Growth, production and productivity of the Arctic sympagic amphipod *Gammarus wilkitzkii*

M. Poltermann*

Alfred Wegener Institute for Polar and Marine Research, Columbusstrasse, 27515 Bremerhaven, Germany

ABSTRACT· The amphipod *Gammarus wilkitzkii* Birula is one of the major macrofauna species permanently inhabiting the subsurface of Arctic sea ice. It reaches an age of 5 yr with a measured maximum body length of 62.3 mm. The growth of this species is best described by the Gompertz growth function, which gives asymptotic final lengths of 69.2 and 64.6 mm respectively for males and females. Individuals of 46 to 52 mm length show the highest individual production, whereas the length class 31 to 36 mm is the most productive within the investigated population. The somatic P/B ratio (productivity) of the investigated *G. wilkitzkii* population (0.398 yr^{-1}) is low compared to other amphipod species from boreal and polar regions. This is discussed with respect to the permanent low water temperature, the low energy content of the food, and the high mortality of juveniles under Arctic sea ice. The overall growth performance, Ψ, of *G. wilkitzkii* is not significantly different from other *Gammarus* species living under boreal conditions. It is therefore assumed that the growth is predominantly determined genetically rather than by environmental conditions.

KEY WORDS: Sea ice · Sympagic amphipod *Gammarus wilkitzkii* · Growth · Overall growth performance · P_s/B ratio · Arctic

INTRODUCTION

Arctic sea ice represents a very dynamic environment which is, among other things, characterised by permanently low temperatures, highly variable salinities and limited and only seasonally available food sources (Carey 1985, Melnikov 1997). Evolutionarily, only a few macrofauna species (> 5 mm) have adapted to life in these unstable and extreme conditions. In terms of biomass *Gammarus wilkitzkii* Birula is the dominant amphipod species permanently inhabiting the underside of Arctic sea ice (Gulliksen & Lønne 1989, Lønne & Gulliksen 1991a,b,c, Melnikov 1997, Poltermann 1998). The biomass can reach 10.12 g m^{-2} with densities of up to 368 ind. m^{-2} (Poltermann 1997). Feeding on ice-produced material and in turn preyed upon by pelagic predators (polar cod) *G. wilkitzkii* represents a key species in the ice-based Arctic food web (Poltermann 1997, 1998, Werner 1997). Earlier studies showed that *G. wilkitzkii* is physiologically well adapted to the high osmotic stress and the very low temperatures under the Arctic sea ice (Aarset & Aunaas 1987, 1990, Aarset 1991). No information, however, is available yet concerning possible adaptations in growth. The present investigation is focused on the analysis of growth and productivity of *G. wilkitzkii*, and a comparison with other amphipod species living under similar or different environmental conditions.

MATERIAL AND METHODS

Sampling of the sympagic amphipod *Gammarus wilkitzkii* (Fig. 1) was carried out in summer 1994 north-west of Franz Josef Land (82° 09' N, 42° 02' E; 82° 23' N, 40° 54' E; 81° 51' N, 41° 17' E) and in the southern part of the archipelago (80° 20' N, 52° 41' E) (Fig. 2). Ice thickness varied from 0.2 to 2.70 m; ice cover was about 40 to 50 %, with a mixture of multi- and first year ice. The ice underside was relatively smooth at all sampling sites; no large pressure ridges were present. Because of the origin of older sea ice,

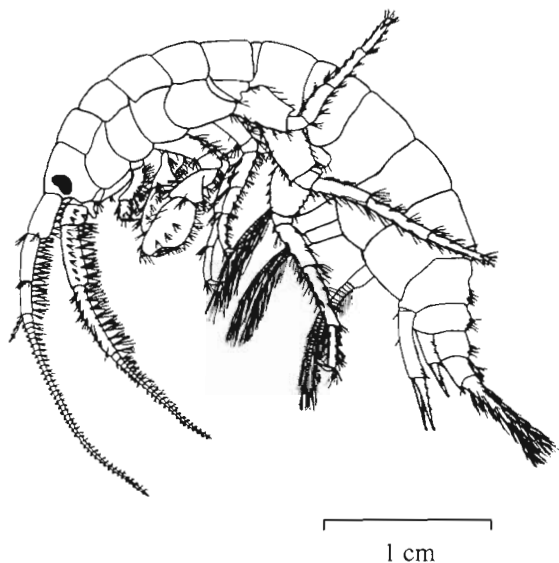*Present address: Norwegian Polar Institute, 9296 Tromsø, Norway. E-mail: michael.poltermann@npolar.no

