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Temperature dependence of Arctic zooplankton metabolism and excretion stoichiometry

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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 O_2 consumption and NH_4-N and PO_4-P excretion, but also to investigate the possible relationships between temperature and the stoichiometry of the metabolic products. Zooplankton metabolic rates increased according to the rising temperature conditions, following the Arrhenius equation. However, the activation energy differed for the various metabolic processes considered. Respiration was the metabolic activity less affected by temperature, followed by NH_4-N and PO_4-P excretion, and as a consequence the values of the C : N, C : P and N : P quotients of the metabolic products were inversely related to temperature. The effects of temperature on the stoichiometry of the excretion products would contribute to modify the nutrient pool available for phytoplankton and induce qualitative and quantitative shifts in the characteristics of primary producers that could possibly translate into 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 (Comisso et al., 2008), with unpredictable though important consequences for such vulnerable ecosystems (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 Nichol, 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-respiration losses, NH_4-N and PO_4-P excretion of Arctic zooplankton, and explore the possible differences in the Arrhenius' activation energy for the different metabolic activities. In a scenario of rising temperatures, the consequences of differential responses by the these metabolic processes would be changes in the C : N : P stoichiometry of the excreted products. If persistent, the progressive changes in the inorganic N and P proportion in the nutrient pool could induce a shift in the phytoplankton communities that could affect the whole Arctic food web.

2 Methods

The study took place in July 2007 during the ATOS-Arctic cruise on board the R/V *Hespérides*, in a network of stations located in the East Greenland current, the Fram strait and NW Svalbard (Fig. 1), in a range of temperature spanning from 1 °C to 6.56 °C (Alcaraz et al., 2010).

Zooplankton metabolism (respiration, NH_4-N and PO_4-P 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 isolated containers and translated to the laboratory, where organisms were washed three times with 0.2 µm-filtered water at "in situ" temperature.

Water for incubation experiments was obtained with a 12 l Niskin bottle from 20 to 40 m depth and filtered with 0.2 µm AcroPack® 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). Aliquots of zooplankton were enclosed in experimental chambers and incubated for 12–24 h in thermostatic baths filtered at "in situ" temperature ±0.1 °C and dim light.

Zooplankton respiration rates were estimated as the decrease in dissolved oxygen concentration during the incubation. The analyses were made with two OXY-4 PreSens® 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. Respiratory C losses were calculated assuming an $RQ = 0.97$ (Omori and Ikeda, 1984).

Excretion rates were estimated in the same incubation experiments as for respiration. NH_4-N and PO_4-P 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 into broad plastic tips closed with 100 µm-mesh in order to avoid extracting zooplankton organisms with the water sample. NH_4-N was analysed by a fluorimetric method described by Kéruel and Aminot (1997), and PO_4-P 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 further measurement of experimental biomass as zooplankton carbon (C_{zoo}) according to Alcaraz et al. (2003; 2010). Biovolume (BV) determinations were made using automatic image analysis (ZooImage®) and the BV-C_{zoo} factor conversion used was that given for Arctic zooplankton by Alcaraz et al. (2010). C-specific metabolic rates were calculated as the quotient between gross respiration and excretion rates (µmol C, N and P day^{-1}) and the corresponding experimental biomass (µmol C_{zoo}). In order to avoid the interference of body mass on specific metabolic rates (Ikeda, 1985), only those experiments in which the average individual zooplankton biomass (I.M.) fell in the range comprised by average I.M. ± SD (13.31 ± 11.6 µmol C ind^{-1}) for the whole study were considered in the analysis. The independence of I.M. from environmental temperature was also verified.

The response of metabolic rates to temperature has been adjusted to the Arrhenius equation,

$$V = V_0 \cdot e^{(E_a/RT)} \tag{1}$$

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; 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 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 (8.6173×10^{-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

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

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 eV into J mol^{-1} is $f = 8.314 \times 10^{-3}(\text{J K}^{-1}\,\text{mol}^{-1})/8.617 \times 10^{-5}(\text{eV K}^{-1}) = 96486.9$.

The metabolic C : N, C : P and N : P quotients were calculated as the ratios between the specific C respiration and NH_4-N and PO_4-P excretion rates for individual experiments and expressed in atoms. The relationships between temperature and the metabolic quotients were estimated as the corresponding linear regression equations.

