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Respiration of adult female *Calanus hyperboreus* (Copepoda) during spring in the North Water Polynya

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***Abstract*:** The respiration rate of adult female *Calanus hyperboreus* was determined in order to assess physiological activity and its relationship to food availability during spring in the North Water Polynya, northern Baffin Bay. The respiration rate increased hyperbolically with increasing ambient chlorophyll *a* (Chl. *a*) concentration regardless of the reproductive status. The increase of respiration with Chl. *a* concentration may be caused by activated feeding behavior. This suggests that all adult females during spring were physiologically active individuals. Possible advantages of the rapid response to food concentration in adult female copepods are discussed.

key words: Copepoda, respiration rate, reproduction, food condition, Baffin Bay

Introduction

The planktonic copepod *Calanus hyperboreus* Krøyer is a key species in Arctic plankton communities because of its abundance and size (Hirche, 1997). This copepod undergoes pronounced seasonal ontogenetic migrations, which consist of ascent during the ice-melting season (summer) for feeding and descent during the ice-forming season (winter) for resting. Usually, female *C. hyperboreus* spawn at depth during the resting phase in early to mid-winter without feeding and complete egg production before the spring phytoplankton bloom (Conover, 1988; Smith, 1990; Hirche, 1997). Gravid females lost most of their lipids and body proteins during the spawning, and most adult females probably die after the spawning (Head and Harris, 1985). However, some females which mature late and either do not become gravid or else produced only a few eggs would survive until the next reproductive season (Conover, 1988; Hirche, 1997). Although late-mature females commonly occur throughout the Arctic to subarctic regions in summer, their abundances and proportions in populations vary considerably (Buchanan and Sekerak, 1982; Longhurst *et al.*, 1984; Hansen *et al.*, 1990; Tande, 1991; Hirche and Niehoff, 1996; Thibault *et al.*, 1999). One possible factor that affects the abundances of adult females during summer is the difference in the amount of lipid accumulation in the CV stage (Conover, 1988). In addition, there is some recent evidence that food concentration during the late spawning season (*i.e.* early spring) affects

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the reproductive status (Melle and Skjodal, 1998), but this has not been studied in detail. In this study, we assess the respiration rate of the adult female *C. hyperboreus* in order to deduce the effect of food concentration on physiological condition during the late spawning season in the North Water Polynya, northern Baffin Bay.

Materials and methods

Sampling and measurements were done aboard the CCGS icebreaker *Pierre Radisson*, at 7 stations of the North Water Polynya from April to May 1998 (Table 1). A quadrangle net (200 μm or 500 μm mesh 1.0 × 1.0 m mouth opening) was used to sample live specimens from bottom to surface, except at Stn. A54 where the tow was from 60 m to the surface. After the net was retrieved, the content of the cod-end bucket was immediately transferred to a large container filled with surface seawater, and undamaged specimens were sorted out for experiments.

The oxygen electrode method (Omori and Ikeda, 1984) was used to determine the oxygen consumption rates. For each experiment, a single copepod was placed in a 3-m*l* water sealed jacketed chamber with filtered seawater, and the decline of dissolved oxygen was measured with the oxygen electrode (Hansatech Instruments, DW2 Liquid-Phase Oxygen Electrode Unit). Oxygen consumption by the copepod was calculated from the mean rate of decline of pO_2 after correcting for the electrode drift with pre-and post-test calibration. The pO_2 did not change in control tests without copepods. The temperature of the chamber was maintained at 0°C by a chilled freshwater flow which was circulated with a pump. At Stn. A35, respiration rates were also measured for 5 individuals which were fed excess amounts of cultured diatom (*Skeletonema costatum*; >10 μg Chl. *a* l^{-1}) for 4 h, in order to determine the effect of food concentration on the respiration rate. All experiments were conducted in darkness. At the end of each experiment, the copepod was rinsed briefly with distilled water, placed in an aluminum pan and dried at 60°C for 48 h for dry weight determination. Dried specimens were used for elemental composition analysis (C and N), with an elemental analyzer (FISONS NA 1500 NCS) using sulfanilamide as a standard.