Fig. 1. The Arctic sympagic amphipod *Gammarus wilkitzkii* Birula 1897

1 cm

which generally drifts through the Franz Josef Land area from the Arctic Basin (Abramov & Zubakin 1993), the amphipods from both sampling areas are considered as 1 population. A diver-operated electric suction pump (Lønne 1988) in combination with a randomly placed standard frame (25×25 cm) were used to remove all animals from the ice underside, brine channels and melting holes. The amphipods were immediately preserved in 4% buffered formaldehyde. Body length of the amphipods was measured along the dorsal line from the tip of the rostrum to the end of the telson using a video-based image analysing system (VIDS III, Mobrey Bestobell) with a measurement pre-

cision of 0.001 mm. For determination of the wet weight (WW) the amphipods were gently blotted and weighed to the nearest 0.001 g. Ash-free dry weight (AFDW) was calculated using the conversion factor WW:AFDW = 6.47, according to Rumohr et al. (1987). All individuals with oostegites were considered as female, those without oostegites as male, and those both without oostegites and smaller than the smallest female as juvenile. The age of *G. wilkitzkii* was estimated by length frequency distribution at 1 mm intervals according to Grant et al. (1987). Differences in the length-weight relation between males and females were tested by ANOVA (95% significance level).

For growth analysis 2 growth models were tested:

von Bertalanffy growth model
$$L_t = L_\infty \cdot \{1 - \exp[-k \cdot (t - t_0)]\} \tag{1}$$

Gompertz growth model
$$L_t = L_\infty \cdot \exp\{-\exp[-k \cdot (t - t_0)]\} \tag{2}$$

where L_t = length, L_∞ = asymptotic final length, k = growth constant, t_0 = age at length 0 and t = age.

Estimation of the growth parameters k and L_∞ was performed by a Ford-Walford-Plot (Ricker 1975):

von Bertalanffy growth model
$$L_{t+1} = a + b \cdot L_t \rightarrow k = -\ln(b); \; L_\infty = a/(1 - b) \tag{3}$$

where a and b = constants

Gompertz growth model $\hspace{3cm}$ (4)
$$\ln(L_{t+1}) = a + b \cdot \ln(L_t) \rightarrow k = -\ln(b); \; L_\infty = \exp[a/(1 - b)]$$

Annual somatic production (P_s) and productivity (P_s/B ratio) of *Gammarus wilkitzkii* were calculated by applying the weight-specific growth rate (WSGR) method, which uses the length-weight relation
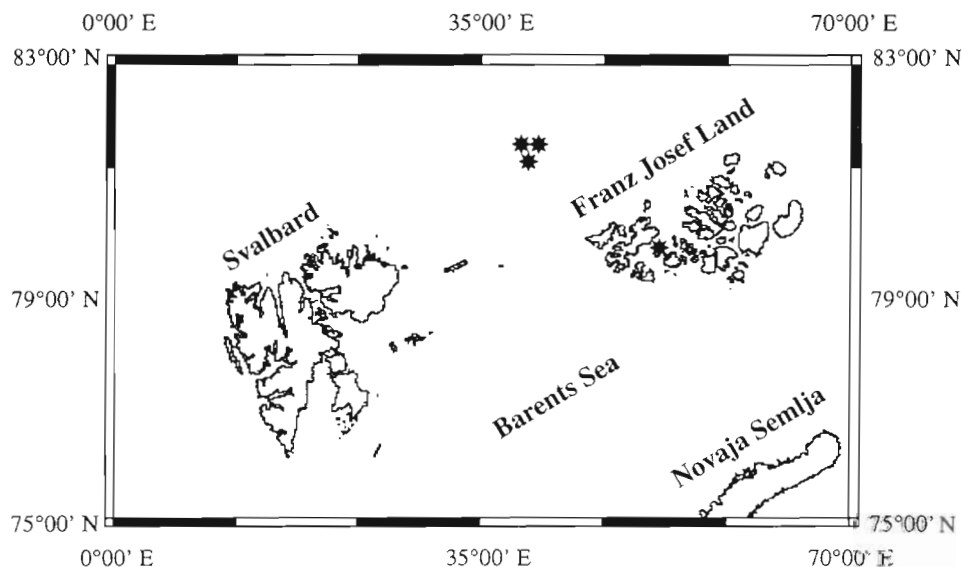