3 Results

The average individual biomass of experimental zooplankton (I.M.) and temperature were not statistically related ($r^2 = 0.04$, $P > 0.21$), therefore we should not expect any interference of I.M. on metabolism. Zooplankton metabolism increased exponentially with temperature, the corresponding determination coefficients of the equations relating temperature and specific metabolic rates being significant (Table 1 and Fig. 2), with exponents increasing from 0.2 (respiration) to 0.26 (P excretion).

The corresponding Arrhenius plots (Eq. 1), in which the logarithms (ln) of the metabolic rates have been plotted against the reciprocal of absolute temperature times the Boltzmann constant ($1/kT$) are shown in Fig. 3. As mentioned above, the slopes of the linear regression equations are equivalent to the E_a in eV. The highest value corresponded to P-excretion rates ($E_a = 1.902$ eV), followed by N-excretion, $E_a = 1.686$ eV and C-respiration, $E_a = -1.293$ eV. However, when comparing the corresponding activation energy values, the differences between C-respiration and N-excretion, or between N- and P-excretion were not statistically significant, and only C-respiration and P-excretion differed statistically (Table 2). Because of the gradient in E_a values, the metabolic activity least affected by temperature was respiration ($Q_{10} = 6.51$), followed by NH_4N and PO_4-P excretion, with Q_{10} values of 11.5 and 15.73 respectively (Table 2).

The atomic C : P and N : P metabolic ratios were inversely related to temperature, the correlation coefficients being higher than the critical r value to validate the null hypothesis $H : r = 0$, $P < 0.05$ (Fig. 4 and Table 3). On average, a temperature increase of 1 °C involves a decline in C : P and N : P ratio by 22 % and 11 %, respectively. For C : N ratios the correlation was not statistically significant. The average atomic C : N : P metabolic ratios across the different temperature conditions, and those corresponding to a predicted temperature rise of 6 °C (Vaquer-Sunyer et al., 2010) are also indicated.

The contribution of the nutrients excreted by zooplankton (Table IV) to the N and P required for the primary production values recorded during the cruise (0.93 $\mathrm{g\,C\,m^{-2}\,day^{-1}}$, Lasternas and Agustí 2010) are indicated in Table 4. The excretion contribution rises from 30 % (average temperature) to more than 70 % for the predicted temperature rise.

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 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 respiration predicts a tendency towards heterotrophy as a consequence of expected temperature rise (Wassmann et al., 2008; Vaquer-Sunyer et al., 2010; Regaudie-de-Gioux and Duarte, 2012). Similarly, increasing temperature could lead to an imbalance between ingestion and respiration in Arctic copepods (Alcaraz et al., 2012) 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-Suñé et al., 2010, Alcaraz et al., 2012).

The results here obtained for zooplankton C-respiration losses and NH_4-N and PO_4-P excretion show the rising traits of what was presumed to be an unimodal response similar to the one found for respiration in different Arctic copepod species by Hirche (1987), and for respiration and ingestion by Tande (1988) and Alcaraz et al. (2012). Nevertheless, these unimodal patterns occurred in experiments made with monospecific copepods, and a temperature acclimation range of 10 °C, while in the present case the experiments corresponded to mixed, acclimatized zooplankton and a narrower (5.5 °C) temperature span.

The activation energy for the metabolic processes here analysed fall in the range found for respiration in Arctic plankton (Vaquer-Sunyer et al., 2010) and copepods (Alcaraz et al., 2012). Lower values, between 0.5 and 0.3 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 the broad temperature range analysed, especially for relatively high E_a values, as mentioned by Huey and Kingsolver (2011).

An important consequence of the diverse E_a values for the analysed metabolic activities was the different Q_{10} values for Crespiration and N- and P-excretion rates. The relationships between the Q_{10} values ($Q_{10\text{-P}} : Q_{10\text{-N}} : Q_{10\text{-C}}$) were 2.4 : 1.7 : 1, respectively. Previous data on zooplankton metabolic response to temperature results in Q_{10} values from 2 to 3 times lower than our estimates (Ikeda and Hing Fay, 1981; Ikeda, 1985; Ikeda et al., 2001) with higher Q_{10} values for N-excretion than for respiration both in Antarctic zooplankton and for a huge collection of zooplankton taxons across a broad span of temperatures and individual body mass.

