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Winter and summer metabolic rates of Arctic amphipods. Preliminary results

INTRODUCTION

The metabolic rates of terrestrial and marine Arctic invertebrates is fairly well known (Remmert, 1980; Opaliński, 1982; Klekowski & Opaliński, 1986, 1989, 1990; Opaliński & Klekowski, 1989; Opaliński & Węsławski, 1989a, b; Piepenburg *et al.*, 1995). However, the above cited literature deals with the summer - Polar Day period, and data on the winter metabolic rates are rather rare. Scarce literature on the planktonic and littoral Antarctic crustaceans (Rakusa-Suszczewski & Klekowski, 1973; Rakusa-Suszczewski, 1990) indicate that winter metabolic rates are lower than summer ones, which is consistent with the generally accepted rule on of the temperature influence on animal metabolism (Prosser, 1973; Duncan & Klekowski, 1975). The aim of the present paper is to answer the question: How does the Arctic marine invertebrate metabolism changes in the course of winter to summer?

METHODS

Animals

Four species of marine littoral and shallow sublittoral amphipod crustaceans were the object of the study (*Gammarus oceanicus, G.setosus, Anonyx sarsi, A. nugax*). All four are common and abundant in the coastal waters of Spitsbergen (Węsławski, 1993a, 1994).

G. oceanicus is an opportunistic omnivorous, Atlantic - boreal species. It occurs in the littoral from the Baltic Sea on the south to Spitsbergen on the north. In Horsund Fjord it is most common between 0 and 2 m depth among stones. Natural temperatures in its environment range from -1.8° C in the winter and spring to +8° C in August in the peak of summer. Salinity ranges from 5 to 34 ppt (Węsławski, 1994). *G.setosus* is an Arctic - boreal species of circumpolar distribution, common throughout the Svalbard archipelago. This species is more cold water compared to the previous one, and is more often found in the inner fjord basins and eastern coast of archipelago, but generally its environmental conditions are the same as for the *G. oceanicus* (Węsławski, 1994).

A sari is necrophagic and carnivorous, Arctic - boreal species. It occurs on soft bottom, between 2 and 30 m depth, where temperature is not exceeding +5° C, and salinity is above 15 ppt.

A.nugax is necrophagic and carnivorous, also an Arctic - boreal species. It occurs on the soft bottom, below 20 m depth, down to 200 m in fjords.Temperature and salinity in its environment stays below +3.5° C and over 33 ppt (Węsławski, 1994). More on the ecology of these species can be found in Opaliński & Węsławski (1989a, b), and Klekowski & Węsławski (1991).

Experimental animals were collected in the intertidal and shallow sublittoral zone in Isbjornhamna, Hornsund Fjord, near the Polish Arctic Station in Hornsund (Southern Spitsbergen, Svalbard, 77°N, 15°E) - Figure 1. A detailed description of the local environment might be found in Węsławski (1993b). Animals were collected with the use of a light dredge between February 1985 and July 1985 (Table 1).

