

Thermal response of ingestion and egestion rates in the Arctic copepod *Calanus glacialis* and possible metabolic consequences in a warming ocean

Ulrike Grote¹ · Anna Pasternak² · Elena Arashkevich² · Elisabeth Halvorsen¹ · Anastasia Nikishina²

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Abstract Climate change is particularly rapid in the Arctic, where water temperatures are predicted to increase substantially with implications for Arctic marine organisms, especially ectotherms such as the calanoid copepod *Calanus glacialis*, a key herbivore in the Arctic marine ecosystem. Feeding depends on temperature, and recent studies indicate different thermal responses in ingestion and respiration implying a possible metabolic mismatch with increasing temperatures. We investigated the thermal response of ingestion and faecal pellet production as an indicator of egestion of the Arctic copepod *C. glacialis* in incubation experiments at five temperatures ranging from 0 to 10 °C and compared the obtained data with published results on temperature dependence of respiration. Copepods were fed ad libitum with the diatom *Thalassiosira gravida*, and algae concentration was assessed prior and after 4 h feeding experiments. Egested faecal pellets were collected and counted. Ingestion and faecal pellet production rates increased linearly (Q_{10} coefficient ~ 1.4 – 1.7 and ~ 1.8 – 4.1 , respectively). No pronounced effect of feeding history (fed vs. starved for 3 days prior to experiment) was found, but responses in both rates were generally less dependent on temperature in the pre-starved experiment. Q_{10} values for ingestion rates were lower than Q_{10} values for published respiration rates (~ 1.8 – 4.6), indicating that metabolic losses increase stronger with increasing

temperature than metabolic gains by ingestion. A persistent imbalance between metabolic losses and energy uptake could lead to reduced fitness for *C. glacialis*, thereby affecting the population dynamics and distribution of this important species in the Arctic.

Keywords Feeding · Temperature · Climate change · Calanoid copepods · Ecophysiology

Introduction

Climate change is affecting temperature patterns globally, and climate models suggest an average warming of sea surface temperatures by at least 1.5 but up to 4.8 °C by the end of the twentieth century (IPCC 2013). Due to its influence on biochemical reaction rates and enzyme activity, temperature has a fundamental control over physiological processes, thereby influencing the survival, growth and reproduction of an organism, especially ectotherms. Enzyme-catalysed reactions typically increase with temperature to a certain point after which they sharply decrease again due to enzyme denaturation. As enzymatic reactions are the base of biological rates, feeding and respiration rates often display a similar unimodal response with temperature (Dell et al. 2011; Kordas et al. 2011). The performance of an organism is therefore likely to change with increasing environmental temperatures.

Changes in temperature appear to be particularly rapid in the Arctic marine ecosystems with warming rates two to four times higher than the global rate (ACIA 2004; IPCC 2007; Screen and Simmonds 2010). This warming trend is expected to continue in the future, as the water temperatures in the Arctic are predicted to increase by 6–8 °C by the end of this century (ACIA 2004; Richardson 2008).

✉ Ulrike Grote
ulrike.grote@uit.no

¹ Department of Arctic and Marine Biology, Faculty of Biosciences, Fisheries and Economics, UiT The Arctic University of Norway, 9037 Tromsø, Norway

² Shirshov Institute of Oceanology, RAS, 117997 Moscow, Russia

Key players of the pelagic food web at high latitudes are copepods of the genus *Calanus*, as they dominate the zooplankton biomass, representing an important link between phytoplankton and higher trophic level organisms, such as fish, seabirds and marine mammals (Conover 1988; Mumm et al. 1998; Daase and Eiane 2007; Falk-Petersen et al. 2009). One important species is *Calanus glacialis*. This relatively large and lipid-rich copepod is an Arctic shelf species (Jaschnov 1970; Conover 1988; Kosobokova 1998), and sea water temperature seems to be an important factor affecting its distribution (Daase and Eiane 2007). In the West Spitsbergen Current, where Arctic and Atlantic water masses mix, the biomass of *C. glacialis* is related to cold water temperatures with a critical threshold ~ 6 °C, above which its presence and biomass decrease (Carstensen et al. 2012).

