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Effects of temperature on the metabolic stoichiometry of Arctic zooplankton

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Abstract. We assessed the relationship between zooplankton metabolism (respiration and inorganic N and P excretion) and "in situ" temperature through a grid of stations representing a range of natural temperature variation during the ATOS-Arctic cruise (July 2007). The objective was to explore not only the direct effects of temperature on zooplankton carbon respiratory losses (hereafter C_R) and NH_4-N and PO_4-P excretion rates (hereafter N_E and P_E, respectively), but also to investigate whether these metabolic pathways responded similarly to temperature, and so how temperature could affect the stoichiometry of the metabolic products. Metabolic rates, normalised to per unit of zooplankton carbon biomass, increased with increasing temperature following the Arrhenius equation. However, the activation energy differed for the various metabolic processes considered. Respiration, C_R, was the metabolic activity least affected by temperature, followed by N_E and P_E, and as a consequence the values of the $C_R : N_E$, $C_R : P_E$ and $N_E : P_E$ atomic quotients were inversely related to temperature. The effects of temperature on the stoichiometry of the excreted N and P products would contribute to modifying the nutrient pool available for phytoplankton and induce qualitative and quantitative shifts in the size, community structure and chemical composition of primary producers that could possibly translate to the whole Arctic marine food web.

1 Introduction

Human-induced climatic changes are driving major ecosystem changes at the global scale, but especially in high-latitude ecosystems. The rising temperatures (ACIA, 2004) are accelerating the rate of loss of Arctic summer sea ice (Comiso et al., 2008), with unpredictable though important consequences for such vulnerable ecosystems (Carmack et al., 2006; Wassmann, 2011). In spite of the uncertainty about what changes will occur in marine Arctic ecosystems in relation to temperature increases, it is very likely that these changes will be especially intense (Smetacek and Nicol, 2005) and not necessarily smooth and reversible. What must be expected are non-linear, abrupt responses, regime shifts and complex trajectories in the evolution of the different tipping elements as defined in Duarte et al. (2012).

Neither the main thresholds setting the limit or tipping point for regime shifts, nor the nature of the future changes, are well known. However, there are insights about how the different sensitivity to rising temperatures of some biological processes could lead to Arctic trophic shifts. In the case of the carbon balance in marine systems (i.e. photosynthesis–respiration, Regaudie-de-Gioux and Duarte, 2012), the higher sensitivity of respiration could lead to a net heterotrophic regime above a certain temperature threshold (Vaquer-Sunyer et al., 2010).

Amongst the Arctic tipping elements, zooplankton play a fundamental role in food webs, linking primary producers

and microheterotrophs with large consumers (Hjort, 1914; Tande and Båmstedt, 1985; Loeng and Drinkwater, 2007), modulating by grazing and respiration the final destination of biogenic carbon (Hirche et al., 1991; Olli et al., 2007), and contributing via excretion to regenerate the nutrient pool available for phytoplankton (Sterner, 1990; Alcaraz et al., 2010).

Respiration and N and P excretion rates in copepods, as any temperature-dependent biological activity in ectotherms, respond between certain temperature limits according to the Boltzmann–Arrhenius model (Loosanoff, 1958; Kordas et al., 2011). However, given the complex nature of the mechanisms involved, the various metabolic pathways could require different activation energies, therefore showing different quantitative responses to similar temperature conditions.

Here, we estimate the response to temperature of C-specific respiration (C_R) and ammonia and phosphate excretion (N_E and P_E) of Arctic zooplankton, and explore the possible differences in the Arrhenius activation energy for the different metabolic activities. The null hypothesis is that the metabolic stoichiometry should not be related to temperature. If rejected, the consequences of different sensitivity to temperature by these metabolic processes would be changes in the $C_R : N_E : P_E$ stoichiometry of the metabolic products in a scenario of rising temperatures. The progressive changes in the inorganic N and P proportion in the nutrient pool could induce a shift in the structural and trophic properties (i.e. taxonomy and chemical composition, Sterner, 1990; Lasternas and Agustí, 2010) of phytoplankton communities that could affect the whole Arctic food web.