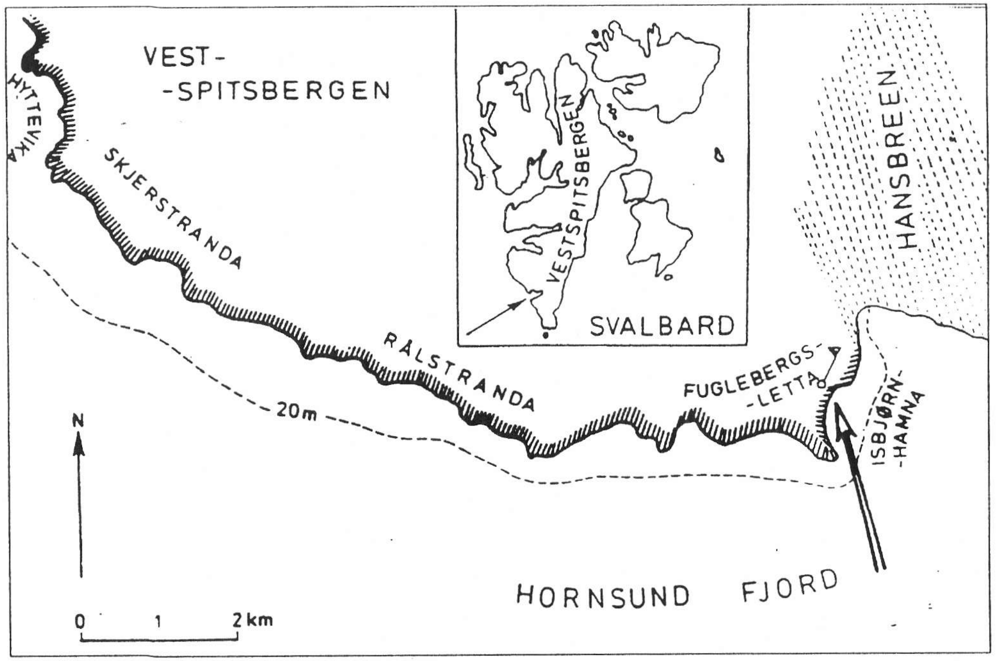

Fig. 1. Hornsund Fjord, Spitsbergen. The arrow indicate place of animal sampling.

Measurement methods

Animals were transported to the laboratory in the Polar Station and placed in aquaria for 5 to 12 hours to adapt for measurement conditions. Oxygen consumption was measured using closed vessels method. Oxygen concentration in vessels was measured with the oxygen sensor OXI 57 (WTW, Germany).

Table 1. Oxygen consumption and metabolic rate in Spitsbergen amphipods. n - number of measurements, T - temperature of measurements (°C), LC - animal body length (mm), W - animal wet weight (mg), R - oxygen consumption (cubic mm per individual per hour), MR - metabolic rate (cubic mm per mg wet wt per hour). Mean values ± Standard Error.

Date	n	T	LC	W	R	MR
Gammarus oceanicus						
Feb. 24	8	-1.0	17.6 ± 2.6	128.5 ± 56.3	20.6 ± 8.8	0.189 ± 0.026
March 28	8	-1.0	26.1 ± 1.3	284.6 ± 38.2	40.6 ± 4.0	0.164 ± 0.029
May 16	9	-1.0	23.2 ± 1.5	227.0 ± 35.7	39.6 ± 3.9	0.177 ± 0.035
May 20	9	0.0	27.9 ±1.4	360.3 ± 53.6	46.8 ± 3.7	0.146 ± 0.018
May 24	9	-1.6	18.5 ± 1.6	132.6 ± 32.0	20.2 ± 3.3	0.175 ± 0.016
June 2	4	-1.0	no data	268.0 ± 40.0	38.0 ± 6.4	0.149 ± 0.022
June 6	6	+1.0	no data	231.2 ± 59.3	32.1 ± 7.7	0.140 ± 0.010
June 12	5	+1.0	26.0 ±1.6	244.0 ± 30.2	22.4 ± 3.3	0.147 ± 0.014
July 4	25	+2.0	no data	249.4 ± 28.1	37.4 ± 4.6	0.150 ± 0.010
Gammarus setosus						
Feb.24	22	-1.6	19.5 ± 1.3	149.7 ± 28.5	20.5 ± 4.4	0.126 ± 0.012
Feb.24	21	0.0	23.1 ± 1.2	245.7 ± 27.8	26.1 ± 2.7	0.120 ± 0.011
March 26	11	-1.0	29.9 ± 0.9	409.6 ± 39.1	52.7 ± 4.2	0.134 ± 0.013
May 28	8	-1.0	28.7 ± 2.3	405.7 ± 84.4	42.3 ± 7.8	0.120 ± 0.016
July 8	26	+2.0	no data	61.0 ± 8.0	10.9 ± 0.9	0.187 ± 0.013
July 15	5	+3.0	no data	89.0 ± 35.0	18.7 ± 6.9	0.212 ± 0.055
Anonyx sarsi						
Feb. 24	33	-1.6	19.4 ±0.7	250.0 ± 22.0	48.2 ±13.3	0.156 ± 0.013
Feb. 27	5	-1.0	17.6 ± 1.7	180.0 ± 35.7	38.2 ±11.2	0.220 ± 0.043
April 2	5	-1.6	18.8 ± 0.9	266.4 ± 24.3	46.2 ± 4.1	0.177 ± 0.017
May 16	5	-1.6	19.6 ± 0.8	292.0 ± 21.8	47.0 ± 5.2	0.159 ± 0.010
May 20	4	0.0	15.8 ± 1.6	155.0 ± 42.5	23.8 ± 7.4	0.149 ± 0.010
May 20	10	+2.0	19.2 ± 1.6	219.2 ± 31.9	39.5 ± 6.9	0.176 ± 0.025
May 24	12	-1.6	17.8 ± 1.4	216.1 ± 40.9	21.4 ± 3.5	0.113 ± 0.019
Anonyx nugax						
April 12	9	+3.0	29.2 1.6	699 ±114	46.7 ± 5.2	0.078 ± 0.011
June 5	23	+1.0	no data	652 ± 72	56.6 ± 6.0	0.085 ± 0.005
July 3	21	+2.0	no data	549 ± 70	44.6 ± 3.9	0.095 ± 0.008
July 15	28	+3.0	no data	658 ± 51	56.8 ± 5.7	0.086 ± 0.006