Feeding is at the base of the performance of an organism, providing energy for metabolism, growth and reproduction, and thus strongly affects its distribution and success. Understanding how feeding rates depend on temperature is therefore crucial in order to understand and predict the impact of climate change on copepod populations in the Arctic. Former studies on temperature dependence of feeding rates in *C. glacialis* are limited (Kjellerup et al. 2012; Alcaraz et al. 2014). Kjellerup et al. (2012) found that specific faecal pellet production of *C. glacialis* females from Disko Bay, western Greenland, increased gradually with temperature (0–10 °C). Unimodal responses in ingestion with increasing temperature (0, 2.5, 5, 7.5, 10 °C) have been reported for this species by Alcaraz et al. (2014). When provided with water from the chlorophyll *a* maximum, *C. glacialis* copepodite stages V (CV) and adult females collected in June 2009 in the Barents Sea at -0.8 °C (average for 0–100 m depth) displayed highest ingestion rates at 2.5 °C, whereas the rates decreased again at the, respectively, higher temperatures. Alcaraz et al. (2014) thus present an in situ scenario, where, in addition to temperature, food concentration and food quality might have affected ingestion rates. Another factor that can affect feeding rates in copepods is the recent feeding history of the animals as starvation prior to the experimental feeding might result in increased grazing rates (e.g. Runge 1980; Båmstedt 1988; Rey et al. 1999). Compensation for lower assimilation rates or deficiencies of nitrogen and protein have been suggested as possible explanations for such a hunger response (Checkley 1980; Hirche 1996) which in turn also may be affected by changes in temperature (e.g. Almeda et al. 2011). To our knowledge, no data exist if *C. glacialis* also increases ingestion in response to starvation or for copepods generally, if the starvation response is similar at different temperatures.

Recent comparisons of consumption and metabolism across different taxa indicated that metabolism frequently

increased more quickly with temperature than did consumption resulting in a metabolic mismatch at higher temperatures (Rall et al. 2010; Lemoine and Burkepile 2012). The case study presented in Alcaraz et al. (2014) suggests that this could also be the case for *C. glacialis* under in situ conditions.

The main objective of this study was to investigate the temperature-induced response in ingestion rates of *C. glacialis*, accounting for the recent feeding history and ad libitum, high-quality food conditions and to discuss the possible metabolic scenarios for increasing temperatures. Additionally, we wanted to investigate the thermal response in faecal pellet production rates as an indicator for egestion.

This was approached by carrying out short-term feeding experiments at five different temperatures (0, 2.5, 5, 7.5 and 10 °C). To study the effect of feeding history, the grazing experiments were performed with animals fed or starved 3 days prior to the experiments. To analyse the physiological performance of *C. glacialis* at increasing temperatures, we compared the obtained ingestion rates with the obtained egestion rates and relevant published data on respiration rates (Hirche 1987; Tande 1988; Ikeda and Skjoldal 1989; Alcaraz et al. 2014). Our hypothesis was that ingestion rates of the cold water species *C. glacialis* increase up to a temperature optimum and are suppressed at the higher end of the investigated temperature range as indicated by preliminary data obtained under in situ conditions (Alcaraz et al. 2014). We also hypothesised that respiration rates may increase more pronounced with temperature than ingestion rates, possibly resulting in a mismatch between consumption and metabolic demands.

Materials and methods

Sampling and maintenance

C. glacialis was collected in Advent fjord (78°16'N, 15°30'E), Svalbard, on 2 July, 2009, for experiment I and on 9 July, 2009, for experiment II by vertical net hauls using a WP2 net (0.25 m² mouth opening, 200- μ m mesh size) fitted with a non-filtering cod end. Hauls were made from 30 m depth at low speed to minimise physical damage and capture stress. Water temperature ranged from 6 to -1.5 °C at 0–30 m depth. After collection, the samples were transferred into 60-L plastic containers filled half way with sea water, large zooplankton species were removed, and the containers were transported to the cool room (2–3 °C) at UNIS (The University Centre in Svalbard). For experiment I, the entire unsorted samples were incubated in filtered sea water with or without food for 3 days. Prior to experiment II, no pre-treatment was applied to the samples.

Fed animals were supplied with high concentrations of the diatom *Thalassiosira gravida* ($\sim 700 \mu\text{g C L}^{-1}$) every 24 h.