Fig. 2. Sampling area of *Gammarus wilkitzkii* carried out in summer 1994 on Franz Josef Land and north-west of the archipelago

$(W = a \cdot L^b)$, length frequency distribution, and growth function (Crisp 1984):

von Bertalanffy growth model
$$\text{WSGR}_i = b \cdot k \cdot (L_\infty - L_t) \qquad (5)$$

Gompertz growth model
$$\text{WSGR}_i = b \cdot k \cdot \ln(L_\infty/L_t) \qquad (6)$$

where i = length class (LC) i and WSGR_i = weight-specific growth rate per LC_i.

P_s for each length class was calculated according to the equation:

$$P_{s_i} = \text{WSGR}_i \cdot W_i \cdot N_i \qquad (7)$$

where W_i = mean individual weight at mean length of the LC_i and N_i = number of individuals per LC_i.

The sum of P_s of each length class (P_s) yields the total somatic production of the investigated population:

$$P_s = \sum P_{s_i} \qquad (8)$$

The annual P_s/B ratio was determined as follows:

$$P_s/B = \sum P_{s_i}/\sum W_i \cdot N_i \qquad (9)$$

To avoid an overestimation of the somatic production of *Gammarus wilkitzkii* by the highly variable gonad weight of the females, only the length-weight relation of males was used for the calculation.
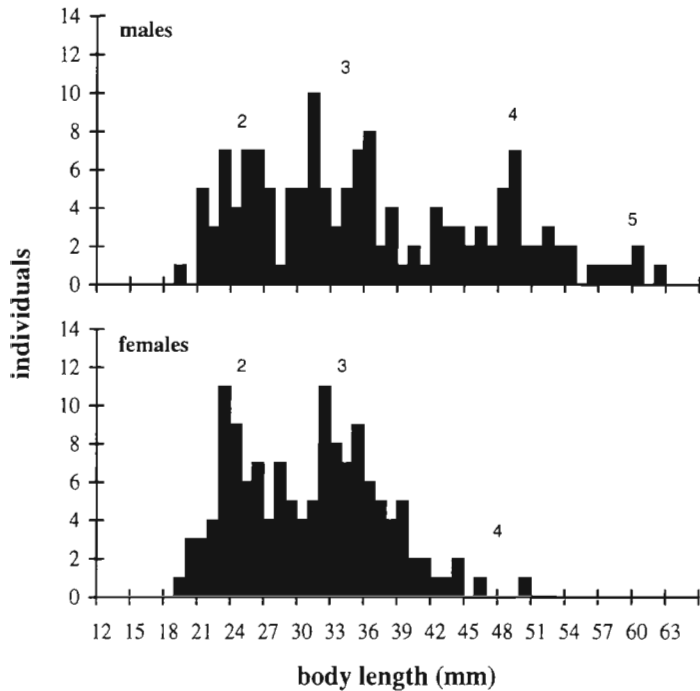

Fig. 4. Length-weight relation of *Gammarus wilkitzkii* (males: n = 129; females: n = 132)

The overall growth performance, Ψ, was calculated according to Brey (1999):

$$\Psi = \log(M_{max}/A_{max}) \qquad (10)$$

where M_{max} = maximum body weight (kJ) and A_{max} = maximum age (yr).