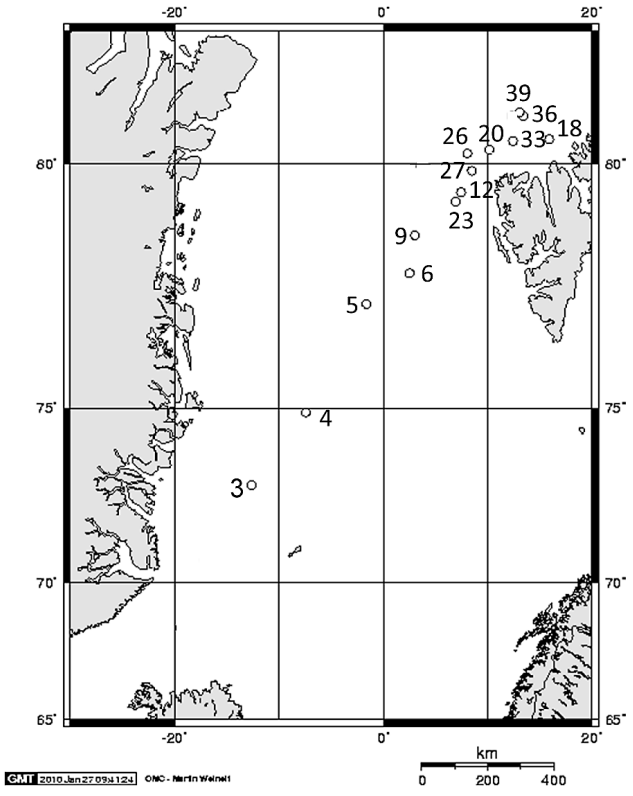

Fig. 1. Map of the study area and position of the sampled stations.

2 Methods

The study is based in the data obtained in July 2007 during the ATOS-Arctic cruise on board the R/V *Hespérides* (Alcaraz et al., 2010), in a network of stations located in the East Greenland Current, the Fram Strait and NW of the Svalbard islands (Fig. 1). Part of the data on zooplankton metabolism (about 70 %), have been selected from those in Alcaraz et al. (2010), according to a given range of average individual biomass, taxonomic composition and "in situ" food condition (concentration of microplankton biomass and proportion of autotrophs) in each incubation experiment, as described below.

2.1 Experimental conditions

Zooplankton metabolism (respiration and ammonia and phosphate excretion) was estimated by incubation experiments of mixed zooplankton as described in Alcaraz (1988) and Alcaraz et al. (1998, 2010). Experimental organisms were obtained by vertical net tows from 75–100 m depth to surface, conducted with a double WP-2 net fitted with 200-µm netting with a 6-L plastic bag as cod end to avoid damaging the organisms. Samples were immediately transferred into thermally insulated containers and transferred to the laboratory. Occasionally occurring larger zooplankters (a few larger amphipods, chaetognaths or coelenterates) were discarded by gently screening the sample through a 20 mm plastic grid submerged in a 2 L jar containing 0.2 µm filtered seawater at "in situ" temperature. The samples were repeatedly diluted with filtered seawater and screened through 200 µm netting in order to remove microzooplankton.

Water for incubation experiments was obtained with a 12 L Niskin bottle from 20 to 40 m depth and filtered with 0.2 µm Acro-Pack® filters. Incubation experiments for simultaneous estimation of respiration and excretion rates were made in 250 mL Pyrex® bottles closed by silicone stoppers holding the O_2 probes and a syringe needle to compensate for pressure changes, as described in Alcaraz et al. (1998, 2010) and sketched in Fig. 1 in Almeda et al. (2011). Experimental bottles contained aliquots of the washed zooplankton samples suspended in filtered seawater, while control bottles contained only filtered seawater. Once confirmed that there were no damaged organisms (i.e. all the organisms showing normal swimming behaviour), experimental and control bottles were incubated for 12–24 h in thermostatic baths at "in situ" temperature ± 0.1 °C and dim light. The incubation of zooplankton in filtered seawater was intended in order to avoid any interference of the feeding conditions during the

experiments (type and biomass of prey, Thor et al., 2002; Saba et al., 2009; Almeda et al., 2011) on the qualitative and quantitative characteristics of the metabolic products.

2.2 Variability sources for zooplankton metabolism other than temperature

Quantitative and qualitative characteristics of metabolic rates are highly controlled, aside from temperature conditions, by individual biomass, the metabolic substrate (determined by the feeding conditions and trophic habit), and by differences taxonomic characteristics. In order to avoid the bias induced on the specific metabolic rates by differences in body mass (Ikeda, 1985), only those experiments in which the average individual zooplankton body mass (IM) fell in the range comprised by average IM $\pm$ SD (13.31 ± 11.6 µmol C ind^{-1}) were considered in the analysis. The possible co-variance between individual body mass (IM) and "in situ" temperature, which would have similarly biased the effect of temperature on metabolic rates, was also analysed. The average IM in the experiments was estimated as the quotient between the experimental zooplankton biomass and the number of organisms, as described below.