All feeding experiments were performed with cultured *T. gravida*. Algae were grown in batch cultures in 2-L Nalgene® bottles using Guillard's marine water enrichment solution (f/2) including silicate. *T. gravida* was maintained at 4–6 °C in a temperature-controlled room with a light/dark regime of 14:10 h.

Experiments

C. glacialis stage V copepodites (CV) were the most abundant developmental stage during the sampling and were used in the experiments. They were sorted under a stereomicroscope into glass containers with filtered sea water (0.2 μm , 70–100 mL) kept in the cool room (2–3 °C) using wide mouth glass pipettes. Copepods were acclimated to the respective experimental temperature by transferring the glass containers into temperature-controlled incubators (Termaks KB 8182) until the water had reached the respective temperature. Depending on the experimental temperature, this took 2–4 h. For experiments, 6–10 *C. glacialis* CV were carefully transferred to 300-mL jars containing $\sim 450 \text{ cells mL}^{-1}$ of *T. gravida* ($\sim 700 \mu\text{g C L}^{-1}$) and incubated in darkness at 0, 2.5, 5, 7.5 and 10 °C (± 0.2 °C) in the temperature-controlled incubators for 4 h. A total of 1–2 jars without copepods served as control. To obtain the food concentrations for incubations, algal cell density in the cultures was counted with a haemocytometer (Fuchs-Rosenthal) and the dilution rates with filtered sea water were calculated.

C. glacialis ingestion rates were assessed in incubation experiments with microscopic cell counts prior to and after the experiment. At the beginning (control treatments) and end (all treatments) of the experiments, 15-mL water samples per replicate were fixed with Lugol's solution (final concentration 1 %). *T. gravida* cells were counted under a light microscope at 10 \times magnification, and three subsamples were counted per replicate. Copepod ingestion rates were calculated according to Båmstedt et al. (2000), as no changes in control cell concentrations during the experiment were detected.

$$I = F \times [C] \quad (1)$$

$$F = \ln(C_0/C_t) \times V/(t \times n) \quad (2)$$

$$[C] = (C_0 - C_t)/(\ln(C_0) - \ln(C_t)) \quad (3)$$

where F is the clearance rate, $[C]$ is the logarithmic mean cell concentration, C_0 is the control end cell concentration, C_t is the experimental end cell concentration, n is the number of individuals and t is the incubation time. To estimate carbon ingestion from ingestion of cells, the

average C content of *T. gravida* cells obtained from CN analysis was used. Volumes of 50–100 mL *T. gravida* culture with known concentrations were filtered on three GF/F filters and analysed for C content in order to calculate the C content of the cells. Samples were prepared and analysed according to Reigstad and Wassmann (1996), with a Leeman Lab 440 elemental analyser. Faecal pellets produced during the experiments were collected and enumerated, and pellet production rate was assessed assuming no diel rhythm in pellet production ($\# \text{ FP ind}^{-1} \text{ d}^{-1}$).

Q_{10} approximations

In order to be able to discuss the effect of increasing temperature on *C. glacialis* performance, we estimated the Q_{10} values for the whole experimental temperature interval (0–10), 0–5, and 5–10 °C using the results from linear regression analysis and compared them with the Q_{10} values estimated from respiration measurements investigating similar temperature intervals (Hirche 1987; Tande 1988; Ikeda and Skjoldal 1989; Alcaraz et al. 2014). If not already presented in the cited studies, Q_{10} values were calculated according to Prosser (1961),

$$Q_{10} = (k_1/k_2)^{10/(t_1-t_2)} \quad (4)$$

where k_1 and k_2 are the ingestion and respiration rates at temperatures t_1 and t_2 , respectively. Respiration rates were presented only graphically in Tande (1988), and we retrieved and analysed (linear regression) the data using WebPlotDigitizer (Rohatgi 2013).

Statistical analysis

Preliminary inspection of the data revealed no unimodal response but approximately linearly increasing ingestion and faecal pellet production rates. The influence of temperature on ingestion rates and faecal pellet production was therefore analysed using linear regression analysis. To investigate the effect of feeding history on ingestion rates and faecal pellet production rates in *C. glacialis* and possible differences between all three experiments, analysis of covariance (ANCOVA) was performed and if applicable, Tukey's honest significant differences (HSD) test specifying the different experiments as the categorical variable. All calculations and statistical analyses were performed in R version 3.0.2 (R Development Core Team 2011).