Higher $Q_{10\text{-P}}$ than $Q_{10\text{-N}}$ has direct consequences for the future evolution of the relative composition of 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 by excretion of NH_4-N and PO_4-P (Table 4) but the N : P ratio of the inorganic excreted products will diminish by half (from an average value of 23.8 at 0 °C to 12.58 at 6 °C Table 3). Given the importance of the organic N and P fraction excreted by zooplankton (Conover and Gustavson 1999; Saba et al., 2009) these effects could be more intense.

Our results suggest that the significant 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 characteristics of the dissolved nutrient pool. According to the high and significant contribution of zooplankton excretion to the phytoplankton nutrient requirements (about 70 % at the predicted 6 °C temperature rise, Table 4), the N : P stoichiometric changes induced by temperature rises could modify fundamental properties of autotrophs like size, taxonomic composition, production, nutritive value, etc. (Sterner, 1990), thus inducing a shift in the food web characteristics that could affect the whole Arctic marine ecosystems.

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Table 1. Exponential equations relating temperature in °C with C-specificrespiration and NH_4-N and PO^4-P excretion rates.

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

Table 2. 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, polychaets 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* (Alcaraz et al., 2012).

Metabolic activity	a	b (E_a, eV)	E_a limits 95 %	Q_{10} (1.0–6.5°C)	r^2	N
C-respiration (1)	50.28	1.292	(0.994–1.586)	6.51	0.51	42
NH_4-N excretion (1)	65.25	1.685	(1.328–2.032)	11.50	0.61	40
PO_4-P excretion (1)	71.59	1.905	(1.715–2.185)	15.73	0.73	44
C-respiration (2)	53.72	1.086	–	3.05	0.94	–
C-respiration (3)	53.07	1.33		3.19	0.94	–
C-respiration (4)		1.05		5.0	0.27	40
C-respiration (5)		1.56		15.5	0.55	19
C-respiration (6)	66.60	1.679	–	11.40	0.77	12

Table 3. 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/N	5.45	−0.252	−0.25	4.58	3.25
C/P	149.7	−18.68	−0.51*	85.7	37.62
N/P	23.8	−1.87	−0.31*	17.0	12.58

Table 4. Comparison of daily nutrient excretions according to the equations at Table 1 for average experimental temperature (2.7 °C), and for predicted 6 °C. Integrated primary production (PP) during the study = 0.93 g C m^{-2} day^{-1} (Lasternas and Agusti, 2010); N and P phytoplankton requirements calculated according C : N : P ratios equal to 106 : 16 : 1 (Redfield et al., 1963). Zooplankon N and P excretion in g m^{-2} day^{-1}, considering the average zooplankton biomass = 12.23 g C_{zoo} m^{-2} (Alcaraz et al., 2010).

	N	P
Phyto requirements	0.164	0.023
Nutrient concentration	1.646	0.269
% consumption	9.947	8.704
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