The biomass of microplankton as carbon at the different stations was considered as a proxy of food for zooplankton (ZF). It was analysed in lugol-preserved water samples settled in Utermöhl chambers. Microplankton organisms from diatoms to auto- and heterotrophic flagellates and ciliates were counted and sized under an inverted microscope, and converted into carbon using the equations of Mender-Deuer and Lessard (2000). The relative contribution of phytoplankton to zooplankton food was estimated as the quotient between >5 µm chlorophyll carbon and total microplankton carbon (C_{CHL}/ZF). A detailed description of the method can be found in Calbet et al. (2011). The taxonomic composition of zooplankton in the experiments was estimated using automatic image analysis and identification software as described below.

2.3 Zooplankton metabolic rates

Zooplankton respiration was estimated as the decrease in dissolved oxygen concentration during the incubation. The analyses were made with two OXY-4 Pre-Sens® oxygen sensors (optodes, Alcaraz et al., 2010) that allowed semi-continuous (every 30 s) measurements of O_2 concentration using 8 O_2 probes (3–5 experimental and 1–3 control chambers, depending on the availability of sensors due to periodic calibration). Respiration rates were estimated as the difference between the slopes of the linear regression equations describing the changes in O_2 concentration during the incubations in experimental and control chambers. Oxygen consumption was transformed into respiratory C losses using a respiratory quotient (RQ, the molar ratio of CO_2 produced to O_2 consumed) of 0.97 (Omori and Ikeda, 1984).

Excretion rates were estimated in the same incubation experiments as respiration. Ammonia and phosphate excretion rates were calculated as the difference in the respective concentrations in experimental and control chambers. At the end of the incubation, water samples were siphoned from the chambers using silicone tubes ending in broad plastic tips enclosed with 100 µm-mesh in order to avoid extracting zooplankton organisms with the water sample. Ammonia was analysed by a fluorimetric method described by Kéruel and Aminot (1997), and phosphate according to Grasshoff et al. (1999).

At the end of the incubations, zooplankton were transferred to vials and fixed in 4 % formalin (final concentration) for automatic counting, biomass (biovolume, hereafter BV) analysis and taxonomic identification as described in Alcaraz et al. (2010) and Saiz et al. (2013). The method consisted in staining the samples with yellow eosin and scanning them in colour, transparency mode, at 2400 dpi. The corresponding images were automatically analysed for number, BV and organism classification into taxonomic groups using the free software ZooImage® (http://www.sciviews.org/zooimage/). The different zooplankton taxa were classified according to an established training set with the Random Forest algorithm. Zooplankton biomass as carbon (C_{ZOO}) was calculated according to BV–C_{ZOO} relationships for Arctic zooplankton: 1 mm^3 BV = 0.080 mg C_{ZOO}. More details can be found in Alcaraz et al. (2003, 2010) and Saiz et al. (2013). Metabolic rates were normalised to per unit of zooplankton carbon biomass (specific metabolic rates) by dividing daily gross respiration and excretion rates (µmol C_R, µmol N_E and µmol P_E day^{-1}) by the corresponding experimental biomass in µmol C_{zoo}. In each experiment, average individual biomass (IM) was calculated by dividing the experimental biomass in µmol C (C_{ZOO}) by the corresponding number of organisms in the experiment.

2.4 Temperature–metabolism relationships

The response of specific metabolic rates to temperature was described by the Arrhenius equation,

$$V = V_0 e^{(-E_a/RT)}, \quad (1)$$

where V is the metabolic rate; V_0 is a constant in the same units as V; E_a is the mean activation energy coefficient, related to the sensitivity of the corresponding metabolic function to temperature; and R is the universal gas constant (equal to 1.986 cal K^{-1} mol^{-1} or 8.3145 JK^{-1} mol^{-1}). The activation energy E_a expressed in eV has been calculated as the slope of the regression equation that explains the relation between the ln of the metabolic rates and the reciprocal of kT, where k is the Boltzmann constant (8.617310^{-5} eV K^{-1}) and T is the absolute temperature.

Q_{10} (the expected increase factor of metabolic rates corresponding to 10 °C temperature increase) has been calculated as

$$Q_{10} = e^{(10\,E_a / RT)}, \quad (2)$$

in which E_a is the activation energy in J mol^{-1}, R is the gas constant and T the average absolute temperature range for which Q_{10} is measured (Raven and Geider, 1988). The factor to transform the units of E_a from eV to J mol is $f = 8.31410^{-3}$ (JK^{-1} mol^{-1})/8.61710^{-5} (eV K^{-1}) = 96486.9.