Results

Environmental conditions

Environmental conditions are summarized in Table 1. At all sampling sites temperature never exceeded zero during the present study (range: −1.7 to −0.1°C). Salinity showed little variation (range: 33.1 to 34.3 PSU; Table 1). Mean Chl. *a* concentration in the euphotic zone (from the surface to the depth of 1% surface light penetration) was fairly low from 21 to 29 April (range: 0.050 to 0.224 μg l^{-1}; Table 1). On 30 April and 4 May (Stns. A47 and A54), Chl. *a* concentration increased to *ca.* 1.2 μg l^{-1}, after which it drastically increased to 7.5 μg l^{-1} at Stn. B18 on 15 May.

Chemical composition and oxygen consumption

Mean dry weights of female *Calanus hyperboreus* ranged from 1.98 to 3.02 mg for gravid females, and from 1.63 to 3.90 mg for non-gravid females (Table 2). The

Table 1. Date, location and environmental conditions of sampling sites in April–May 1998.

Stn. No.	Date	Location	Sampling depth (m)	T (°C)	S (PSU)	Chl. *a* ($\mu g\ l^{-1}$)
A44	Apr. 21 1998	76°23′N 77°25′E	0–320	−1.7 to −0.6	33.1 to 33.9	0.050
A49	Apr. 24	76°17′N 74°45′E	0–480	−1.7 to −0.1	33.3 to 34.3	0.224
A35	Apr. 28	77°00′N 75°02′E	0–500	−1.7 to −0.3	33.1 to 34.3	0.173
A31	Apr. 29	77°00′N 77°13′E	0–200	−1.7 to −0.9	33.1 to 33.8	0.081
A47	Apr. 30	76°19′N 75°53′E	0–330	−1.7 to −0.2	33.4 to 34.1	1.201
A54	May 4	76°17′N 71°54′E	0– 60	−1.7	33.5 to 33.6	1.284
B18	May 15	77°50′N 73°09′E	0–166	−1.4 to −0.3	33.5 to 33.9	7.517

T= temperature range for the sampling depth interval
S= salinity range for the sampling depth interval
Chl. *a* = mean chlorophyll *a* concentration from surface to the depth of 1% surface light penetration.

Table 2. Dry weight, chemical composition (carbon and nitrogen) and C:N of adult female *Calanus hyperboreus* in the North Water Polynya. Values are means ± one standard deviation.

Stn.	Date	No. of replicates	Reproductive status	Dry weight (mg)	Carbon (%DW)	Nitrogen (%DW)	Body C: N
A44	Apr. 21	3	Non-gravid	1.63 ± 0.68	30.2 ± 9.1	5.1 ± 2.7	6.6 ± 2.0
A49	Apr. 24	9	Non-gravid	2.45 ± 0.68	34.0 ± 10.4	7.0 ± 2.6	5.4 ± 2.3
		9	Gravid	3.02 ± 0.64	43.0 ± 6.5	7.2 ± 2.1	6.2 ± 1.2
A35	Apr. 28	3	Non-gravid	1.95 ± 0.26	36.2 ± 11.1	6.4 ± 0.4	5.8 ± 2.0
		3	Gravid	1.98 ± 0.36	45.5 ± 4.9	6.1 ± 1.5	7.6 ± 1.1
A31	Apr. 29	2	Non-gravid	2.43	46.8	6.3	7.4
		1	Gravid	2.35	62.0	9.2	6.7
A47	Apr. 30	4	Non-gravid	1.71 ± 0.50	48.9 ± 12.5	9.7 ± 3.8	5.5 ± 2.2
		5	Gravid	2.48 ± 0.92	48.5 ± 2.3	7.3 ± 1.3	6.8 ± 1.5
A54	May 1	5	Non-gravid	2.53 ± 0.41	38.7 ± 4.8	7.2 ± 0.6	5.5 ± 1.0
B18	May 15	7	Non-gravid	3.90 ± 1.05	52.7 ± 3.3	6.6 ± 0.5	8.0 ± 1.0

amounts of C and N in *C. hyperboreus* are expressed as percentages of dry weight. In gravid females, C varied from 43.0 to 62.0% DW, and N from 6.1 to 9.2% DW; in non-gravid females, C varied from 30.2 to 52.7% DW, and N from 5.1 to 9.7% DW (Table 2). Although mean CN ratio was higher in gravid females (6.8) than in non-gravid females (6.3), the highest ratio (8.0) was recorded in non-gravid females from Stn. B18 where Chl. *a* concentration was highest.