Single animals were examined at natural environmental temperatures, controlled within an accuracy of 0.5° C. Erlenmayer flasks of 200 cm were used as the respirometric vessels. The present paper is based on the data from 338 measurements. Details on sampling dates and the number of measurements for each species are given in Table 1.

As the criterion for the seasonal change from winter to summer, we took the rise of temperature in surface coastal waters from -1.88°C (winter) to -1.0°C (Węsławski & Adamski, 1987; Węsławski *et al.*, 1988; Węsławski, 1993b). In 1985 this took place in the turn of May to June, when the maximum of chlorophyll 'a' abundance was observed (Węsławski *et al.*, 1988).

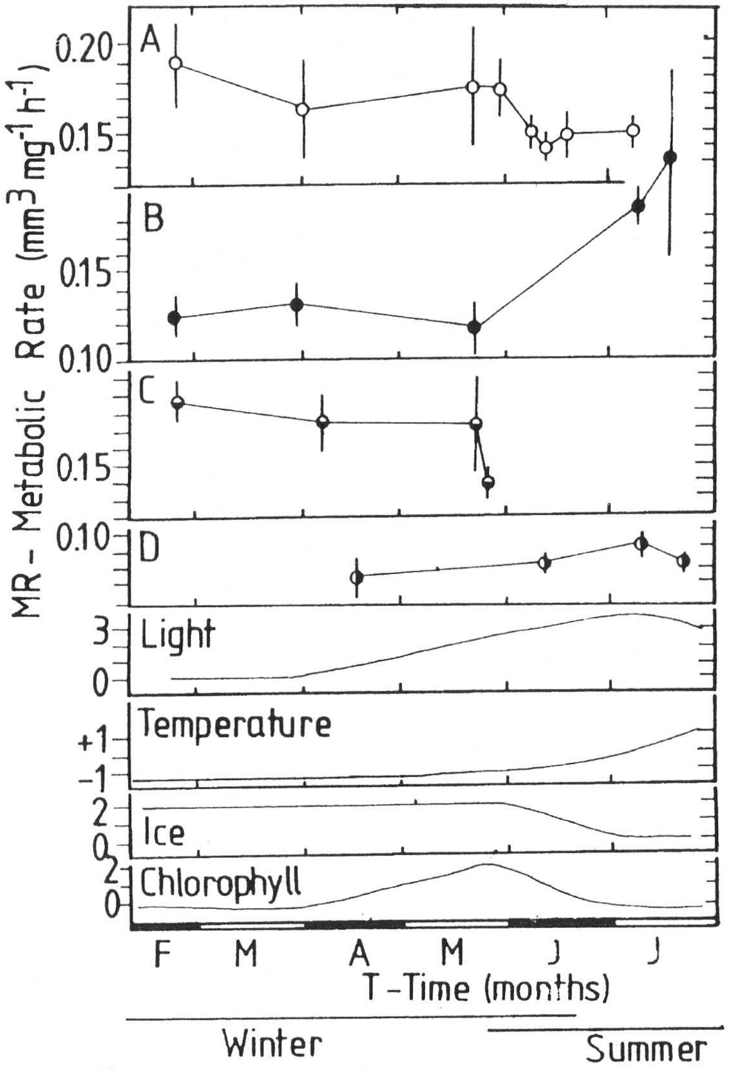

Fig. 2. Seasonal changes of metabolic rate in Spitsbergen coastal water amphipods and seasonal changes of some environmental factors in Hornsund Fjord coastal waters. A - *Gammarus oceanicus*, B - *Gammarus setosus*, C - *Anonyx sarsi*, D - *Anonyx nugax*. Light - in arbitrary units (o - polar night, 1 - night longer than day, 3 - day longer than night, 4 - polar day), Temperature in °C, Ice - in arbitrary units (0 -fast ice, 1 - pack ice, 2 - open water), Chlorophyll - in mg m . Environmental data after Węsławski *et al*. (1988).