Results

Mean ingestion rates and faecal pellet production rates are presented in Table 1. The Q_{10} values are presented in Table 2.

Table 1 Mean faecal pellet (FP) production and daily ingestion rates (I) of *Calanus glacialis* copepodites stage V (CV) for experiment I (Exp. I), pre-fed (f) and pre-starved (s), and experiment II (Exp. II), at five experimental temperatures (T), number of copepods per replicate (n), number of replicates (r)

| Exp. | T (°C) | n | r | FP (ind ⁻¹ d ⁻¹) | I (µg C ind ⁻¹ d ⁻¹) |
|-------|----------|-----|-----|---|---|
| I (f) | 0 | 10 | 3 | 12.88 ± 3.56 | 47.86 ± 10.67 |
| | 2.5 | 10 | 3 | 25.60 ± 0.53 | 89.24 ± 2.51 |
| | 5 | 10 | 3 | 30.40 ± 4.52 | 82.28 ± 5.14 |
| | 7.5 | 10 | 3 | 34.80 ± 5.10 | 85.84 ± 4.32 |
| | 10 | 10 | 3 | 46.16 ± 4.62 | 93.72 ± 6.21 |
| I (s) | 0 | 10 | 3 | 17.13 ± 2.94 | 79.89 ± 8.13 |
| | 2.5 | 10 | 3 | 30.87 ± 3.71 | 84.84 ± 2.05 |
| | 5 | 10 | 3 | 35.14 ± 2.88 | 99.62 ± 3.08 |
| | 7.5 | 10 | 3 | 44.88 ± 191 | 81.89 ± 1.86 |
| | 10 | 10 | 3 | 38.38 ± 6.54 | 99.27 ± 7.81 |
| II | 0 | 6 | 4 | 25.80 ± 0.97 | 68.35 ± 5.68 |
| | 2.5 | 6 | 4 | 34.53 ± 5.79 | 57.15 ± 9.01 |
| | 5 | 6 | 4 | 31.37 ± 1.55 | 63.01 ± 6.25 |
| | 7.5 | 6 | 4 | 45.75 ± 3.97 | 68.95 ± 4.49 |
| | 10 | 6 | 4 | 55.25 ± 2.43 | 99.59 ± 4.10 |

Ingestion

Daily ingestion rates of *C. glacialis* generally increased with increasing temperature (Fig. 1). In experiment I, when animals were fed for 3 days prior to the experiments, ingestion rates increased significantly with temperature (linear regression, $R^2 = 0.45$, $p = 0.007$, Fig. 1a). When animals were starved for 3 days prior to the experiments, ingestion rates did not increase significantly with temperature (linear regression, $R^2 = 0.20$,

Table 2 *Calanus glacialis* Q_{10} values calculated for ingestion (I) and faecal pellet production (E), for experiment I (Exp I), pre-fed (f) and pre-starved (s) and experiment II (Exp II), and for respiration

| Stage | T range (°C) | Q_{10} this study | | | Q_{10} respiration | Reference | |
|-------|--------------------|---------------------|-----------|--------|----------------------|-------------------------------------|-------------------------|
| | | Exp I (f) | Exp I (s) | Exp II | | | |
| CV | 0–10.0 | 1.49 | ns | 1.45 | (I) | This study | |
| | 0–5.0 | 1.65 | | 1.50 | | | |
| | 5.0–10.0 | 1.35 | | 1.40 | | | |
| | 0–10.0 | 3.05 | 2.03 | 2.12 | (E) | This study | |
| | 0–5.0 | 4.09 | 2.29 | 2.43 | | | |
| | 5.0–10.0 | 2.27 | 1.79 | 1.85 | | | |
| | | 0–5.0 | | | 4.60 | | Hirche (1987) (Table 3) |
| | | 5.0–10.0 | | | 4.39 | | |
| | 0–6.0 ^a | | | 4.37 | | Alcaraz et al. (2014) (Figure 2) | |
| AF | –0.5–3.5 | | | 3.43 | | Ikeda and Skjoldal (1989) (Table 2) | |
| | –1.5–10.0 | | | 1.82 | | Tande (1988) (Figure 2) | |

^a Alcaraz et al. (2014) found a unimodal thermal response in respiration rates, and the Q_{10} has been calculated for the temperature range below the optimum temperature

