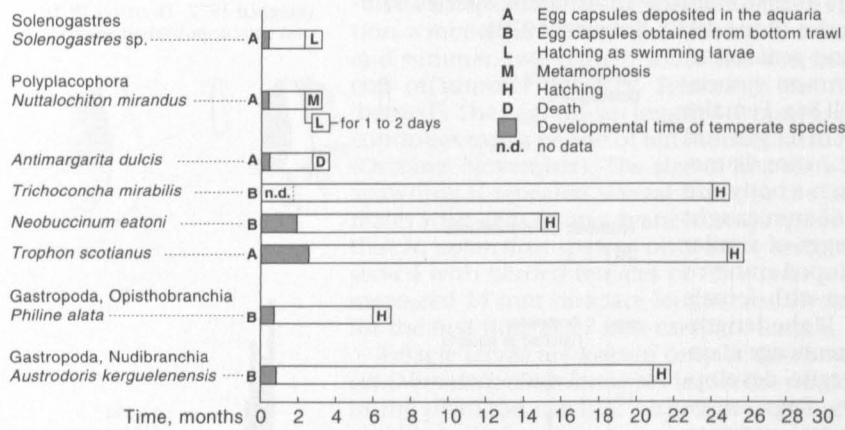


Figure 8.
Embryonic and intra-capsular developmental time of Antarctic molluscs in comparison to temperate species.

Intra-capsular development (*Gastropoda*). All gastropods studied in the aquaria had a lecithotrophic, intra-capsular development. Metamorphosis occurs within the egg capsules, and shelled juveniles are the first free-living stages. The exceptions are the prosobranch families Capulidae and Lamellariidae which have planktotrophic larvae (see Table 3 and Figure 8).

In comparison to temperate species with intra-capsular development the egg sizes of the Weddell Sea gastropods are considerably larger, and the developmental time from depositing the egg capsules till hatching of the juveniles is extended up to 30 times.

Table 3.
Aquadria observations on the reproduction of Antarctic molluscs.

Species	Reproductive mode*	Adult size, mm	Egg mass/capsule size diameter or width/length, mm	No. of eggs spawned/No. of eggs per capsule	Diameter of eggs, μ m	Diameter of eggs of temperate species with intra-capsular metamorphosis	No. of hatchlings per capsule	Height of juvenile shell, mm
<i>Solenogastres</i> sp.	s.e. A	100	-	550	625-775	110-260 (Hadfield 1979)	-	-
<i>Nuttalochiton mirandus</i>	s.e. A	120	-	150-200	920-960	120-420 (Pearse 1979)	-	-
<i>Margarella refulgens</i>	e.m. A	6	-	66; 105	390-460	140-160 (Lebour 1937)	-	-
<i>Margarella</i> sp.	e.m. A	8	13	200	510-560	140-160 (Lebour 1937)	-	-
<i>Antimargarita dulcis</i>	e.m. A	10	14	380	390-490	260-300 (Fretter 1984)	-	-
<i>Torellia mirabilis</i>	e.c. A	35	9	580	420-460	n.d.	25-30	1.9
<i>Torellia smithi</i>	e.c. A	28	7	480	390-450	n.d.	-	-
<i>Neobuccinum eatoni</i>	e.c. B	80	10	-	-	200-300 (Fretter 1984)	1	7.5
<i>Trophon scotianus</i>	e.c. A	75	19	140	900-1.100	480 (Lebour 1937)	110-120	1.7
<i>Trophon shackletoni</i>	e.c. A	45	9	10-11	700-800	480 (Lebour 1937)	10-25	-
<i>Harporvoluta charcoti</i>	e.c. B	75	16	-	-	n.d.	3-5	6.1
<i>Aforia magnifica</i>	e.c. A	150	20	20-30	1.700-1.800	n.d.	-	-
<i>Newnesia antarctica</i>	e.c. B	30	6	-	-	200 (Hadfield & Switzer-Dunlap 1984)	1	1.9
<i>Philine alata</i>	e.m. A	15	16	150; 350	400-600	200 (Hadfield & Switzer-Dunlap 1984)	63	0.5
<i>Austrodoris kerguelenensis</i>	e.c. B	120	30/>50	>2000	1.500-1.900	200-300 (Hadfield & Switzer-Dunlap 1984)	1	2.6

* s.e., spawned eggs; e.m., egg embedded in gelatinous mass; e.c., egg capsule. A, spawned in aquaria; B, obtained from bottom trawl.