The metabolic $C_R : N_E$, $C_R : P_E$ and $N_E : P_E$ quotients were calculated as the ratios between the specific corresponding metabolic rates in individual experiments and expressed in atoms. The daily average nutrient supply by zooplankton excretion during the cruise was estimated by multiplying the N_E and P_E times the average zooplankton biomass (12.23 g C_{zoo} m^{-2}, Alcaraz et al. 2010). Their contribution to the nutrients required by phytoplankton was calculated according to the primary production values during the cruise (0.93 g C m^{-2} day^{-1}, Lasternas and Agustí, 2010), assuming Redfield's C : N : P phytoplankton ratios (Redfield et al., 1963).

The relationships between temperature and the metabolic quotients, as well as those with the mentioned sources of variability (IM, ZF, C_{CHL}/ZF), were analysed using JMP® 7.0 software.

3 Results

3.1 Co-variance between temperature and other sources of metabolism variability

The relationship between average temperature (0–100 m depth integrated values) and the average individual zooplankton biomass (IM) is represented in Fig. 2. IM values ranged from 4.67 µmol C ind^{-1} (St. 19) to 22.84 µmol C ind^{-1} (St. 29), and were not significantly related to temperature ($r^2 = 0.0204$, $n = 30$, Fig. 2). Temperature, zooplankton food (ZF, µg C L^{-1}) and proportion of autotrophs in ZF (C_{CHL}/ZF) at the experimental stations are indicated in Table 1. Neither of these two variables were significantly correlated to temperature (temperature–ZF, $r^2 = 0.008$, $n = 12$; temperature–C_{CHL}/ZF, $r^2 = 0.002$, $n = 12$), Table 2.

The most abundant taxonomic zooplankton group in the experiments were copepods, which represented more than 93 % of the organisms, followed by chaetognaths with a minor contribution, less than 4 %, and amphipods, 1.9 %. As average, herbivorous copepods (Saiz et al., 2013), euphausiids and appendicularians accounted for more than 94 % of the experimental zooplankton, while carnivores like amphipods, chaetognaths and cnidarians contributed only to 5.5 %. In general, the proportion of the different groups was quite similar in all the incubations (Table 3).

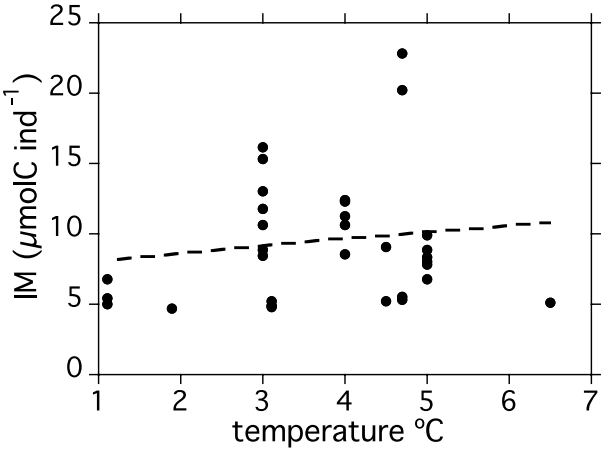

Fig. 2. Relationships between temperature and average experimental IM. The corresponding regression equation was IM = 7.4 + 0.51 T, $r^2 = 0.021$, $n = 30$.

3.2 Temperature and zooplankton metabolism

Zooplankton metabolism increased exponentially with temperature, the corresponding determination coefficients of the equations relating temperature and specific metabolic rates being significant (Table 4 and Fig. 3), with exponents rising from 0.2 (C_R) to 0.26 (P_E).

The plots using the Arrhenius equation (Eq. 1) are shown in Fig. 4. The highest slope of the linear regression equations, (equivalent to the E_a expressed in eV, and related to sensitivity to temperature) corresponded to P_E ($E_a = 1.905$ eV), followed by N_E ($E_a = 1.685$ eV) and C_R ($E_a = 1.292$ eV). However, when comparing the corresponding E_a values, the differences between C_R and N_E, or between N_E and P_E, were not statistically significant, and only C_R and P_E differed statistically (Table 5). Because of the gradient in E_a values, the metabolic activity least affected by temperature was C_R ($Q_{10} = 6.51$), followed by N_E and P_E, with Q_{10} values of 11.5 and 15.73, respectively (Table 5).

