

Temperature and the chemical composition of poikilothermic organisms

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Summary

1. Temperature strongly affects virtually all biological rate processes, including many central to organismal fitness such as growth rate. A second factor related to growth rate is organismal chemical composition, especially C : N : P stoichiometry. This association arises because high rates of growth require disproportionate investment in N- and P-rich biosynthetic cellular structures. Here the extent to which these factors interact is examined – does acclimation temperature systematically affect organismal chemical composition?

2. A literature survey indicates that cold-acclimated poikilotherms contain on average 30–50% more nitrogen [N], phosphorus [P], protein and RNA than warm-exposed conspecifics. The primary exception was bacteria, which showed increases in RNA content but no change in protein content at cold temperatures.

3. Two processes – changes in nutrient content (or concentration) and in organism size – contribute to the overall result. Although qualitatively distinct, both kinds of change lead to increased total catalytic capacity in cold-exposed organisms.

4. Temperature-driven shifts in nutrient content of organisms are likely to resonate in diverse ecological patterns and processes, including latitudinal and altitudinal patterns of nutrient content, foraging decisions by organisms living in strong temperature gradients, and patterns of biodiversity.

Key-words: Acclimation, growth, nitrogen, phosphorus, stoichiometry

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Introduction

Temperature profoundly affects growth and its underlying processes (von Bertalanffy 1960; Cossins & Bowler 1987; Hochachka & Somero 1984; Gillooly *et al.* 2001). For poikilotherms, rising temperature leads to increasing rates of biochemical processes, physiological processes (e.g. heart rate) and life-history characteristics such as development time and foraging rate. A second factor, chemical composition (in particular C : N : P stoichiometry), also now appears to be related to growth rates (Elser *et al.* 1996; Sterner & Elser 2002). To supply tissues with the right materials at high rates, rapidly growing organisms must maintain high concentrations of catalytic units in their cells, especially nitrogen-rich proteins and phosphorus-rich

rRNA. Proteins contain about 17% N by mass and often make up a large fraction of total organismal N (Elser *et al.* 1996). Likewise, RNA is about 10% P by mass and often accounts for most of total organismal P (Elser *et al.* 2000b; Sterner & Elser 2002). Thus, rapidly growing organisms often have high N and P content (Elser *et al.* 2000b).

An important but unresolved question is the extent to which these factors interact – does changing temperature lead, in general, to changing chemical composition? A rich literature has established that poikilothermic organisms acclimated to low temperatures often show extensive internal reorganization (Hochachka & Somero 1984), including larger cell size or body size (Atkinson 1994; Partridge *et al.* 1994; Van Voorhies 1996), increased enzyme activity and altered membrane composition (Hazel & Prosser 1974; Hazel 1995), and proliferation of intracellular mitochondria and lipid droplets (Sidell 1998). However, it remains unclear whether these individual effects, in aggregate, result in strong stoichiometric signals at the whole-organism level. The answer is important to understanding the

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fundamental biochemical processes occurring in organisms. In addition, if temperature systematically alters the chemical composition of individuals, these effects may be readily apparent in ecological patterns and processes involving N and P. Here we examine this question using data on organismal composition compiled from a literature survey.

The data set

Data expressed in terms of elements (N and P) or macromolecules (protein and RNA) were compiled from the literature (see Appendix A for a list of species in the survey and a link to a fuller online description of the data). Data were accepted only if they reflected a major fraction of total N and P or total protein and RNA – thus excluding data on concentration or activity of particular enzymes (Hazel & Prosser 1974; Pearcy 1977; Sidell 1977). Similarly, data on RNA or P were included only if they were likely to reflect the bulk of RNA or P (e.g. rRNA, ribosomes, total RNA but not tRNA or mRNA). In addition, data were included if individual organisms, or suborganismal parts, were exposed to temperatures differing on average by at least 5 °C.

We also noted whether data were expressed as contents or amounts, a distinction prompted by the diversity of units presented in the literature. Contents refer to percentage by mass (usually dry) of some constituent, whereas amounts refer to the total mass of that constituent in an individual organism. Some units are ambiguous – whether they represent contents or amounts depends on the scale at which they are viewed; in these cases, we assigned the unit as a concentration or an amount based on how the authors used it in the text.