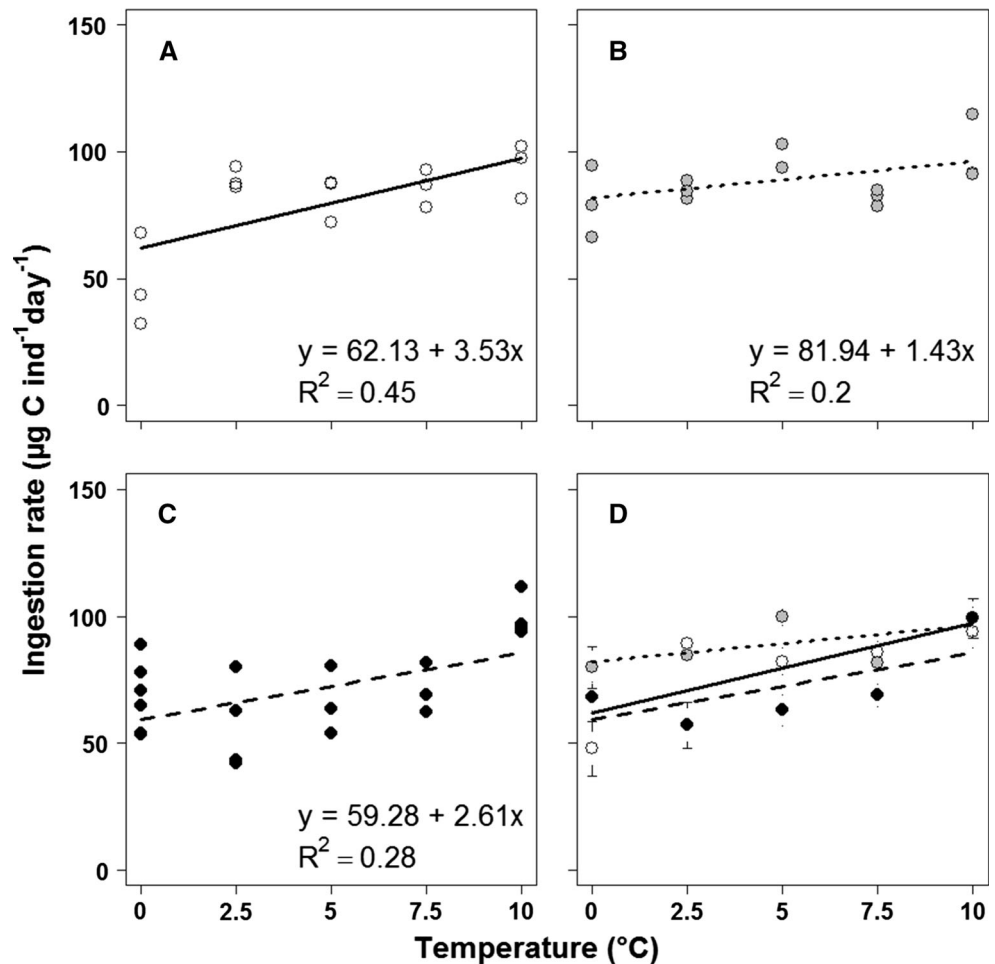
$p = 0.10$, Fig. 1b). Even though the fed treatment increased significantly and the starved treatment did not, no significant difference could be detected between the two feeding treatments, neither in slopes (ANCOVA, $F_{1,26} = 2.38$, $p = 0.13$) nor in intercepts (ANCOVA, $F_{1,26} = 3.75$, $p = 0.06$). In experiment II, ingestion rates increased significantly with temperature as well (linear regression, $R^2 = 0.28$, $p = 0.012$, Fig. 1c). No difference could be detected in the effect of temperature as the slopes in all three experiments did not differ significantly (ANCOVA, $F_{2,46} = 0.99$, $p = 0.38$, Fig. 1d). Ingestion rates estimated from experiment II were significantly lower than the ingestion rates from the starved treatment in experiment I (Tukey's HSD test, $p = 0.003$, Fig. 1d).