RESULTS

Length frequency distribution and age estimation

The length frequency distribution of the investigated *Gammarus wilkitzkii* population allowed a distinction to be made between a maximum of 4 cohorts for males and 3 cohorts for females (Fig. 3). Considering the 2 identifiable cohorts of juveniles (see Fig. 6a) and only 1 reproduction cycle yr^{-1} (Steele & Steele 1975) the maximum age of this species is estimated as 5 yr for males and 4 yr for females. The smallest female was 19.5 mm long, the largest 49.7 mm and the largest male 62.3 mm. The smallest free-living juveniles were 3.2 mm long.

Growth, production and productivity

The length-weight relation of *Gammarus wilkitzkii* was significantly different for males and females (ANOVA, p < 0.05) (Fig. 4). For the same body length, females showed a higher WW than males.

Growth of *Gammarus wilkitzkii* was described best by the Gompertz growth function, yielding L_∞ of 69.2 and 64.6 mm for males and females, respectively. The Gompertz growth function estimates the maximum age

Fig. 3. Length frequency distribution of *Gammarus wilkitzkii* (males: n = 144; females: n = 134). Age estimation (given in years above bars) is based on cohorts
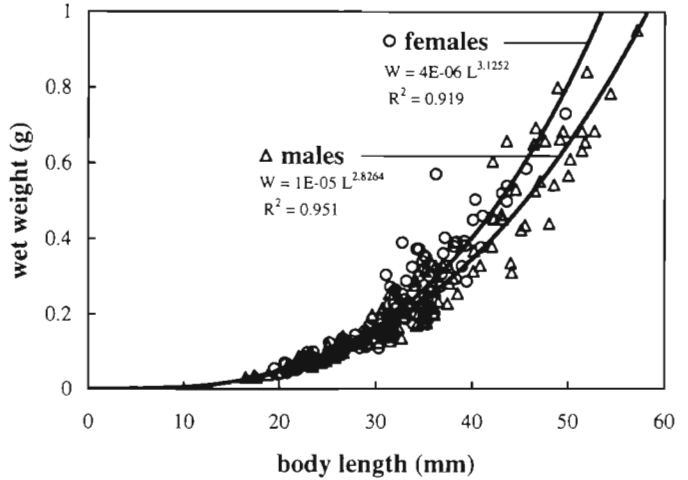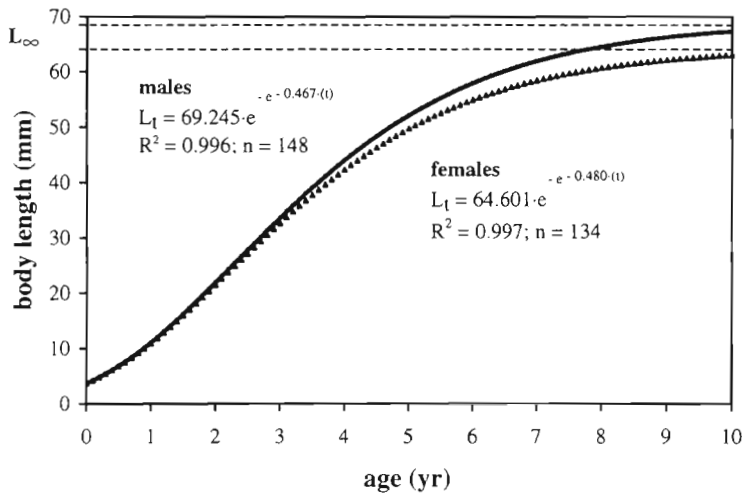
Fig. 5. Gompertz growth function for the Arctic sympagic amphipod *Gammarus wilkitzkii* (L_∞ = asymptotic final length)

attained by *G. wilkitzkii* to be about 9 to 10 yr (Fig. 5). Based on this model the ages of the largest male and female investigated were calculated to be 4.8 and 3.1 yr, respectively. The asymptotic lengths calculated by the von Bertalanffy growth function showed negative values (–246.0 and –3728.6 mm for males and females, respectively) and therefore this model was unusable.

