Antarctic Isopoda (Crustacea: Peracarida): Stress in a polar environment?

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Introduction

Isopods are an important element of the crustacean fauna of the Southern Ocean. While the large decapods that are so common in shallow habitats of warmer seas are absent Antartica - with the exception of a few species of shrimps (Arntz & Gorny 1991) - brooding peracarids, especially the Amphipoda and Isopoda, occur with a large number of species nearly everywhere, from the sub-fast-ice communities to the deep-sea benthos. Today about 230 species of isopods are known from the continental shelf of Antarctica. This diversity suggests that cold might per se be no stressing factor for poikilotherm animals. Nevertheless the polar climate seems to be a disadvantage for many taxa. Most fish families do not occur in the Southern Ocean, several taxa of Malacostraca, Mollusca, Echinodermata etc. are absent. While most terrestrial animals obviously can not survive on the Antarctic continent because of the absence of food, the marine mammals and birds need adaptations to reduce and compensate the loss of heat and the marine invertebrates must adapt to the extreme seasonality and the slowness of biological processes at low temperatures. Studies on the biology and systematics of the Isopoda help to understand the peculiarites of this ecosystem.

Environmental conditions

The physical properties of the Southern Ocean are rather uniform throughout the year, the temperature fluctuating between about +1 and -2°C, the salinity between 34 and 35 ppm (e.g. Hellmer & Busch 1985). A pronounced vertical stratification does not exist, large changes in temperature that serve as barriers in other oceans are absent. Very important is the seasonality of light intensity and of the extension of the sea ice. Phytoplankton blooms are rich, but restricted to a few weeks per year (e.g. von Bodungen et al. 1988). Secondary production depends entirely on these blooms, the input of terrigenous organic material is of no importance, virtually absent in most coastal areas (review e.g. in Hempel 1985).

Peculiarities of the Antarctic benthos-

Species diversity is unexpectedly high in taxa as Porifera, Polychaeta, Amphipoda, Isopoda, Bryozoa and Acidiacea, distinctly higher than in the Arctic Ocean (Knox & Lowry 1977). This is one reason why research on benthic ecology is so difficult and why we are very interested in the

compilation of taxonomic monographs, for which only specialists remain as potential authors. The reasons for the high diversity discussed in literature are the age of the ecosystem, the predictable seasonality and relative stability of climatic conditions, which allow evolutionary adaptation (e.g. Lipps Hickman & Speciation might also be a consequence of low mobility and slow reproduction. An indication for the existence of this mechanism is polymorphism in widely distributed species (e.g. Wägele 1986) (Fig. 1).

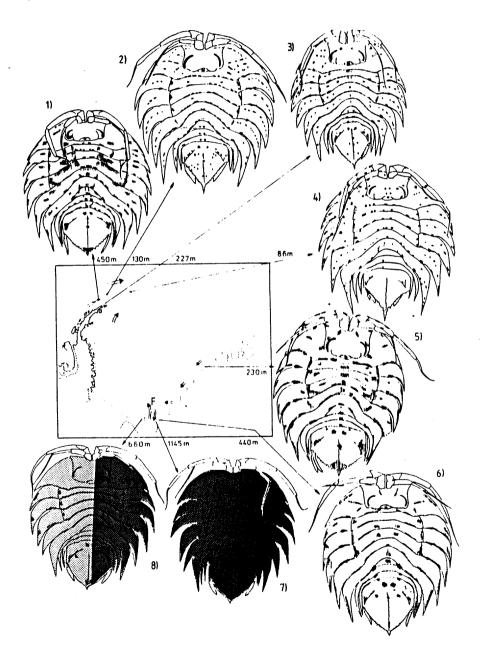
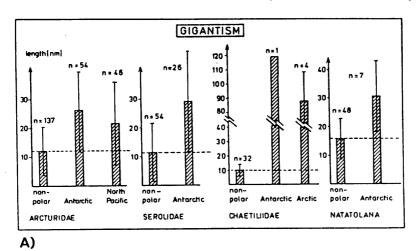


Fig. 1: Polymorphism of Ceratoserolis trilobitoides. Within local populations morphology varies little (from Wägele 1986).
F: Filchner depression; arrows: currents

Most invertebrates are endemic for Antarctica (summary in Brandt 1991), probably also a consequence of the age and of the singular climate of the ecosystem.

The trophic relationships and productivity in the benthic communities are still poorly known. Standing stock is high (e.g. Jazdzewski et al. 1987), but hitherto observed cases of slow growth suggest that this biomass has accumulated in many years and has a low turnover. Interestingly suspension feeders (sponges, bryozoans, hydrozoans, dendrochirotid are dominant in terms of biomass holothurians) continental shelf of many areas (e.g. Voß 1988); and are by specialized Amphipoda, Asteroidea, Nudibranchia (e.g. Coleman 1989, 1991, Dayton et al 1974, H. Wägele 1989, 1990). Another frequent mode of nutrition is necrophagy (e.g. Pressler 1986): a large number of species can be collected with baited traps. In deeper water an important source of energy must be detritus originating from sedimentation. This depends of the seasonal productivity of phytoplankton and has been studied e.g. in the Bransfield Street (von Bodungen et al. 1987).



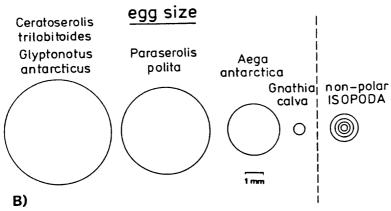


Fig. 2: A: Average maximum length of isopod taxa from Antarctica in comparison with other regions. Note that species from colder oceans (Antarctica, North Pacific, Arctic) are larger than other species.