The atomic $C_R : P_E$, $C_R : N_E$ and $N_E : P_E$ metabolic ratios were inversely related to temperature. For $C_R : P_E$ and $N_E : P_E$ ratios, the correlation coefficients were higher than the critical r value to validate the null hypothesis, $H_0 : r = 0$, $P < 0.05$ (Fig. 5 and Table 6), while for the $C_R : N_E$ ratio the correlation was not statistically significant. On average, a temperature increase of 1 °C involved a decline in $C_R : P_E$ and $N_E : P_E$ ratio by 22 % and 11 %, respectively. The atomic $C_R : N_E : P_E$ metabolic ratios corresponding to the average temperature conditions, and those corresponding to a predicted temperature rise of 6 °C, are also indicated (Table 6).

The contribution of the nutrients excreted by zooplankton to the N and P required for primary production are indicated in Table 7. The current nutrient supplied by zooplankton excretion is about 30 % of the N and P required by phytoplankton. However, this contribution would rise to 70 % and 78 %,

Table 1. Average temperature (Temp, average 0–100 m depth, °C), concentration of potential zooplankton food (total microzooplankton carbon, ZF, µg C L^{-1}) and proportion of >5 µm chlorophyll carbon, C_{CHL}, in microplankton (C_{CHL}/ZF) at the experimental stations. ND: No data. From Calbet et al. (2011).

Station	Temp	ZF	C_{CHL}/ZF
3	1.00	61.18	0.07
4	0.80	38.31	0.20
5	4.00	33.83	0.14
6	3,.48	40.42	0.51
9	3.92	8.77	0.44
12	5.02	13.88	0.24
18	4.18	82.38	0.13
20	1.67	43.02	0.24
23	5.70	119.50	0.16
26	4.90	ND	ND
27	6.56	39.60	0.58
33	4.76	34.70	0.85
36	3.43	ND	ND
39	4.24	17.70	0.23

Table 2. Relationships between temperature in °C and microplankton biomass, here considered as zooplankton food, ZF, in µg C L^{-1}, and the proportion of autotrophs in ZF, Auto-C/ZF.

Regression equation	r^2	n
ZF = 38.6 + 1.54 T	0.008	12
Auto-C/ZF = 3.2 + 0.05 T	0.002	12

respectively, of the N and P required for the predicted temperature rise (Table 7).

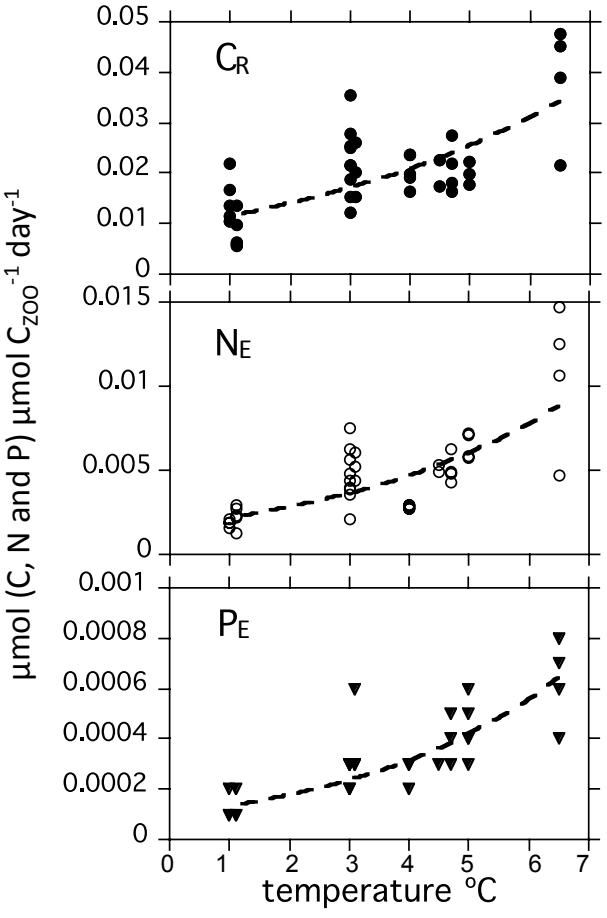

Fig. 3. Relationships between temperature and respiration (C_R), ammonia excretion (N_E) and phosphate (P_E) excretion rates.

4 Discussion

The response of different biological processes to thermal variability has been frequently used to reveal the general trends by which ecosystems could respond to changing temperature conditions (Dell et al., 2011). By tracing the values of biological processes across a range of temperatures, it is possible to characterize, by simple parameters like the activation energy E_a or the Q_{10} value, the physiological patterns that will emerge as a consequence of expected temperature changes (Aldridge et al., 1995; Caron et al., 1986).