When data from multiple temperatures were reported, we used measurements from the highest and lowest temperature treatment groups, except when the authors indicated that these temperatures were outside the normal operating range. Temperature treatments (all shifts between 5 and 30 °C in magnitude) may have been experimental (i.e. laboratory acclimation) or seasonal (i.e. field acclimatization), a restriction excluding populations or species distributed *spatially* across temperature gradients. Most acclimation times were in the order of weeks. We did not attempt to evaluate degree of acclimation, as the rapidity of acclimatory adjustments will depend on, among other factors, taxonomy, metabolic rate and life history. Instead, we simply assumed that authors knew their organisms well enough to determine when they were ‘acclimated’.

From each study we extracted data on chemical composition of organisms exposed to high and low temperatures and, for each pair of measurements, calculated a ratio of the value from the cold-acclimated organism to the value from the warm-acclimated organism (intraspecific comparisons only, see link in

Appendix). The ratios were subsequently \log_{10} -transformed. When multiple tissues were assayed from a particular species, we used the arithmetic mean of the cold/warm ratios for each tissue. This calculation is strictly accurate only when tissues each contain the same amount of the biomolecule or element (or the same fraction of the total amount). Ideally, the values should be weighted according to the fraction of total biomolecule or element contained by each tissue; in practice, however, there were never enough data to make this calculation. When species were tested independently in separate publications, species’ mean values were calculated as the arithmetic mean of \log_{10} -transformed ratios. This method discounts the very high ratios published for some species, thus providing conservative estimates of compositional shifts in those species.

Results

Organisms in the collected studies were exposed to high and low temperatures that differed, on average (\pm SEM), by 15.3 ± 0.5 °C. Altogether 75 species were represented: 21 plants, 25 animals, 20 algae, 8 bacteria and 1 yeast. For N-containing compounds (pooled data on N and protein), we found data for 69 species total. The mean \log_{10} ratio (\pm SEM) was 0.119 ± 0.019 . Cold-exposed tissues thus had, on average, 32% ($= 10^{0.119}$) more N or protein than warm-exposed tissues ($t_{77} = 6.22$, $P < 0.001$). The degrees of freedom are greater than the species count because, for nine species, data were available on both N and protein separately. For P-containing compounds (pooled data on P and RNA), data were available on 41 species. The mean \log_{10} ratio was 0.173 ± 0.033 . Cold-exposed tissues thus had, on average, 49% ($= 10^{0.173}$) more P or RNA than warm-exposed tissues ($t_{43} = 5.30$, $P < 0.001$). Data on both P and RNA were available for three species.

The result did not depend strongly on whether the currency considered was N and P or protein and RNA (Fig. 1). The means of the \log_{10} values of N and protein were both significantly higher than zero (N: mean \log_{10} ratio = 0.125 ± 0.043 , $10^{0.125} = 33\%$, $t_{23} = 2.96$, $P < 0.01$; protein: 0.119 ± 0.021 , $10^{0.119} = 32\%$, $t_{52} = 5.76$, $P < 0.001$, respectively) but not significantly different from each other ($t_{75} = 0.13$, $P = 0.89$). In the survey, the mean values of the distributions of P and RNA were both positive (P: mean \log_{10} ratio = 0.306 ± 0.166 , $10^{0.306} = 102\%$, $t_5 = 1.84$, $P = 0.12$; RNA: mean \log_{10} ratio = 0.152 ± 0.027 , $10^{0.152} = 42\%$, $t_{37} = 5.52$, $P < 0.001$). The increase in P was not statistically significant, perhaps for lack of power. The means of the \log_{10} values of P and RNA also did not differ significantly from each other. These data support our assumption (above) that N and protein, and P and RNA, are strongly coupled currencies.