Fig. 6a shows the length frequency distribution of the investigated population of *Gammarus wilkitzkii*, with length classes 11 and 23 mm including the highest number of individuals. Amphipods with a body length of 46 to 52 mm showed the highest individual somatic production, with an increase of 0.019 g AFDW yr^{-1} (Fig. 6b), whereas the length class 31 to 36 mm were most productive within the investigated population (Fig. 6c). The calculated P_s/B ratio for *G. wilkitzkii* was 0.398 yr^{-1} with a total somatic production of 3.601 g AFDW yr^{-1}. In the Franz Josef Land area with a mean biomass of 10.12 g WW m^{-2} (Poltermann 1997), total somatic production sums up to 0.623 g AFDW m^{-2} yr^{-1}.

DISCUSSION

The maximum age of *Gammarus wilkitzkii* is estimated to be at least 5 yr. Thus *G. wilkitzkii* can be regarded as an amphipod species with a long lifetime (Gurjanova 1951).

Age estimations for the largest amphipods, derived from both the length frequency distribution and the Gompertz growth function, correspond well for males (both about 5 yr); for females, the observed variability in age estimation (4 and 3 yr, respectively) might be due to characteristics of the reproduction cycle. Females are carrying eggs and juveniles in brood

pouches for at least half the year (Barnard 1959, Melnikov 1997), releasing the juveniles in April and May (Melnikov 1997, Poltermann 1997). They do not moult during this time and hence exhibit reduced growth. Considering 2 to 3 possible reproduction cycles during a female's lifetime (Poltermann 1997), growth can be reduced for a total period of at least 1 to 1.5 yr. This explains the high individual variability in growth and age estimation of females.

Only 3 other amphipod species, the large *Bovallia gigantea* (Bone 1972) and *Eusirus perdentatus* (Klages 1993), both from Antarctica, and the deep-sea amphipod *Eurythenes gryllus* (Ingram & Hessler 1987), are known to have lifespans similar to or exceeding that of *Gammarus wilkitzkii*. Living under comparable environmental conditions (low temperature, strong seasonality in food availability) they reach an age of 5, 8 and 9 yr, respectively. As reported by Arntz et al. (1994), species living in environments with permanently low temperatures show an increase in body size and lifespan compared to species in temperate waters. *G. wilkitzkii* can be regarded as a further example of this tendency. In comparison, the systematically closely related species *G. oceanicus*, which lives in temperate waters, reaches a body size of only 38 mm and has a lifespan of about 2.2 yr (Luppova 1991).

One ecological significance of a long lifespan can be to guarantee the reproductive success of a species (Sainte-Marie 1991). Once a year, *Gammarus wilkitzkii* produces a relatively high number of large eggs (149 to 187; $\varnothing$ 0.7 to 0.8 mm; Steele & Steele 1975, Poltermann 1997). However, to accumulate sufficient energy for egg production from the food resources available under the sea ice during the short Arctic summer is presumably difficult. Hence, to secure the survival of the population, several reproduction cycles are necessary, which is guaranteed by the long lifespan of *G. wilkitzkii*.