In the case of biological processes crucial for the metabolic balance of plankton systems (i.e. photosynthesis and total ecosystem respiration), the higher E_a for total plankton respiration predicts a tendency towards heterotrophy as a consequence of temperature rise (Wassmann et al., 2008; Vaquer-Sunyer et al., 2010; Regaudie-de-Gioux and Duarte, 2011). Similarly, increasing temperature could lead to an imbalance between ingestion and respiration in Arctic copepods (M. Alcaraz, unpublished data) that could affect the basic pattern of matter and energy flow in Arctic plankton ecosystems. Both the changes in plankton metabolism (shift from eutrophic to net heterotrophic ecosystem) and the copepod energy balance (respiration losses higher than ingestion) appear to take place at relatively low temperature increases (Vaquer-Sunyer et al., 2010).

4.1 Sources of bias in the response of metabolism to temperature

Temperature is by no means the only factor controlling zooplankton metabolic rates. Both the quantitative response and quality of metabolic products are highly dependent on body size (Ikeda, 1985), so any covariance between temperature and individual biomass (IM) would bias the metabolic response to temperature. During our experiments average IM was not related to temperature (Fig. 2), so no bias could be expected. However, the variability of IM for a given temperature would translate in the variability observed in the response of metabolic rates to temperature.

The incubation of zooplankton in filtered seawater also prevented any bias in metabolism due to food abundance

Table 3. Average temperature (Temp, °C) and taxonomic composition (%) of zooplankton in the incubation experiments at the different stations. Amphi: Amphipods; Append: Appendicularians; Chaet: Chaetognaths; Cnid: Cnidarians. Euph: Euphausiaceans; Copep: Copepods. AVG: Average contribution of each taxon.

Station	Temp	Amphi	Append	Chaet	Cnid	Euph	Copep
3	1.00	1.61	0.50	0.50	0.10	0.00	97.28
4	0.80	1.05	0.45	2.25	0.30	0.00	95.96
5	4.00	1.00	3.73	1.72	0.29	0.43	92.83
6	3.48	1.78	0.96	2.94	0.03	0.17	94.12
9	3.92	1.56	0.78	2.34	0.00	0.00	95.31
12	5.02	2.87	0.44	6.52	0.33	0.22	89.61
18	4.18	1.17	0.12	0.37	0.00	0.06	98.28
20	1.67	3.05	0.86	4.01	0.10	0.38	91.60
23	5.70	3.04	0.20	3.14	0.00	0.30	93.31
26	4.90	2.00	0.46	3.77	0.06	0.06	93.66
27	6.56	3.59	0.35	4.06	0.08	0.23	91.69
33	4.76	1.30	0.74	8.37	0.37	0.19	89.02
36	3.43	0.97	1.17	7.18	0.19	0.39	90.10
39	4.24	2.15	1.60	0.87	0.05	0.25	95.08
AVG		1.94	0.88	3.43	0.14	0.19	93.42

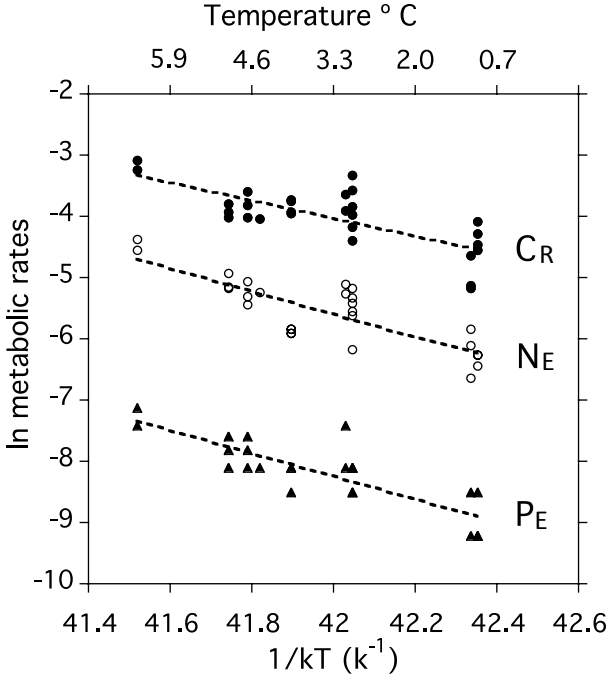

Fig. 4. Arrhenius plots for specific respiration (C_R) and excretion rates (N_E and P_E). Abscissae: 1000 (1/K; down) and temperature (°C; up). Ordinates: ln specific metabolic rates in µmol (C_R, N_E and P_E) µmol C_{zoo}^{-1} day^{-1}.