RESULTS

Gammarus oceanicus

The metabolic rates were lowest at the turn of the seasons (June 6th) and reached 0.140 mm/mg/h, while highest values were observed in the peak of the winter (February 25th) and reached 0.189 mm/mg/h, which makes a statistically important difference (Table 1). The *G. oceanicus* metabolic rates decrease steedily from winter to summer, with a clear drop in the beginning of June (Fig. 2a). The metabolic rates of *G. oceanicus* calculated for the winter period (Feb. 24th - June 2nd) were higher than for summer (June 6th - July 4th), and changed respectively from 0.171 to 0.148 mm /mg/h (Table 2). This clear picture gets worse when we compare not the mean values, but regression lines calculated for the oxygen consumption dependence on body mass (Fig. 3). It was found that large animals of weight over 200 mg showed the same level of metabolic rates in winter and in summer, while small animals of body mass below 100 mg showed higher winter metabolic rates compared to summer ones. The regression lines show the same pattern: intercept 'a' is high in winter animals (0.73), and is low in summer (0.14), with a very high regression coefficent (1.00) (Table 3).

Table 2. Comparison of metabolic rate (MR - cubic mm per mg wet wt per hour) of Spitsbergen amphipods in winter and in summer. T - temperature (°C), n - number of measurements, W - animal wet weight (mg), R - animal oxygen consumption (cubic mm per individual per hour), MR - metabolic rate (cubic mm per mg wet wt per hour). Mean values ± Standard Error.

Season (date)	T	N	W	R	MR
Gammarus oceanicus					
Winter (Feb.24 - June 2)	-1.6 to 0.0	58	220.3 ± 18.6	32.3 ± 2.2	0.171 ± 0.009
Summer (June 2 - July 4)	-1.0 to +2.0	31	254.3 ± 24.2	36.9 ± 3.8	0.148 ± 0.014
Winter + Summer	-1.6 to +2.0	83	233.2 ± 15.5	34.5 ± 2.1	0.165 ± 0.007
Gammarus setosus					
Winter (Feb.24 - May 20)	-1.6 to 0.0	62	260.7 ± 22.7	30.9 ± 2.6	0.124 ± 0.006
Summer (July 8 - July 15)	+2.0 to +3.0	39	130.1 ± 28.6	17.7 ± 2.6	0.206 ± 0.015
Winter + Summer	-1.6 to +3.0	93	193.5 ± 18.2	24.4 ± 2.0	0.159 ± 0.009
Anonyx sarsi					
Winter (Feb. 24 - May 20)	-1.6 to +2.0	81	225.4 ± 13.1	34.7 ± 2.3	0.165 ± 0.008
Anonyx nugax					
Winter (April 12 - June 5)	+1.0 to +3.0	32	663.5 ± 82.3	49.2 ± 5.3	0.082 ± 0.007
Summer (June 5 - July 15)	+1.0 to +3.0	72	580.3 ± 41.9	47.8 ± 3.5	0.089 ± 0.003
Winter + Summer	+1.0 to +3.0	82	568.2 ± 65.9	43.6 ± 4.7	0.087 ± 0.004

Gammarus setosus

The reverse situation was observed in *Gammarus setosus*. The lowest metabolic rates were observed in the middle of the winter (Feb. 24th), and the highest in late summer (July 15th): respectively 0.120 and 0.212 mm/mg/h (Table 1). After the relatively stable winter metabolic rates, the summer values increase sharply (Fig. 2b). The mean metabolic rate of *G. setosus* calculated for the summer period is 0.206 mm/mg/hr (July 8th - July 15th), almost twice as high as the winter one: 0.124 mm/mg/hr (Feb. 24th - May 20th) (Table 2). Relation of oxygen uptake to body weight in *G. setosus* was similar to that in *G. oceanicus*, and large animals (100-200 mg weight) expressed almost the same metabolic rates in winter and in summer (Fig. 4). In small animals (below 100 mg) metabolic rates were higher in summer than in winter (contrary to the results with *G. oceanicus*). The intercept „a" in regression equations shows