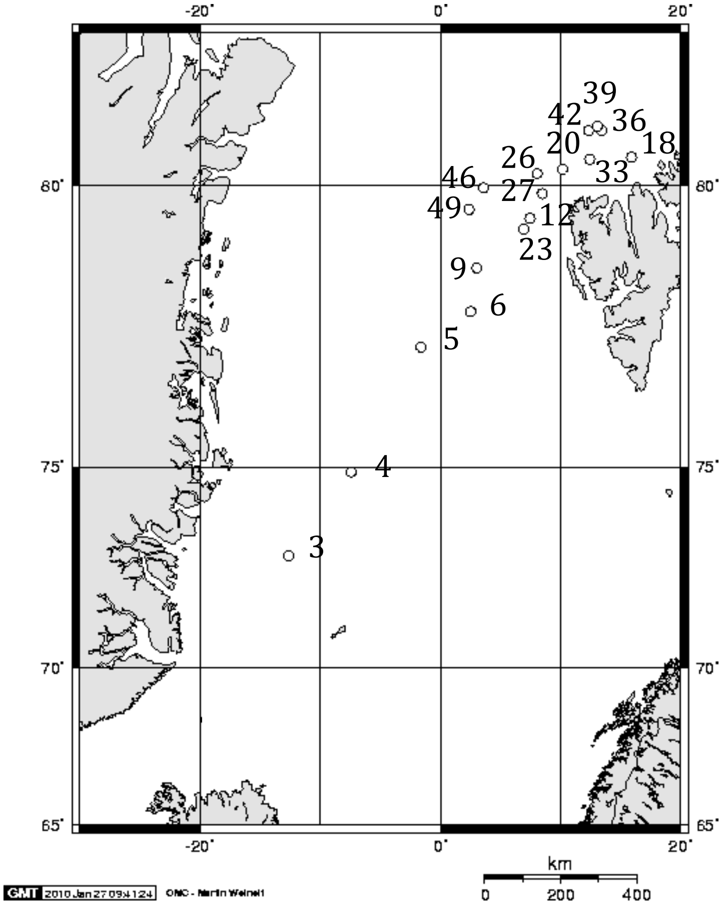

Fig. 1. Map of the study area and position of the sampled stations.

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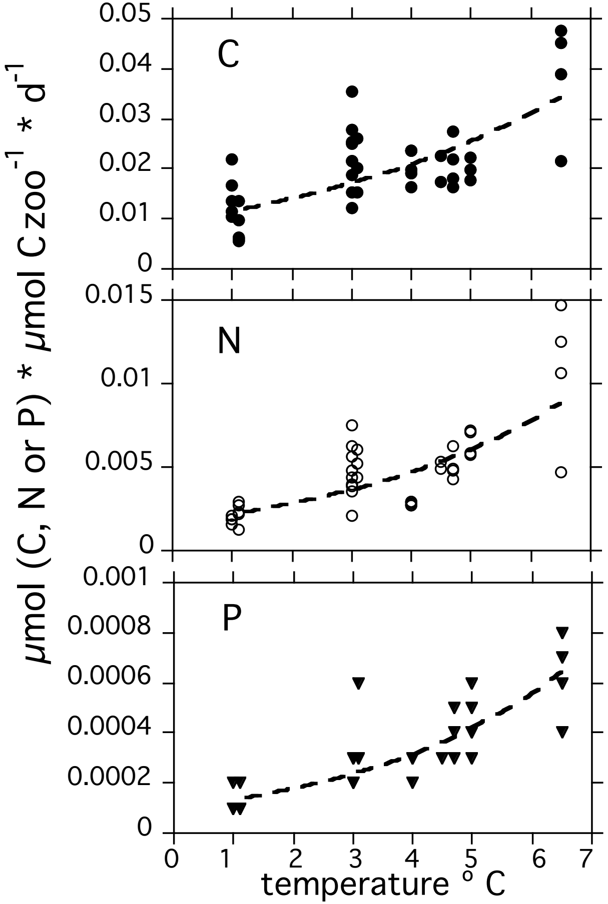

Fig. 2. Relationships between temperature and C-specific respiration and N- and P-excretion rates.