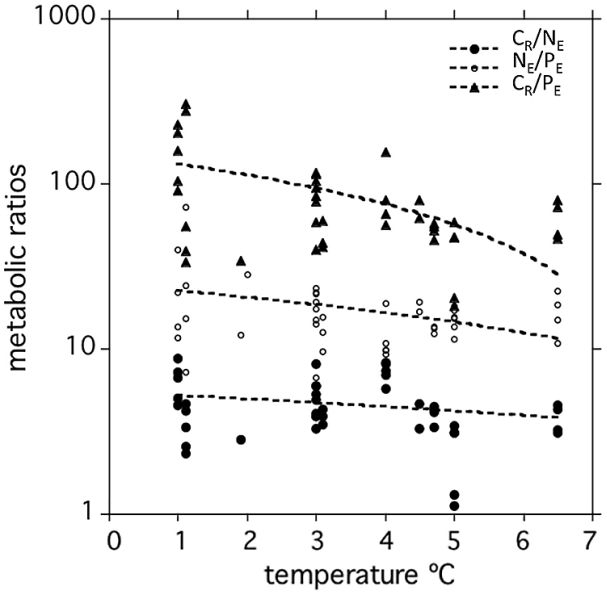

Fig. 5. Linear relationship between temperature and $C_R : N_E$, $N_E : P_E$ and $C_R : P_E$ ratios in atoms. Ordinates are in log scale. Metabolic rates as in Fig. 3.

and composition. Although in these conditions the increase of metabolic rates associated with feeding (the Specific Dynamic Action, SDA, Grisolia and Kennedy 1966) was excluded, the relative proportion of the metabolic products would not have changed in the short incubation time (12–24 h, Ikeda, 1977). Similarly, the lack of relation between "in situ" temperature and food concentration and composition (Table 2) precluded any bias in the response of zooplankton metabolism to temperature.

Differences in the taxonomic composition and trophic habit of zooplankton when mixed samples are incubated are additional sources of variability in the metabolic rates (Mayzaud and Conover, 1988). In our case, there was an

Table 4. Exponential equations relating temperature in °C (t) with C respiration (C_R) and NH_4-N (N_E) and PO^4-P (P_E) excretion rates.

Metabolic activity	Equation	r^2	N
C Respiration	$C_R = 0.0093 \times e^{(0.20 \times t)}$	0.52	42
N Excretion	$N_E = 0.0017 \times e^{(0.26 \times t)}$	0.59	40
P Excretion	$P_E = 9.8 \times 10^{-5} \times e^{(0.29 \times t)}$	0.67	44

Table 5. Activation energy (eV), Q_{10} for the temperature range explored, determination coefficient and number of data corresponding to the metabolic processes represented in the plots of Fig. 3, and previous data from other authors: (1): This work (in parentheses the E_a limits for the 95 % significance). (2): Average values for mixed Arctic and Antarctic zooplankton (euphausiids, amphipods, polychaetes and copepods, Hirche, 1984, Table 2). (3): Average values for several Arctic copepods (Hirche, 1987). (4): Surface Arctic plankton (all experiments, Vaquer-Sunyer et al., 2010). (5): Surface Arctic plankton (Spring, Vaquer-Sunyer et al., 2010). (6): *Calanus glacialis* (M. Alcaraz, unpublished data)

Metabolic activity	(E_a, eV)	E_a limits 95 %	Q_{10} (1.0–6.5 °C)	r^2	N
C_R (1)	1.292	(0.994–1.586)	6.51	0.51	42
N_E (1)	1.685	(1.328–2.032)	11.50	0.61	40
P_E (1)	1.905	(1.715–)2.185	15.73	0.73	44
C_R (2)	1.086	–	3.05	0.94	–
C_R (3)	1.331	–	3.19	0.94	–
C_R (4)	1.05	–	5.0	0.27	40
C_R (5)	1.56	–	15.5	0.55	19
C_R (6)	1.679	–	11.40	0.77	12

absolute dominance of herbivorous zooplankton taxa (mainly copepods, euphausiids and appendicularians), while the proportion of carnivores (chaetognaths, cnidarians and amphipods) was negligible. Although the trophic habit of the experimental organisms was mostly herbivorous, and the proportion of the different taxa across the experimental stations was relatively constant (Table 3), the variability observed in the response of metabolism to temperature was likely a consequence of the mixed character of the experimental community.