Gammarus wilkitzkii exhibits a low growth rate, needing 5 yr to reach its maximum size. This is strongly supported by the fact that the oxygen consumption rates of this species are the lowest measured among Arctic and subarctic benthic amphipods (Werner et al. 1999). A low growth rate is also reported to be typical for organisms inhabiting polar regions (Arntz et al. 1994). Limited food availability and a low basic metabolism due to the permanently cold water temperatures are regarded as main factors responsible for the slow growth of polar organisms (Kanneworff 1965, Bone 1972, Bregazzi 1972, Rakusa-Suszczewski 1972, Perry 1975, Sagar 1980, Clarke 1988, Brey & Clarke 1993).
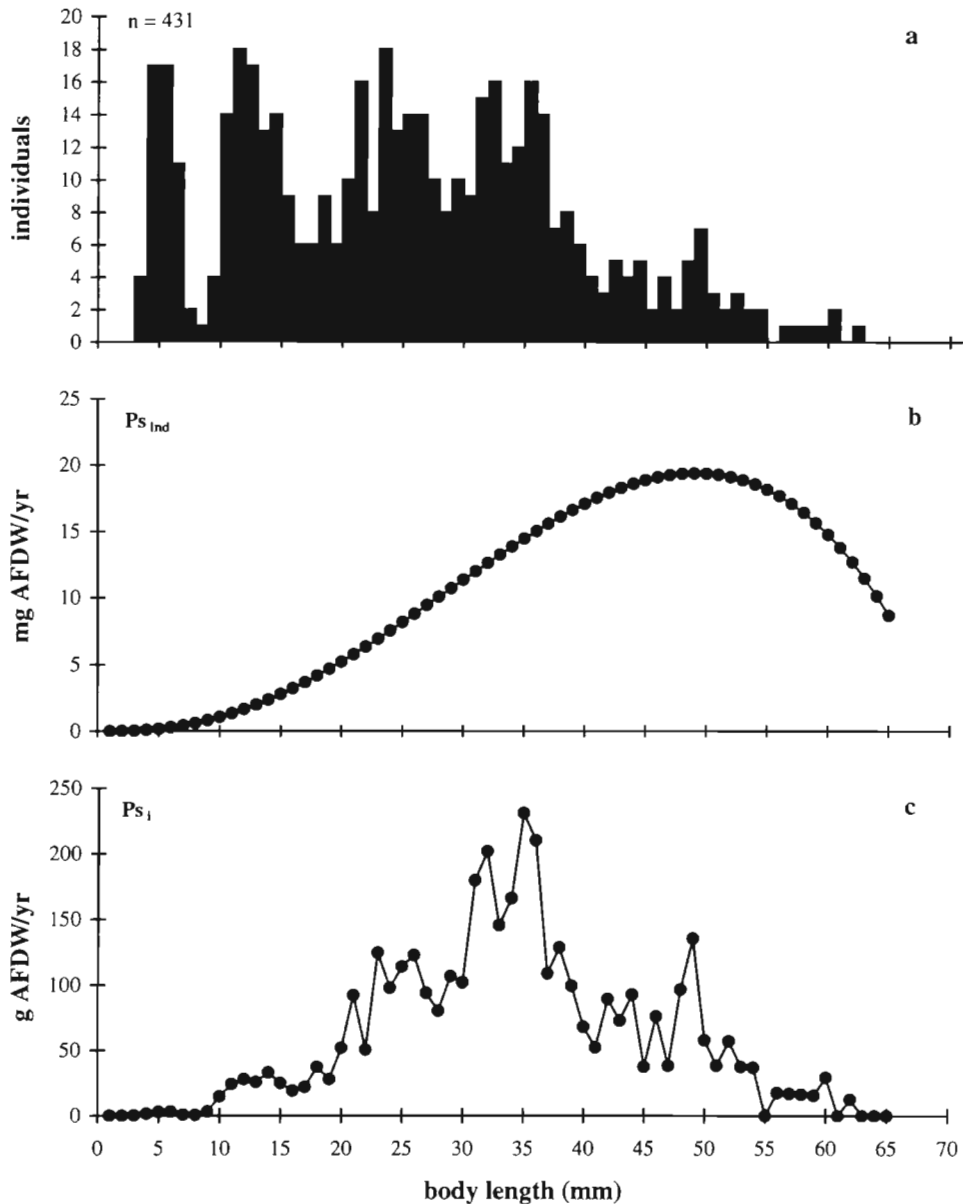
Fig. 6. (a) Length frequency distribution, (b) individual somatic production, $P_{s\,ind.}$, and (c) somatic production of the different length classes, P_{s_i}, of the investigated population of *Gammarus wilkitzkii* (AFDW: ash-free dry weight)