Number and size of the juveniles in relation to the size of the female show that the expenditure of energy must be very high for the female. In some cases (e.g. *Lissarca notorcadensis*) the visceral mass of the female is reduced in size, and the juveniles fill up the whole mantle cavity. Large eggs found in the ovaries of several females with juveniles indicate a continuous reproduction. Brooding appears to occur only in 12 species from 4 families. The reproductive mode of the other bivalve species from the Weddell Sea is still unknown.

Lecithotrophic larvae (Solenogastres and Polyplacophora). The lecithotrophic larvae of one unidentified solenogastran species and of the polyplacophoran *Nuttallochiton mirandus* were studied for the first time. The eggs of the Weddell Sea species spawned in the aquaria, are the largest known for both groups. The developmental time (Figure 8) is three to seven times longer than in temperate species.

Planktotrophic larvae (Gastropoda). Except for the larva of the limpet *Nacella concinna* which is confined to low Antarctic shallow waters (White 1984), two larval types ('Echinospira' and 'Limacosphaera') are the only meroplanktonic gastropod larval forms known from the Antarctic Ocean. They were first described as 'unknown prosobranch larvae' by Pelseener (1903) and Simroth (1914). Species identification of both larval types was carried out by SEM analysis of the protoconch ('Echinospira' - *Capulus subcompressus*) and by rearing through metamorphosis ('Limacosphaera' - *Marseniopsis mollis* and *M. conica*), respectively. The latter show special adaptations to the Antarctic environment such as utilisation of embryonic deposits during low phytoplankton concentrations. In aquaria they extended their larval phase up to one and a half year.

Echinoderms (holothurians and echinoids)

Echinoderms are of special interest in the Antarctic since many species have free-living larvae (White 1977, 1984, Pearse et al. 1990). However, most of these are non-feeding benthic or pelagic larvae (e.g. *Porania* spp. or *Acodontaster* spp, Pearse et al. 1990); only a few species have real pelagic feeding larvae (e.g. *Odontaster validus* and *Sterechinus neumayeri*; Pearse et al. 1986, 1990).

In the south-eastern Weddell Sea no pelagic echinoderm larvae have been found to date. Detailed studies have been made of two holothurians, *Psolus dubiosus* (Ludwig & Heding 1935) and *Ekmocucumis steineni* (Ludwig 1898), and the echinoid *Sterechinus antarcticus* (Gutt 1991, Gutt et al., in press, Brey & Gutt 1991, Brey 1991).

The two holothurians are predominantly sessile suspension feeders living on the Antarctic shelf. The ovaries of both species contain 2 or 3 cohorts of oocytes of differing developmental stage. However, the gonads of *E. steineni* are filled with mature eggs or sperm in late winter (October) and mostly devoid of mature reproductive products in summer (January/February) whereas no such seasonal difference has been found for *P. dubiosus*. In addition, juveniles of the latter species which are brooded between the tentacles do not exhibit seasonal differences in size (Figure 9).

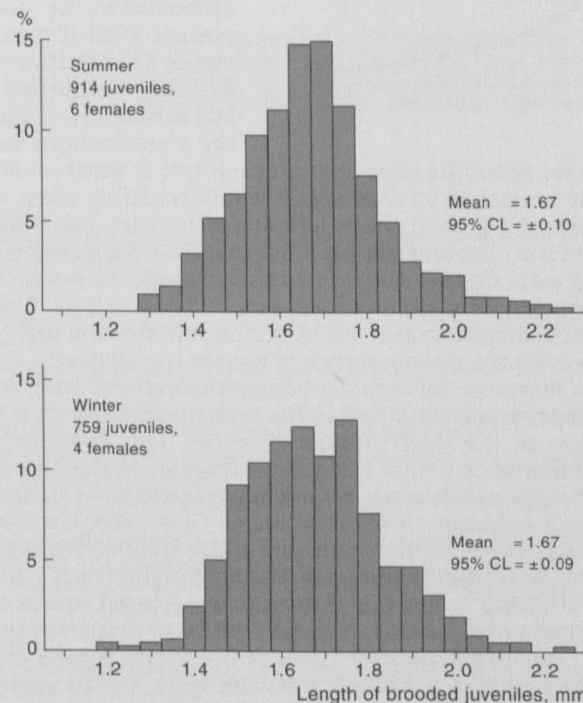


Figure 9. Frequency distributions of brooded juveniles of *Psolus dubiosus* in summer (914 juveniles from six females) and in winter (759 juveniles from four females). No significant difference ($p = 0.05$) between mean length in summer and winter (Gutt 1991).