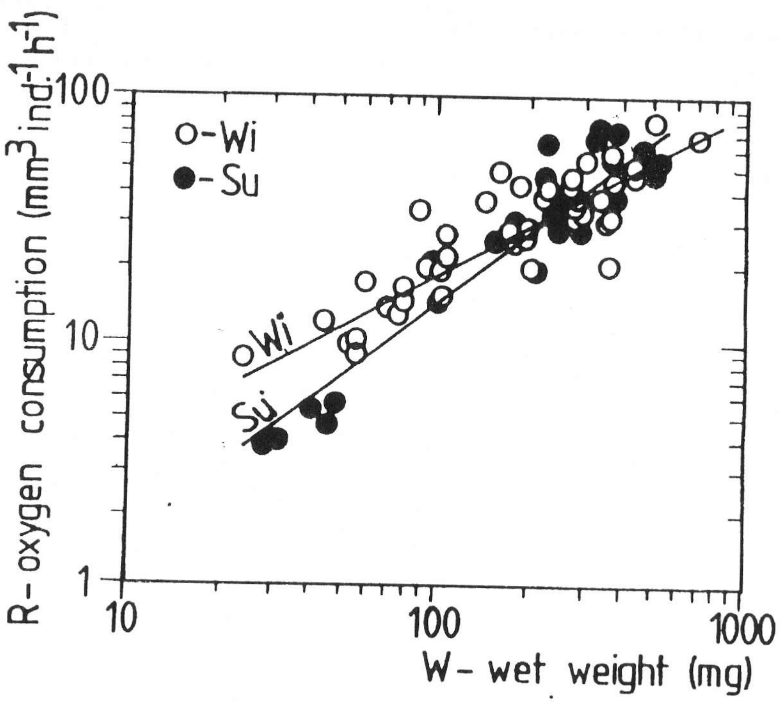

Fig. 3. The dependence between animal wet weight (W) and oxygen consumption (R) in *Gammarus oceanicus* from Hornsund Fjord in winter (Wi) and in summer (Su). See also Table 3.

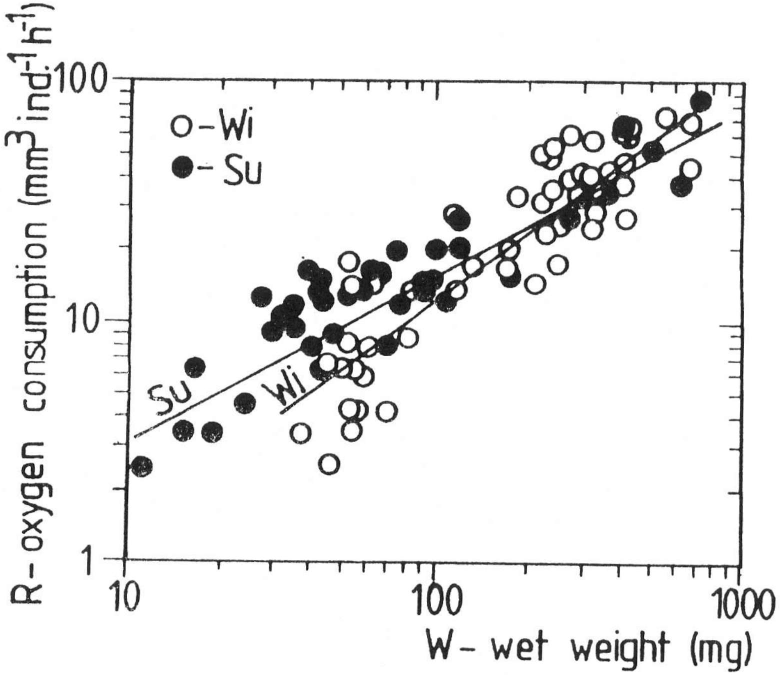

Fig. 4. The dependence between animal wet weight (W) and oxygen consumption (R) in *Gammarus setosus* from Hornund Fjord in winter (Wi) and summer (Su). See also Table 3.

Table 3. The dependence between oxygen consumption (R - cubic mm per individual per hour) and body wet weight (W - mg) in Spitsbergen amphipods in winter and in summer. General formula R = a W^b. n - number of measurements.