In April respiration rates varied from 0.32 to 2.08 $\mu l\ O_2\ ind^{-1}\ h^{-1}$ for gravid females (mean 0.76), and 0.18 to 1.45 $\mu l\ O_2\ ind^{-1}\ h^{-1}$ for non-gravid females (mean 0.60). Respiration rates of non-gravid females were increased in May, and ranged from 0.56 to 1.73 (mean 0.98); those of gravid females were not measured (Table 3). Because of the methodological difference, *i.e.* the narrow chamber in this study prevents free movements of copepods, these values are slightly lower than in previous Arctic studies (Table 3). There are no clear relationships between respiration rate and temperature, dry weight, carbon and nitrogen, but respiration is significantly related to Chl. *a* concentration (Fig. 1). In individuals fed excess food, respiration rates were 3.4 times (per ind) and 2.7 times (per DW) as high as those of individuals without excess food (Fig. 2).

Table 3. Mean and range of the respiration rate in adult female *Calanus hyperboreus* during spring in the North Water Polynya Values from previous studies are also shown for comparison.

Location	Month	Expt T (°C)	Respiration rate ($\mu l\, O_2\, ind^{-1} h^{-1}$)	Body DW (mg)	Reproductive status	References
North Water Polynya	April	0	0.60 (0.18–1.45)	2.17	Non-gravid	Present study
North Water Polynya	April	0	0.76 (0.32–2.08)	2.54	Gravid	Present study
North Water Polynya	May	0	0.98 (0.56–1.73)	3.90	Non-gravid	Present study
Barrow Strait	March–April	−1	1.9*	?	Gravid	Head and Harris (1985)
Barrow Strait	March–April	−1	1.5*	?	Non-gravid	Head and Harris (1985)
Gulf of Maine	April	4–6	1.28	1.26	Non-gravid	Conover and Corner (1968)
Gulf of Maine	May	4–6	3.07	2.69	Non-gravid	Conover and Corner (1968)
Barents Sea	May–June	1.3	1.49	3.95	?	Ikeda and Skjodal (1989)

*Read from their Fig.4.

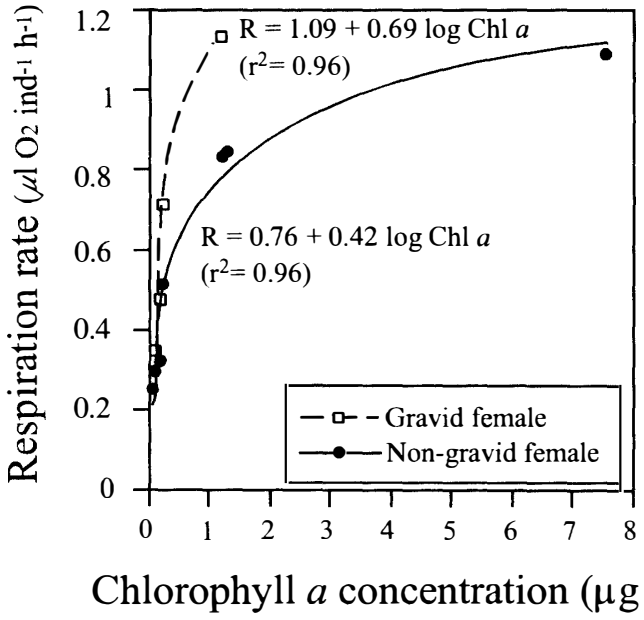

Fig. 1. Relationships between mean chlorophyll *a* concentration in the euphotic zone (1% surface light penetration) and respiration rate of adult female *Calanus hyperboreus* in the North Water Polynya during April–May 1998.