Temperature-driven shifts in composition occur broadly across taxa. Three of four groups (plants, animals, and algae and yeast) contained significantly more nitrogen following cold exposure, and all groups contained

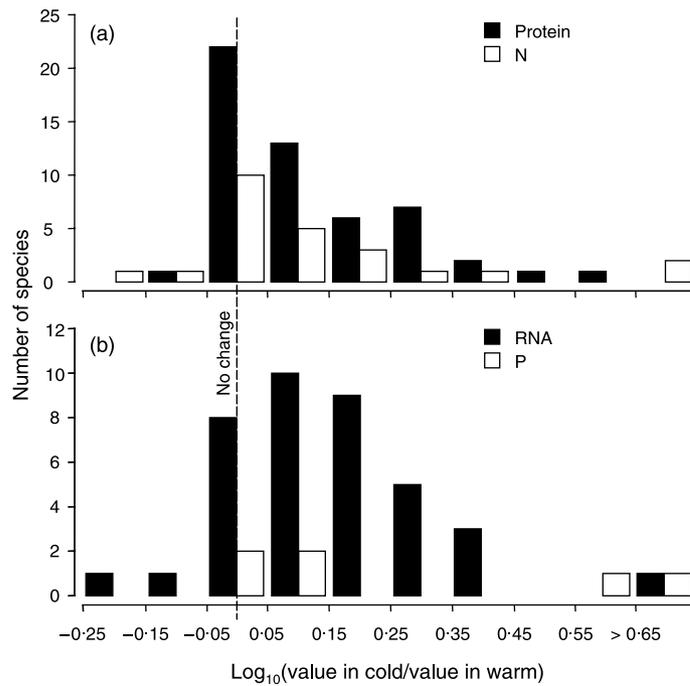


Fig. 1. Histograms of the effects of acclimation to different temperatures on N or protein composition (a) and P or RNA composition (b) in poikilothermic organisms. Data in (a) are partitioned into two groups, those from studies measuring protein concentration or amount and those from studies measuring nitrogen concentration or amount; similarly, data in (b) are partitioned into those from studies measuring RNA and those measuring phosphorus concentration or amount. For each species, we calculated a ratio of the measurement at the cold acclimation temperature divided by the measurement at the warm acclimation temperature; and to normalize the data, we \log_{10} -transformed all ratios. Data bins in the histograms are centred on 0, 0.1, 0.2, etc. and are 0.1 units wide, e.g. the bin centred around zero extends from -0.05 to $+0.05$.

Table 1. Summary of cold-induced shifts in the composition of major groups of poikilothermic organisms (number of species in parentheses after mean values)

	N and protein		P and RNA	
	Mean \log_{10} ratio (\pm SEM)	Mean increase	Mean \log_{10} ratio (\pm SEM)	Mean increase
Plants	0.145 ± 0.038 (19)	39.6%**	0.176 ± 0.044 (12)	50.2%**
Animals	0.109 ± 0.029 (24)	28.5%**	0.099 ± 0.027 (15)	25.7%**
Algae and yeast	0.129 ± 0.042 (21)	34.6%**	0.250 ± 0.146 (6)	78.0%
Bacteria	-0.006 ± 0.012 (5)	-1.4%	0.198 ± 0.078 (8)	54.9%*

* $P = 0.05$; ** $P < 0.01$.

more P after cold exposure (Table 1, Fig. 2). The separate groups, with the exception of bacteria, thus showed systematic effects of temperature on chemical composition. For algae and yeast, the mean increase in P-containing compounds, though large (78% = $10^{0.250}$), was not significantly different from zero, probably reflecting small sample size ($N = 6$). The primary exception to the overall pattern was bacteria, which showed no evidence for increased N or protein in the cold.

We considered correcting the data by the magnitude of difference between maximum and minimum acclimation temperatures. However, the utility of such an

analysis depends on there being a clean relationship between the two variables. In fact, the magnitude of the shift in composition was unrelated to the magnitude of the temperature shift (Fig. 3). The relationship was positive for N and protein, but the slope was not significantly different from zero (best-fit line: \log_{10} ratio = $0.065 + 0.0036 * \text{temperature shift}$; $F_{1,74} = 1.02$, $P = 0.3$). For P and RNA, the relationship was flat (best-fit line: \log_{10} ratio = $0.165 + 0.0006 * \text{temperature shift}$; $F_{1,41} = 0.0006$, $P = 0.9$).