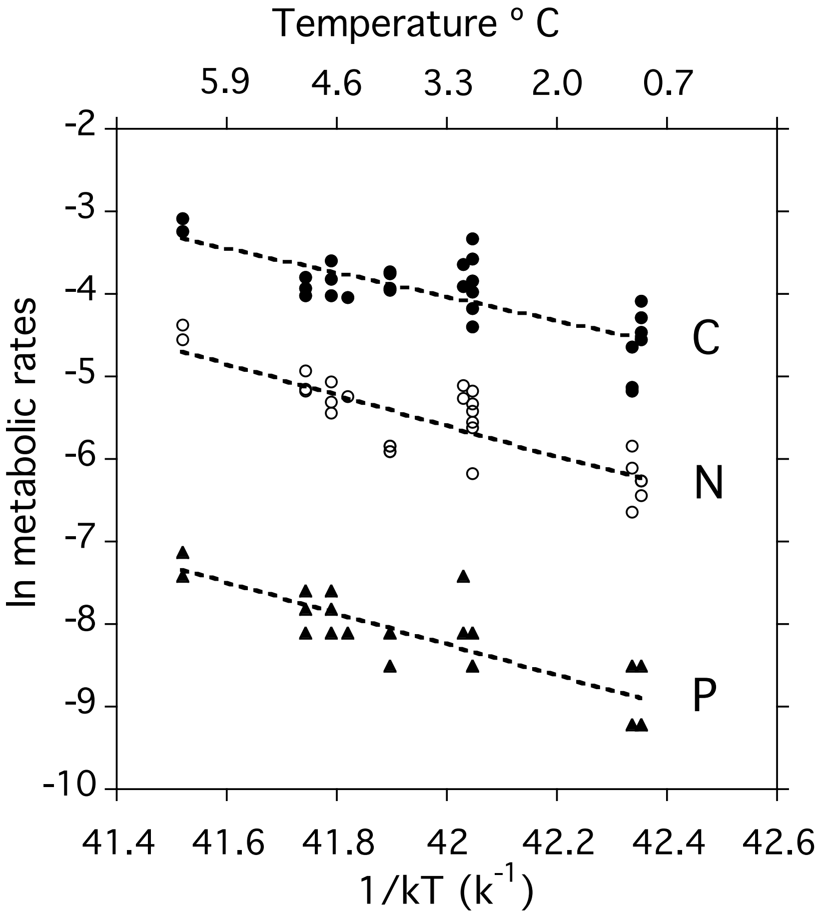

Fig. 3. Arrhenius plots for specific C losses and N and P excretion. Abscissae: 1000·(1/K) (down); °C (up). Ordinates: ln metabolic rates in µmol (C, N or P) µmol C_{zoo}^{-1} day^{-1}.

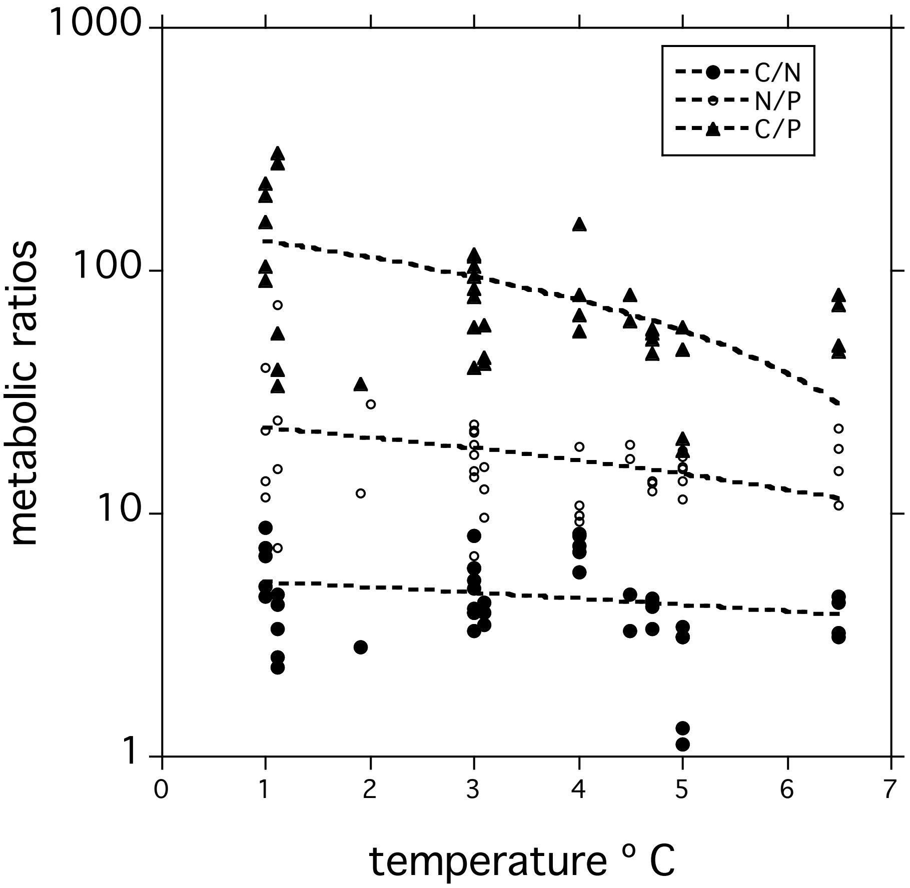

Fig. 4. Linear relationship between temperature and C : N, N : P and C : P metabolic ratios. Ordinates are in log scale. Metabolic rates as in Fig. 3.