Faecal pellet production

Faecal pellet production rates of *C. glacialis* followed the same trend as daily ingestion, with production increasing with temperature in both treatments in experiment I (linear regression; pre-fed, $R^2 = 0.76$ and $p < 0.001$, pre-starved, $R^2 = 0.55$ and $p = 0.002$, Fig. 2a, b, respectively) and experiment II (linear regression; $R^2 = 0.69$, $p < 0.001$, Fig. 2c). Again, no difference could be detected between the two feeding treatments, neither in slopes nor in intercepts (ANCOVA; $F_{1,26} = 1.07$ and $p = 0.31$, $F_{1,26} = 1.58$ and $p = 0.22$, respectively, Fig. 2a, b). Faecal pellet production was significantly lower in the pre-fed treatment of experiment I as compared to experiment II (Tukey's HSD test, $p = 0.002$, Fig. 2d), but with no difference between all three experiments in regard to the effect of temperature (ANCOVA, $F_{2,46} = 0.06$, $p = 0.57$, Fig. 2d).

calculated from the literature: (1) Hirche (1987) (2) Alcaraz et al. (2014) (3) Ikeda and Skjoldal (1989) (4) Tande (1988)

Fig. 1 Ingestion rates of *Calanus glacialis* CV in relation to experimental temperatures in two feeding experiments. Lines indicate linear regression lines. **a** experiment I pre-fed treatment, ($p = 0.007$), **b** experiment I pre-starved treatment ($p = 0.099$), **c** experiment II no pre-treatment ($p = 0.012$), **d** mean values of all three experiments. Error bars indicate standard error