Discussion

Respiration rates of the adult female *Calanus hyperboreus* significantly increased with increasing Chl. *a* concentration before the spring phytoplankton bloom. The increase of respiration was high at Chl. *a* <1 $\mu g\ l^{-1}$. The results of experiments with fed

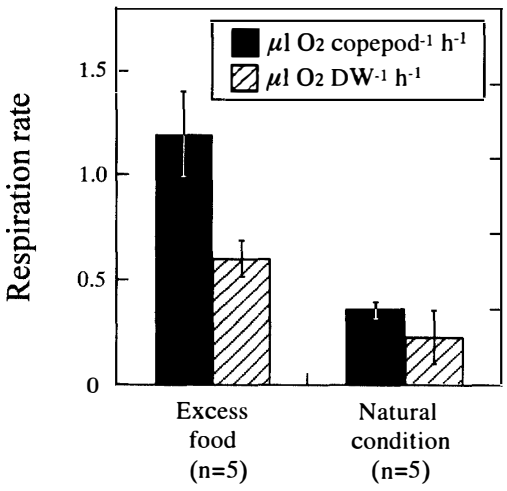

Fig. 2. Respiration rate of adult female *Calanus hyperboreus* (non-gravid) under excess food and natural seawater without any food supplement in the North Water Polynya on 28 April 1998. Vertical bars represent one standard deviation.

copepods indicate that this increase was directly caused by feeding, resulting from the increase of Chl. *a*. In general, respiration is lower in copepods living in water with an inadequate supply of food than in an area with high food availability (Marshall, 1973). In the adult female *C. hyperboreus*, an increase of respiration during the phytoplankton bloom was often reported, the availability of food being the most important factor that determined the level of respiration (Conover, 1962; Conover and Corner, 1968; Conover and Gustavson, 1999). In fact, a clear positive linear relation with the ambient Chl. *a* concentration was also observed in the gut pigment contents of *C. hyperboreus* during the same cruise (H. Hattori, pers. comm.). Hence, adult female *C. hyperboreus* became physiologically active when it encountered increased Chl. *a* concentration during April–May.

The increase of respiration with increasing Chl. *a* observed in adult female *Calanus hyperboreus* occurred regardless of the reproductive status, although the rate was higher in gravid than non-gravid females, as reported by Conover (1962). This response to food suggests that adult females during spring were not a spent population, but physiologically active individuals. Since females in this season are considered to be individuals which mature late or do not become gravid, there may be several advantages to the sensitive physiological response to Chl. *a* concentration. First, the sensitive response to the increased food would support supplemental reproduction for gravid females. Although *C. hyperboreus* is generally known to show a pre-bloom spawning strategy by using lipid reserves, the importance of secondary egg production during the bloom was recently emphasized (Melle and Skjodal, 1998). In our cruise, given that egg production in *C. hyperboreus* was confirmed to last until May, *i.e.* the onset period of the phytoplankton bloom (L. Fortier, pers. comm.), part of the gravid females would reproduce eggs by utilizing the phytoplankton. In fact, it was shown that *C. hyperboreus* produce more than 2000 eggs with food but, under starvation, spawned around 450 eggs (Conover, 1967). Second, the sensitive response to the food increase can be used to

accumulate lipid reserves during the ice-melting season. According to Conover (1988), adult females which molted from the lean CV stage must take an extra season to fatten before spring. Therefore, early onset of extensive feeding by a lean adult female would ensure enough lipid accumulation for maturation and egg production during the coming season. In this study, the increase of body CN ratio with increase of Chl. *a* concentration in non-gravid females supports this view.

It follows that the rapid increase in respiration rate as a response to high Chl. *a* concentration may be an adaptation to increase recruitment in Arctic environments, where the productive period of phytoplankton is limited. In Resolute Passage, old copepodite stages of *C. hyperboreus* hardly utilize ice algae, and there is little feeding by this species during the ice-covered period before the end of May (Conover *et al.*, 1991). Therefore, adult female *C. hyperboreus* in the polynya would take advantage of the early food supply for reproduction and growth in the area where the phytoplankton bloom begins early. Increase of favorable condition of this largest copepod leads to better food for fish, birds, and mammals, of which food mainly consists of or is derived from copepods (Ainley and DeMaster, 1990). The results of our study suggest that secondary production in the adult female *C. hyperboreus* was affected by the timing of the onset of phytoplankton bloom as well as its intensity and duration. Consequently, timing of phytoplankton bloom, even though their growth rates are low, should be an advantage of polynyas which have central importance to pelagic marine organisms in the Arctic (Ainely and DeMaster, 1990).

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