Season	n	W	R	Regression intercept a	Regression coefficient b	Regression r^2
Gammarus oceanicus						
Winter	58	220	32.6	0.73	0.71	0.7904
Summer	31	254	36.9	0.14	1.00	0.8702
Winter + Summer	82	233	24.5	0.42	0.81	0.8110
Gammarus setosus						
Winter	62	261	30.9	0.13	0.98	0.8400
Summer	39	130	17.1	0.80	0.66	0.8290
Winter + Summer	93	193	34.5	0.43	0.77	0.7904
Anonyx sarsi						
Winter	81	225	34.7	0.36	0.83	0.5375
Anonyx nugax						
Winter	32	663	49.2	0.57	0.69	0.6708
Summer	72	580	47.8	0.16	0.90	0.9109
Winter + Summer	82	568	43.6	0.16	0.89	0.9435

low values in winter (0.13) and in summer (0.80), with regression coefficents b=0.98 for winter and b=0.66 in summer (Table 3).

Anonyx sarsi

The metabolic rates of this species were measured in winter only (Feb. 24th - May 24th). They ranged between 113 to 220 mm /mg/h (Table 1). From the middle of winter to the late winter a slight decrease of *A. sarsi* metabolism was observed (Fig. 2c).

Table 4. Metabolic rate (MR - cubic mm per mg wet wt per hour), the dependence between oxygen consumption (R - cubic mm per individual per hour) and body wet weight (W - mg) (general formula R = aW^b) in some polar invertebrates in the winter and in the summer. The difference between winter and summer metabolic rate (W/S) is indicated in percent.

Species	Season	Temperature °C	MR	W/S %	Regression a	Regression b	Author
Gammarus oceanicus	winter	-1.6to 0.0	0.171	-	0.73	0.71	present paper
	summer	-1.0 to +2.0	0.148	-13	0.14	1.00	present paper
Gammarus setosus	winter	-1.6 to 0.0	0.124	-	0.13	0.98	present paper
	summer	+2.0 to +3.0	0.206	+66	0.80	0.66	present paper
Anonyx nugax	winter	+1.0 to +3.0	0.082	-	0.57	0.69	present paper
	summer	+1.0 to +3.0	0.089	+8	0.16	0.90	present paper
Paramoera walkeri	winter	-1.9	0.050	-	0.09	0.71	Klekowski et al 1973
	summer	-1.2	0.090	+80	0.10	0.65	Rakusa-Suszczewski, Klekowski 1973
Euphausia superba	winter	-1.8	0.060	-	0.08	0.95	Rakusa-Suszczewski 1990
	summer	0.0	0.074	+23	0.10	0.95	Rakusa-Suszczewski 1990

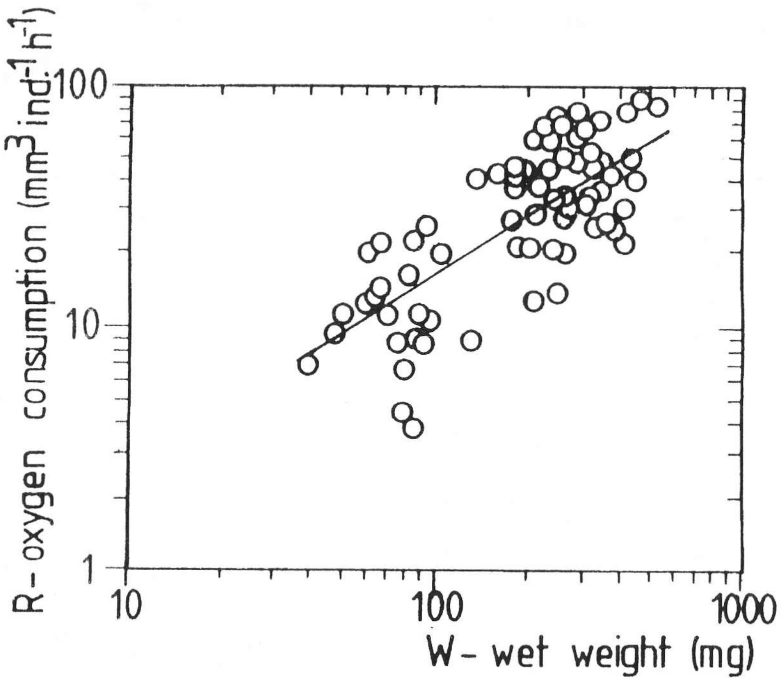

Fig. 5. The dependence between animal wet weight (W) and oxygen consumption (R) in *Anonyx sarsi* from Hornsund Fjord in winter. See also Table 3.