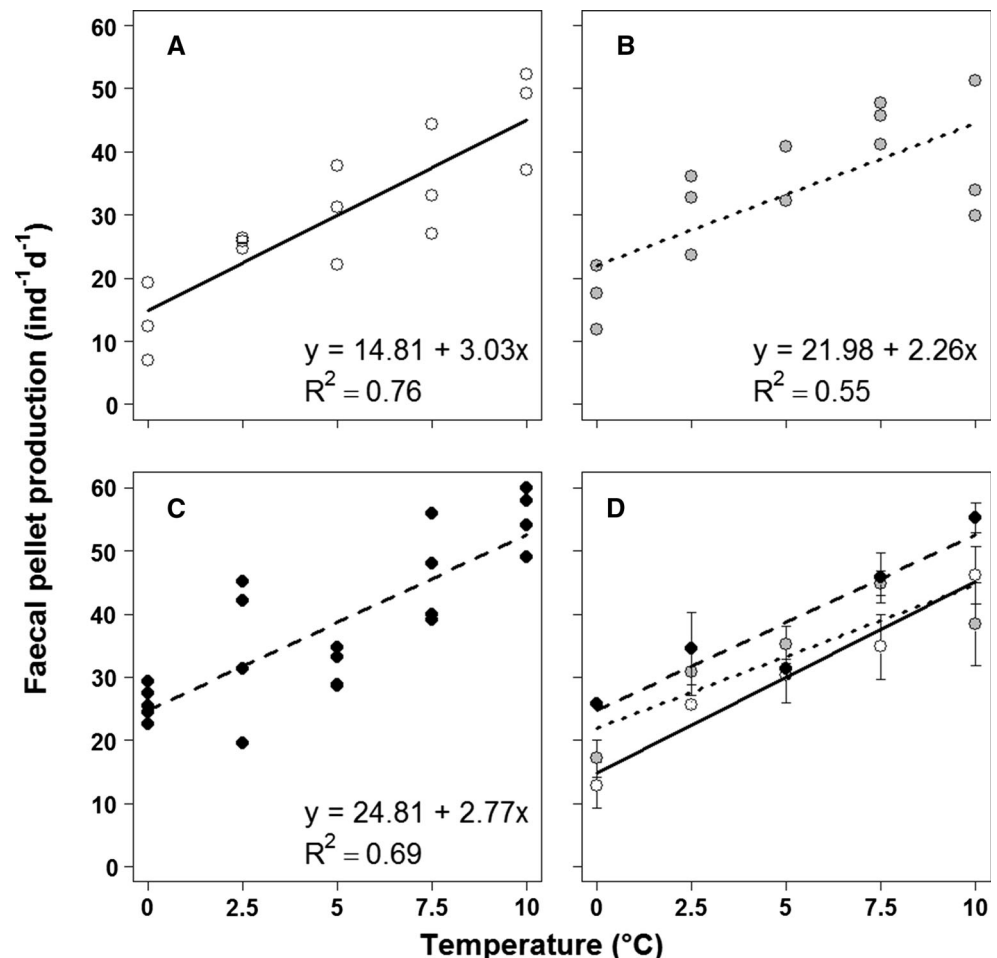
Discussion

Thermal response

Biological rates often increase with temperature to a certain point (the temperature optimum) after which they decrease again (Kordas et al. 2011). Ingestion rates of *C. glacialis* in the present study increased linearly within the studied temperature range (0–10 °C) without any apparent temperature optimum. Møller et al. (2012) found optimum temperatures of 12.2 and 13.6 °C for clearance rates of *Calanus finmarchicus* and *Calanus helgolandicus*, respectively, which both have a more southern distribution than *C. glacialis*. It is therefore possible that a suppression in feeding of *C. glacialis* from Advent fjord might have occurred at temperatures around or above 10 °C. Alcaraz et al. (2014) found optimum temperatures for ingestion at 2.5 °C in *C. glacialis* CV from the central Barents Sea in June. This locality is characterised by cold Arctic water and has a narrower temperature range over the season (Lind and Ingvaldsen 2012, and references therein),

compared to the Advent fjord, which is strongly influenced by warmer Atlantic water flowing along the West Spitsbergen coast. *C. glacialis* populations from the central Barents Sea and the Advent fjord will thus experience different thermal acclimation regimes throughout their feeding season, which could explain the difference in the thermal response between the present study and Alcaraz et al. (2014). Temperature only partly explained the variation in the obtained ingestion rates (45 and 28 % in exp. I (pre-fed) and exp. II, respectively). In our analysis, we could not account for two factors that could affect ingestion rates of copepods, within-stage variation in copepod size and within-stage variation in ingestion rates (Båmstedt 1984, 1988). Generally, ingestion rates are increasing with increasing body size in copepods (e.g. Bautista and Harris 1992; Barquero et al. 1998), and variability in size within stage CV of *C. glacialis* can be high (Gabrielsen et al. 2012). However, experiments investigating individual ingestion rates of *C. glacialis* CV feeding on identical *T. gravida* cell concentrations as used in our experiments indicate individual variation of 42 % independent of body

Fig. 2 Faecal pellet production of *Calanus glacialis* CV in relation to experimental temperatures in two experiments. Lines indicate significant linear regression lines. **a** experiment I pre-fed treatment ($p < 0.001$), **b** experiment I pre-starved treatment ($p = 0.002$), **c** experiment II ($p < 0.001$), **d** mean values for all three experiments. Error bars indicate standard error



size (Morozov et al. 2013). Even though we present group data of 6–10 individuals, much of the remaining variation could be ascribed to individual variability.

Feeding history and conditions

During our grazing experiments, *C. glacialis* received ad libitum concentrations of monocultures of *T. gravida*, a common diatom in the spring bloom in the Barents Sea (Degerlund and Eilertsen 2010). The results should therefore represent maximum ingestion and egestion rates. The high ingestion and faecal pellet production rates found during this study, as well as high egg production rates (Pasternak et al. 2013), confirm this and also the suitability of *T. gravida* as food for *C. glacialis*.

C. glacialis ingestion rates found during this study were within the range reported for stage CV feeding in nature (Tande and Båmstedt 1985; Hansen et al. 1990; Båmstedt et al. 1991) or higher (Pasternak et al. 2008). Faecal pellet production rates correspond well to in situ estimates (Pasternak et al. 2002; Seuthe et al. 2007). Our estimated ingestion and egestion rates have to be regarded as

maximum values as animals probably are not feeding 24 h per day and experimental food concentrations were very high. Our findings for *C. glacialis* agree well with a compilation of maximum ingestion rates for calanoid copepods in the laboratory (Saiz and Calbet 2007).

Previous studies have reported higher feeding rates for pre-starved *Calanus pacificus* females compared to pre-fed females (Runge 1980; Hassett and Landry 1983, 1990) and Rey et al. (1999) found higher faecal pellet production rates in pre-starved than in pre-fed *C. finmarchicus* females. Here, we could not detect an effect of feeding history on feeding and faecal pellet production rates of *C. glacialis* stage CV apart from different significances in thermal responses of feeding rates. Generally, the effect of temperature was least pronounced in the pre-starved experiment, indicating a possible temperature dependence of the starvation response.