Inhabiting the Arctic sea ice, *Gammarus wilkitzkii* is exposed to an environment characterised by extreme physical and biological conditions, such as temperatures close to the freezing point, highly variable salinities and a seasonally limited food supply during the short Arctic summer (Carey 1985, Melnikov 1997). Obviously, *G. wilkitzkii* is evolutionarily adapted to live under such conditions. The question arises as to whether its low growth rate is one such adaptation. The individual growth of an organism is a non-linear process and can be described only by non-linear functions (Brey 1999). Therefore, for comparison among

species, growth functions are not suitable. The species-specific overall growth performance, Ψ (Brey 1999), is an index describing the time in which an organism reaches its maximum weight and is independent of a species-specific growth function. The comparison of Ψ among salt and freshwater amphipods (Gammaridea) from boreal and polar regions shows that *Gammarus* species in general have a higher overall growth performance than other genera (Fig. 7). Within the genus *Gammarus*, however, Ψ of *G. wilkitzkii* is not significantly different from boreal species (ANOVA, $p > 0.05$). According to Brey (1999) Ψ of sys-
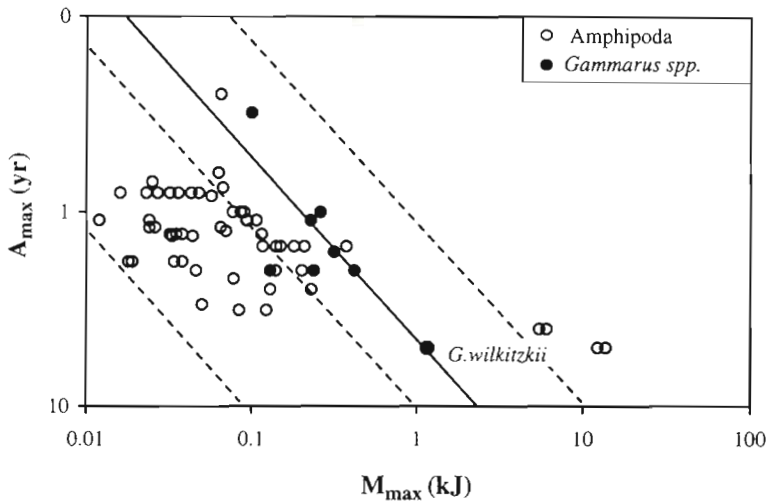
Fig. 7. Auximetric grid comparing overall growth performance, Ψ, of amphipod species from boreal and polar regions. Diagonal lines indicate equal values of Ψ. ●: species of the genus Gammarus—G. pulex, G. pseudolimnaeus, G. aequicauda, G. mucronatus (data collection: T. Brey)

tematically closely related species is primarily determined genetically rather than being dependent on the environmental conditions. This obviously also applies for amphipods of the genus Gammarus, and within those for G. wilkitzkii.

Somatic productivity of the sympagic amphipod Gammarus wilkitzkii is rather low compared to other amphipod species from polar and boreal habitats (Fig. 8). The P_s/B ratio is mainly influenced by environmental factors such as temperature and food, but also by the proportion between small and large individuals within the population (Brey 1994). In the following sec-
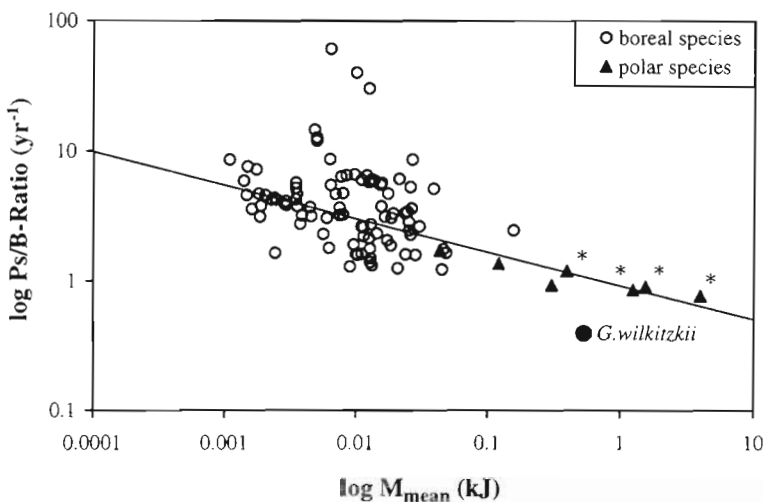

Fig. 8. Annual somatic P_s/B ratio of Gammarus wilkitzkii in comparison to amphipod species from boreal and polar regions (data collection: T. Brey) (*: P_s/B ratio of Bovallia gigantea; Thurston 1970, Bone 1972)

tions, these factors are discussed in detail for G. wilkitzkii.