Gonad maturation in the two holothurian species seems to last up to 24 months. Up to 400 mature eggs were produced per g body weight in *E. steineni* and up to 40 per g body weight in *P. dubiosus* (wet weight of females 1-9 g in either case). Egg sizes are large; mature eggs in the ovaries measure up to 1.0 mm diameter in *E. steineni* and up to 1.3 mm in *P. dubiosus*. Duration of embryonic development is not exactly known but is at least several months.

Up to now it has not been possible to estimate growth although the calcareous sclerites exhibit distinct growth rings. Maximum length found was about 12 cm for *E. steineni* and about 6 cm for *P. dubiosus*.

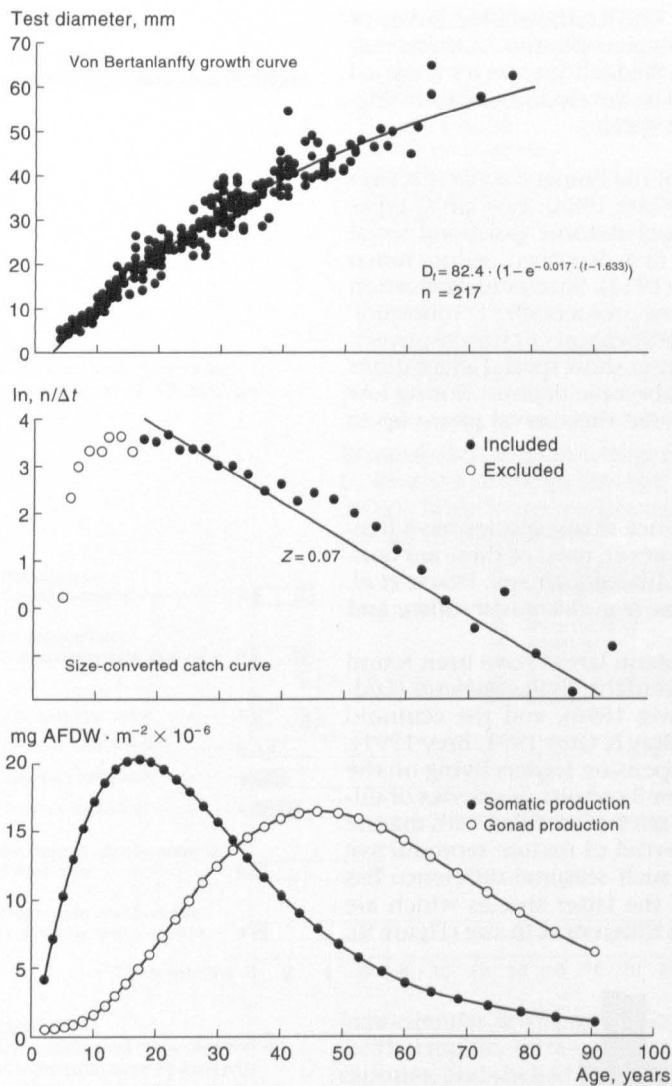


Figure 10. *Sterechinus antarcticus*: Von Bertalanffy growth, size-converted catch curve, and age-specific distribution of somatic and gonadal production in the population.

have about the same annual amplitude as waters at 600 m depth in our high Antarctic investigation area which is influenced by 'deep warm water' from the Weddell Sea (cf. Figure 2). The regularity with which this inflow occurs throughout the year is surprising and implies a tidal rhythm. Shallower waters (≈ 300 m) corresponding to areas close to the continental ice edge, however, are characterized by extremely constant temperatures between -1.6 and -1.8 °C during most of the year and wider oscillations around -1.5 °C during summer and early autumn. These coincide largely with the disappearance of the sea ice cover and the pulse of primary production in that area. This apparent difference between shallower-shelf and deeper-shelf (and slope) areas should affect the fauna; furthermore, it makes a uniform characterization of the 'high Antarctic' versus 'low Antarctic' conditions difficult. Benthic biomasses are high in both these areas (Mühlenhardt-Siegel 1988, Voss 1988), but there is a shift towards a higher proportion of epifaunal suspension feeders in the high Antarctic (Arntz *et al.* 1990, Gutt 1988, Gutt & Vogel 1988, Gerdes, unpubl. data). High benthic biomasses in the Weddell Sea as compared to other oceans must not be considered a consequence of high primary production in the euphotic zone but rather a result of slow growth, delayed sexual maturity and longevity of the fauna (White 1984) combined with low predation pressure (DeBroyer 1977).