Q_{10} and metabolic mismatch

Q_{10} values calculated from linear regression for ingestion of *C. glacialis* were relatively low in both experiments, lower than Q_{10} values calculated for published respiration rates

(Hirche 1987; Ikeda and Skjoldal 1989; Alcaraz et al. 2014) but approximately similar to Tande (1988). This indicates that respiration could have a higher thermal sensitivity than ingestion for *C. glacialis*. As feeding and respiration were estimated in separate experiments, we have to treat the comparisons with caution. The best agreement is probably achieved with Hirche (1987), as the time of year and in situ temperature during collection of animals were similar to this study and the same stage has been investigated.

Q_{10} values calculated from linear regression for faecal pellet production were higher than Q_{10} values calculated for ingestion (Table 2). Total egestion is, in addition to the number of faecal pellets produced per unit time, a function of faecal pellet volume and density, which we did not assess here. However, as a single food type and constant, high food concentrations were used during the experiments, we assume that faecal pellets did not change considerably in volume and density during our experiments. A decrease in assimilation efficiency with increasing temperature could thus explain the observed stronger increase in faecal pellet production compared to ingestion. This would lead to less of the ingested food being used for somatic growth and metabolism and a relatively higher egestion with increasing temperature.

As respiration and egestion contribute to the metabolic losses (together with excretion), a strong increase in both processes with increasing temperature might negatively affect growth (and reproduction in adults) if not balanced by a similar increase in ingestion. Less energy could then be allocated to growth and reproduction at higher temperatures as compared to lower temperatures. In accordance with this, a decrease in egg production rates at experimental temperatures above 5 °C has recently been shown for *C. glacialis* females (Pasternak et al. 2013). If the metabolic expenditures are not covered by ingestion, this mismatch between consumption and metabolism might thus severely reduce species fitness as has been shown recently in a number of studies across different taxa (Angilletta et al. 2010; Donelson et al. 2010; Lemoine and Burkepile 2012). Our study indicates the possibility of such a metabolic mismatch for the Arctic *C. glacialis* with increasing temperatures.

Future considerations

C. glacialis is a rather long-lived copepod with a 1–3 year life cycle with stages CIV and CV as the main overwintering stages (Conover 1988; Kosobokova 1998; Arnkværn et al. 2005). Long-term acclimatisation to experimental conditions in order to account for possible genetic adaptation to increasing temperatures would demand long-term cultivation, which was not within the scope of the present study. The copepods used in the experiments were

acclimated for 2–4 h to their respective experimental temperature. At the experimental temperatures 0, 2.5 and 5 °C, the acclimation time was within 1 h per 1 °C change, whereas the acclimation time for the experimental temperatures 7.5 and 10 °C might have been too short to be able to exclude thermal stress affecting the outcome of the experiments. The experimental results presented here therefore add to our knowledge how *C. glacialis* are functioning in the present variable environment (e.g. 6 °C to –1.5 °C at 0–30 m). In addition, the generally high ingestion rates obtained during the experiments do not indicate suppression in feeding due to pronounced thermal stress.

Due to their long life cycle (50–100 generations within 100 years), the potential of *C. glacialis* for genetic adaptation to the predicted high rate of temperature increase (6–8 °C within the next 100 years) is probably limited. However, the fact that feeding increased linearly without an apparent temperature optimum in this study, whereas previous work, investigating the same temperature range, has identified a temperature optima at ~2.5 °C for *C. glacialis* CV and adult females (Alcaraz et al. 2014), indicates plasticity in this trait, possibly related to thermal acclimation. Local populations of *C. glacialis* are also known to exist in relatively warm environments (Kosobokova 1999; Niehoff and Hirche 2005). This indicates that *C. glacialis* has the capacity to buffer a certain level of temperature increase. Whether this plasticity is also expressed in earlier life stages, and whether it encompasses the full range of temperature change predicted for the future, will be of importance for predicting the performance and role of this species in a warming Arctic. Future studies on the plasticity of optimal feeding temperatures investigating different seasons, locations and life stages combined with respiration measurements could gain valuable information. A persistent imbalance between metabolic losses and energy uptake could lead to reduced fitness for *C. glacialis*, possibly affecting the population dynamics and relative distribution of this important species in the marine Arctic.

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