Temperature

The metabolic rate of marine invertebrates is generally positively correlated to water temperature (Clarke 1991, Brey 1999). The low temperatures below Arctic sea ice (–1.65 to –1.7°C, Melnikov 1997) could explain the low P_s/B ratio of Gammarus wilkitzkii in comparison to amphipod species from temperate latitudes, but not compared to the Antarctic species Bovallia gigantea (Fig. 8). The noticeable difference in productivity between these 2 polar species must be caused by factors others than temperature.

Food

Food availability and food quality are important factors influencing individual growth and productivity of a population. A strong seasonal variability in food availability and food quality may result in a generally lower productivity of polar compared to boreal species. The higher P_s/B ratio of Bovallia gigantea in comparison to Gammarus wilkitzkii could be due to differences in their feeding strategies. B. gigantea is a typical predator and, as such, has a year-round supply of food of high energy content (Bone 1972, Iken 1995). G. wilkitzkii predominately feeds on detritus, animal remains, and ice algae (Poltermann 1997, Werner 1997). G. wilkitzkii is less dependent on the primary productivity cycle by feeding mainly on detritus, which is available year round, and hence food limitations may be less important than for many other polar organisms. Still, the energy content of this diet is low (Begon et al. 1989, Penzlin 1989) compared to the diet of B. gigantea and, furthermore, is subjected to seasonal oscillations in availability. This likely causes the lower P_s/B ratio of G. wilkitzkii compared to B. gigantea.

Size distribution within the population

A large proportion of small individuals, which are characterised by a high

increase in body mass in a short time, results in a high P_s/B ratio of a population (Brey 1994). In the investigated population of *Gammarus wilkitzkii* only a comparatively small number of juveniles (<19 mm) (Fig. 6a) have been found, only insignificantly increasing the P_s/B ratio. The low number of juveniles may have the following causes: (1) Small amphipods were not sampled quantitatively, or live at other places. (2) *G. wilkitzkii* produces only a small number of juveniles annually. (3) The number of females within the population is low. (4) The mortality of juveniles is very high.

Samples were taken randomly with a non-selectively working suction pump. Therefore, small individuals were sampled in the same manner as large ones. No differences in the small-scale distribution between juveniles and adults could be observed at the sampling sites. The reported annual mean of 145 juveniles female^{-1} (Poltermann 1997), which is considered to be very high for amphipods (Sainte-Marie 1991), and a male:female ratio of 1:0.9 (Poltermann 1997) indicate that reproduction-specific features are not likely to be responsible for the low productivity of the *Gammarus wilkitzkii* population. High mortality of juveniles after their release from the female brood pouch seems to be a more likely factor, influencing the P_s/B ratio negatively. Mortality of juveniles will probably increase considerably if they are released at sub-optimal food conditions and/or when there is high pressure from predators (e.g. polar cod, cannibalism). Also, juveniles are probably physiologically more sensitive to unstable environmental conditions (e.g. changes in salinity) than adults and might therefore be more strongly subjected to natural selection.

Summary and conclusion

Gammarus wilkitzkii exhibits a long lifespan with a low growth rate compared to most other, especially boreal, amphipod species. The discussion above showed that these findings are mainly related to the peculiarities of its polar environment—combined effects of extremely low water temperature and strongly seasonally variable food availability and food quality. However, the high frequency of occurrence and biomass under Arctic sea ice (Poltermann 1998) demonstrates its successful adaptation to this specific habitat. High mortality, especially of juveniles, which influences the productivity of the population negatively, is compensated by high fecundity and by several reproduction cycles during a long lifespan.

The species-specific overall growth performance, Ψ, of *Gammarus wilkitzkii* is determined genetically and is not significantly different to boreal *Gammarus* species. To ensure this overall growth performance, *G.*

wilkitzkii has to compensate for the limitations of permanently low water temperature and oscillation in food availability and quality. It has adapted successfully to these conditions by exhibiting a low growth rate but reaching a high age and a very large body size.

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