Due to the pack-ice cover of the south-eastern Weddell Sea throughout most of the year material is only available from Austral summer and spring. In many cases we have no direct indications as to what happens in winter, e.g. cessation of growth or interruption of gonad development. For this reason, a combination of different approaches is necessary, including the analysis of ovary development, the study of morphological characteristics and their changes with increasing size, aquarium observations on live specimens and their offspring, and length-frequency distributions combined from several expeditions. However, a synthesis of this approach yields interesting features.

All Weddell Sea macrobenthic fauna investigated to date show some adaptation in their life cycles to this environment, but the degree of their dependence on the restricted period of primary production and sedimentation of organic matter differs

Sterechinus antarcticus is the predominant regular sea urchin on the lower shelf and slope of the south-eastern Weddell Sea. Between 100 and 1200 m water depth, abundance and biomass of this species are about $0.02 \text{ ind} \cdot \text{m}^{-2}$ and $5 \text{ mg AFDW} \cdot \text{m}^{-2}$ (Brey & Gutt 1991). *S. antarcticus* shows distinct growth lines in the half pyramids of the Aristotle's lantern which were interpreted as annual growth marks. If this assumption holds true, a von Bertalanffy growth function can be fitted to age-diameter data (Figure 10), indicating that these echinoids need 50 years to grow to a diameter of 40 mm and may reach a maximum age of about 75 years (Brey 1991).

From the growth curve and a representative size-frequency sample ($n = 1113$, based on 92 trawl hauls), annual total mortality of *S. antarcticus* was estimated to $Z = 0.07$ (Figure 10), annual P/B ratio and production (somatic and gonadal) were estimated to $0.12 \cdot \text{y}^{-1}$ and $0.6 \text{ mg AFDW} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$, respectively (Brey 1991).

Discussion

In comparing environmental data for the south-eastern Weddell Sea with data from the South Orkney Islands (60°S) (Clarke *et al.* 1988), it appears that differences exist in a shortening of the productive period rather than in the absolute lowness of water temperatures and the range of their oscillations. At Signy Island the productive period, characterized by strong diatom blooms, lasts for 10-12 weeks from about mid-December to February. In the south-eastern Weddell Sea it is considerably shorter as is shown by the sudden and pronounced difference in the flux rates at the beginning of December 1989 (Figure 3). This is also confirmed by earlier investigations (Nöthig 1988, v. Bodungen *et al.* 1988). Sea surface temperatures near Signy oscillate between ≈ -2 and >0 °C (Clarke, loc. cit.), showing a pronounced seasonal pattern. However, they

with species. One strategy (applied e.g. by the shrimps *C. antarcticus* and *N. antarcticus*, and the holothurian *E. steineni*) uses the improved food conditions in Antarctic summer both for gonad development and growth, and releases the larvae one year later when conditions are favourable again. The shrimp larvae are well developed when they are released; those of *N. antarcticus* hatch as a Zoea 2 stage. The two shrimp species living in shallower water actively migrate to shallow parts of the shelf, where the larvae are provided with a maximum of food (in terms of quality and quantity), and also the females of the deep-water shrimp *N. lanceopes* migrate into shallower water to release their larvae which may remain close to the sea-floor. There is evidence that even this deep-water species uses the short plankton bloom to provide its larvae with suitable food. A case where the disconnection from the production cycle has been achieved is the holothurian *P. dubiosus* which reproduces non-seasonally, achieving this independence by fewer, larger eggs and brood protection. A number of bivalves (e.g. *Philobrya sublaevis*, *Lissarca notorcadensis*) behave very much the same way. Independence is even more striking in the case of the Limacospaera larva of the gastropod *Marseniopsis* spp. which is able to alternate between planktotrophic feeding and subsistence on its own reserves. Finally, most of the amphipods are almost completely disconnected from the high Antarctic seasonal cycle as they are scavengers, predators, or detritus feeders which brood their young, and different species release their juveniles into the environment as fully developed organisms throughout the year (own unpubl. results). There may be a change in feeding habits with growth, e.g. from detritus feeding to scavenging, but larval stages which essentially need fresh phytoplankton are thus avoided. Brooding highly-developed young in a brood pouch is a long-established character not only of amphipods but also of the peracarid group in general (Hennig 1986), and may have contributed considerably to the success of these crustaceans in the Antarctic.

The present paper seems to indicate that trends described in the literature for a gradient from low latitudes to low Antarctic regions continue into the high Antarctic. These are features such as long gonad and embryological development, reproduction late in the life cycle and only once to a few times per individual, suppression of free-living larval stages, brood protection, slow growth and longevity. Some cases described in this paper are extremes on their respective scales but more data are necessary in order to determine whether this holds true in each individual case.

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