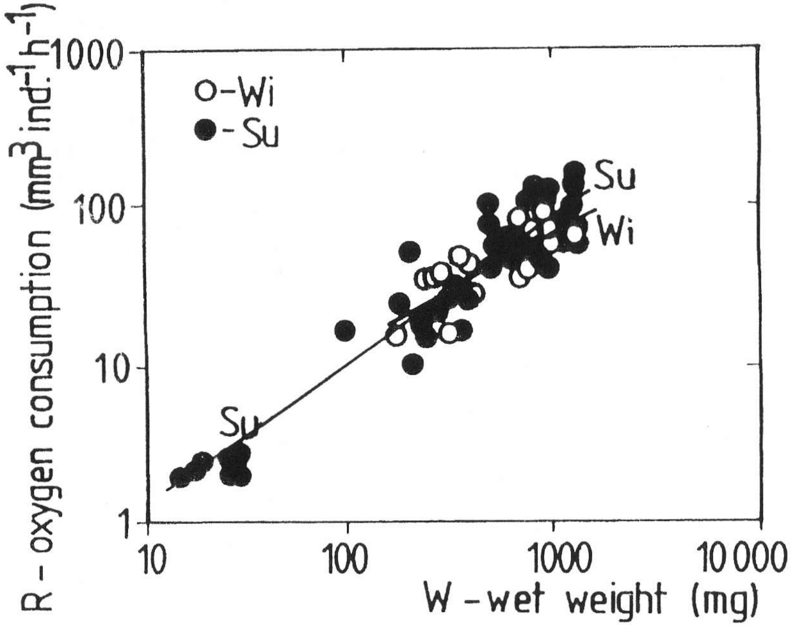

Fig. 6. The dependence between animal wet weight (W) and oxygen consumption (R) in *Anonyx nugax* from Hornsund Fjord in winter (Wi) and summer (Su). See also Table 3.

The mean metabolic rate of *A. sarsi* in winter was 0.165 mm /mg/h (Table 2). The correlation of oxygen consumption and body mass in *A. sarsi* is illustrated in Figure 5 and Table 3.

Anonyx nugax

The lowest metabolic rates of this species were found in winter (April 12th) and the highest in summer (July 5th), 0.078 and 0.095mm mg/h respectively (Table 1). The mean summer metabolic rates of *A. nugax* (June 5th and July 15th) were similar to the mean winter values (April 12th - June 5th) and ranged respectively from 0.089 to 0.082 mm /mg/h (Table 2, Fig. 2d). The relation of oxygen consumption to body weight in *A. nugax* is shown by the differences in winter and summer values of intercepts ‘a’ (0.57 to 0.16) and coefficients ‘b’ : 0.69 and 0.9 respectively (Table 3), however the measurements of adult animals showed almost identical regression lines (Fig. 6). The differences of regression parameters come from the low metabolic rates of juvenile specimens, observed in summer.

Presented results show all possible metabolic reactions connected with the change of seasons: the metabolism may drop from winter to summer *(G.oceanicus)*, it may grow (G. setosus) or remain stable (*A. nugax*). The observed differences of metabolic rates in winter and summer are the effect of juvenile animals metabolism, the adults expressed an even level of metabolism from winter to summer.

DISCUSSION

Seasonal change from winter to summer is connected with the change of important environmental parameters like temperature, salinity, light, and food resources. The High Arctic region shows especially drastic changes of these parameters (Węsławski *et al.*, 1988; Węsławski, 1994).

How may poikilothermic animals react to those changes?

The increase of poikilothermic animals metabolic rates from winter towards summer seems to be a natural reaction caused by an increase in water temperature (Klekowski *et al.*, 1973; Opaliński, 1979a,b; Opaliński & Klekowski, 1992), increased sun radiaton (Opaliński & Klekowski, 1991), food resources (Opaliński, 1991; Percy, 1993; Vernberg & Vernberg, 1993; Chapelle *et al.*, 1994), or the salinity drop caused by the ice melt (Klekowski & Opaliński, 1993). Such metabolic rates, which increase from winter to summer, have been observed among Antarctic animals. *Paramoera walkeri* (Amphipoda) metabolism expressed a summer increase of metabolic rates of 80% compared to winter values, and antarctic krill (*Euphausia superba*) showed a 23% increase (Table 4).

A rate of 8% increase of the metabolic rate from winter towards summer in *A. nugax* was statistically unimportant, while *G. oceanicus* expressed a decrease of metabolic rate of 13% (Table 4).

Further analysis is needed for answering the question of what are the specific external and internal factors, changeable from winter to summer, that might be responsible for the metabolic rates seen in Arctic littoral amphipods. This will be the subject of future studies.

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