B: Egg size of Antarctic isopods in comparison with other species.

Biology of Antaractic Isopoda

When collecting specimens from trawl samples or by SCUBA diving one of the first impressions is that many species of invertebrates attain an unusual large size. Among isopods the largest species of the Paranthuridae, Chaetiliidae, Arcturidae, Serolidae und Gnathiidae live in Antarctica. To show that gigantism is a rule and not a subjective impression, the average maximal length of non-polar species can be compared with that of polar species (Fig. 2). The correlation between large size and low temperature even has an effect within populations of a single species: southern populations of Ceratoserolis trilobitoides have larger (but fewer) eggs than populations from Subantarctic localities (Wägele 1987). This is accordance with Thorson's rule (Thorson 1936, 1950).

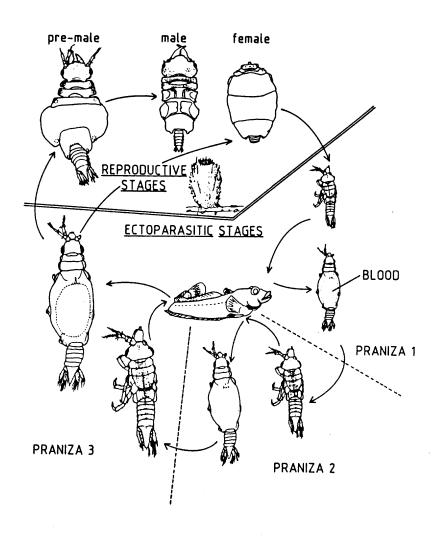


Fig. 3: Life cycle of the Antarctic fish parasite Gnathia calva (after Wägele 1988).

It can be expected that low temperatures induce a retardation of all biological processes. The study of life cycles is logistically difficult, but some data support the suspicion that life in cold water is slow. While isopods of the North Sea usually live for 1 year, summer generations only for few months, the life cycles of Antarctic species take much longer.

The large valviferan Glyptonotus antarcticus is probably sexually mature after 5 or more years; females of Paraserolis polita produce the first brood after 28 months, while the larger serolid C. trilobitoidas needs 3.5 to 4 years, Gnathia calva 3 - 4 years (Fig. 3), Aega antarctica more than 10 years to mature and spawn (Wägele 1987, 1990). In view of the comparatively lower number of eggs it is not surprising that the production of eggs per minimum generation time is very low in Antarctic species (Table 1). Slow growth and low fecundity indicate that Antarctic populations must have a much lower regenerative potential than populations of related species in warmer seas.

In this context it is interesting that metabolic adaptions to cold water seem to be absent, at least according to respiration measurements (e.g. Luxmoore 1984). Anti-freeze protection has not been studied.

In view of this slow life cycles the gigantism of many species is paradoxical. Faster reproduction should be possible when maturity is reached at a smaller size, coldwater species should have a selective advantage with a reduced body size. Obviously the ecosystem favours K-selection: concurrence is in a stable environment more important a factor than the reproductive rate. Many Antarctic species have the typical features of K-selected organisms: longevity, large body size, low reproductive rates (see e.g. Pearse 1969, Ralph & Everson 1972, Arntz & Gorny 1991). Slowness as a physiological effect of low temperatures can not easily be discerned experimentally from evolutionary adaptations to a stable environment.

Genetic adaptations need time to evolve. This time was available in the Southern Ocean. Polar conditions exist for at least 25 m.y. since the formation of the circumpolar current, which isolated Antarctica thermically (and faunistically) (Kennett 1977, Barker et al. 1988). Fluctuations of the extension of the ice sheet must have had an effect on the availability of food and space, but not on water temperature. It is obvious that the species diversity, the peculiarities of morphology and life cycles are the result of a long period of evolution in a polar environment. Temperature stress in the sense of factors that reduce fitness within this ecosystem has not been detected; those species that survived the cooling of the Southern Ocean evolved to a highly specialized, adapted fauna.

That such a speciation really took place has recently been shown (Wägele, in press). A phylogenetic - biogeographic

analysis revealed that the Antarctic Serolidae evolved in situ, isolated of populations of the neighbouring continents (South America and Australia). Offsprings of an older Gondwana fauna still survive in a disjunct area of cold-temperate climate (tips of southern continents), a distribution that must be explained with vicariance by continental drift.

Table 1 Average number of eggs produced per day of minimum generation time by 1000 females

(bold = Antarctic species, italics = stygobionts)

(for references see Wägele 1987, 1988, 1990)

species	eggs, day
Asellus hilgendorffi (25°C) 780
Idotea baltica (Sommer	•
Idotea baltica	580
Idotea baltica (Winter	
Idotea chelipes (Somme	
Asellus hilgendorffi (•
Asellus aquaticus	290-300
Idotea chelipes (Winte	r) 282
Idotea chelipes (Somme	r) 259
Glyptonotus antarcticu	s 210
Idotea chelipes (Winte	r) 177
Sphaeroma hookeri	160
Asellus aquaticus	150-160
Saduria entomon	132
Dynamene bidentata	120-130
Asellus aquaticus	82
Idotea pelagica	80
Excirolana braziliensi	s (Sommer) 79
Gnathia calva	71
Eurydice pulchra (Wint	er) 61
Limnoria lignorum	55
Cyathura carinata	55
Excirolana braziliensi	s (Winter) 52
Gnorimosphaeroma insul	are 44
Proasellus cavaticus	21- 30
Serolis polita	28
Ceratoserolis trilobit	oides 11

Aega antarctiaStenasellus virei

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