4.2 Response of metabolic processes to temperature

The activation energy for the metabolic processes analysed here falls in the range found for respiration in Arctic plankton (Vaquer-Sunyer et al., 2010) and copepods (M. Alcaraz, unpublished data). Lower values, between half and one third of our results, have been obtained for heterogeneous taxonomic ensembles, different biological activities, and contrasting environments (0.65 eV, Dell et al., 2011). The differences could be due to the systematic variation of E_a across broad temperature ranges, especially for relatively high E_a values as mentioned by Huey and Kingsolver (2011). However, the lack of homogeneity in the data set (the high variance of metabolic rates, and the short span of environmental temperature, typical of the Arctic ocean), clearly bias the slopes of the Arrhenius plots (E_a values). Nevertheless, the relative differences between metabolic processes appear as statistically significant.

Table 6. Parameters of the linear regression equations relating temperature in °C and the metabolic quotients (atoms). *: Significant correlations ($p > 95$ %). Avg: Quotients for the average "in situ" temperature. 6 °C: Quotients for a temperature increase of 6 °C.

	a	b	r^2	Avg	6 °C
C_R / N_E	5.45	−0.252	−0.25	4.58	3.25
C_R / P_E	149.7	−18.68	−0.51*	85.7	37.62
N_E / P_E	23.8	−1.87	−0.31*	17.0	12.58

Table 7. Comparison between the N and P daily required by phytoplankton for primary production, and zooplankton supply ($g\,m^{-2}\,day^{-1}$) and contribution to phytoplankton requirements (%) at average temperature (2.7 °C) and for predicted 6 °C increase.

	N	P
Phyto. requirements	0.164	0.023
Zoo. excretion (avg)	0.049	0.007
Zoo. excretion (6 °C)	0.115	0.018
% PP zoo. nutrient supply (avg)	29.885	29.890
% PP zoo. nutrient supply (6 °C)	70.482	77.830

An important consequence of the diverse E_a values for the analysed metabolic activities was the different Q_{10} values for C-respiration and N- and P-excretion rates. The relationship between the Q_{10} values (Q_{10}-P_E : Q_{10}-N_E : Q_{10}-C_R) was 2.4 : 1.7 : 1. Previous data on zooplankton metabolic response to temperature result in Q_{10} values from 2 to 3 times lower than our estimates (Ikeda and Hing Fay, 1981; Ikeda, 1985; Ikeda et al., 2001) for a huge collection of zooplankton taxa and across a broad span of temperatures and individual body mass. One of the reasons for the uncommonly high Q_{10} values here obtained is the short temperature range for which those Q_{10} have been estimated. Aside from the variability of E_a as mentioned in Huey and Kingsolver (2011), given a constant E_a, Q_{10} is inversely related to the average absolute temperature range for which it is estimated (see Eq. 2). It is worth mentioning that Q_{10} differences between metabolic rates of zooplankton are by no means rare. Ikeda and Hing Fay (1981), Ikeda (1985), and Ikeda et al. (2001), amongst others, also obtained higher Q_{10} values for N_E than for C_R, agreeing with our results. Nevertheless,

the same statistical problems as discussed in relation to E_a (i.e. the non-homogeneity of the data set and the short span of temperature) would explain the anomalous Q_{10}. In any case, in spite of the variability induced by the heterogeneous character of the experimental organisms and the short spread of the data, the different sensitivity of the metabolic processes to temperature seem to be confirmed by the statistical significance of the differences between the thermal coefficients.

Higher Q_{10}-P_E than Q_{10}-N_E has direct consequences for the future evolution of the relative proportion of N and P in the inorganic nutrient pool available for phytoplankton (Sterner, 1990; Alcaraz et al., 2010). A temperature rise of 6 °C in the Arctic Ocean (Vaquer-Sunyer et al., 2010) would not only increase by a factor of 2.5 the average daily nutrient turnover rates of N_E and P_E (Table 7), but the N : P ratio will diminish by half (from an average value of 23.8 at 0 °C to 12.58 at 6 °C, Table 6). Given the important contribution of organic N and P compounds in the products excreted by zooplankton (Conover and Gustavson, 1999; Saba et al., 2009), these effects could be more intense.

In spite of the anomalous Q_{10} values derived from the high variance of metabolic rates, and the short span of data sets, our results suggest that the changes in the proportion of the N and P supplied by zooplankton excretion as a consequence of temperature increases would modify the proportion and quality of the dissolved nutrient pool. Due to the significant contribution of zooplankton excretion to phytoplankton nutrient requirements (according to the estimated Q_{10} values, about 70 % at the predicted 6 °C temperature rise, Table 6), the N : P stoichiometric changes induced in the dissolved nutrient pool by temperature rises could modify fundamental properties of autotrophs. Changes in cell size, taxonomic composition, production, nutritive value, etc. (Sterner, 1990), could induce a shift in the food web characteristics that would affect the whole Arctic marine ecosystems.

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