For the analyses above, data expressed as contents (per dry mass, etc., 76% of measurements) and as amounts (per cell, per organ, etc., 24% of measurements)

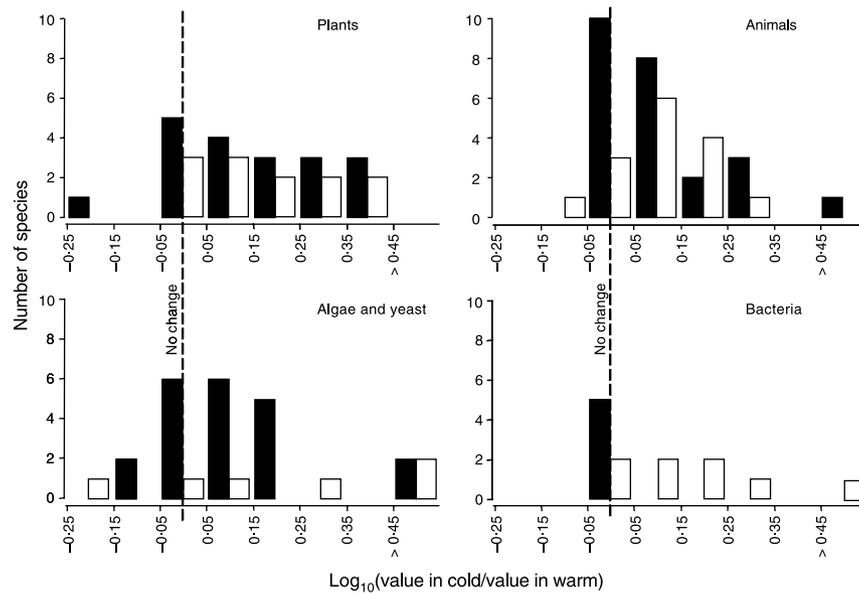


Fig. 2. Nutrient composition of species acclimated to different temperatures in four broad taxonomic groups. Within each group, data on protein and N were pooled (■), as were data on RNA and P (□). Plants, animals, and algae and yeast had significantly higher values of protein and N following cold exposure, and all groups showed higher values of RNA and P following cold exposure (the increase in algae and yeast was not significant, probably because of the small sample size; see Table 1). Protein and N in bacteria were the exception to the overall pattern, showing no evidence for temperature-induced change.

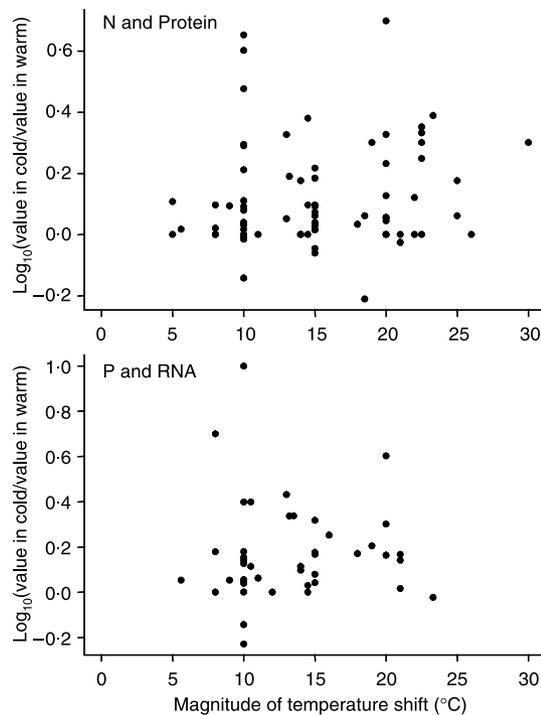


Fig. 3. Relationship between magnitude of temperature difference and magnitude of shift in composition. Neither slope was significantly different from zero (see text for statistics).

were pooled. We analysed the effect of this distinction by partitioning the data into two groups (contents and amounts) and, within each group, calculating for each species a mean ‘nutrient content’ ratio, defined as the mean value of the \log_{10} ratios for N- and P-containing

compounds. Both kinds of data indicated significant cold-induced increases in catalytic material (Fig. 4). The mean nutrient content ratio for data expressed as contents was 0.105 ± 0.017 ($27.4\% = 10^{0.105}$; $t_{63} = 6.11$, $P < 0.001$), and the mean ratio for data expressed as amounts was 0.185 ± 0.039 ($53\% = 10^{0.185}$; $t_{24} = 4.73$, $P < 0.001$). However, studies measuring total amounts per individual or cell, on average, recorded significantly larger cold-induced increases in nutrients than studies measuring contents per cell or individual ($t_{87} = 2.17$, $P = 0.03$). The mean temperature treatments for the two groups was not different (15.4 ± 0.6 °C and 14.9 ± 1.0 °C, respectively, $P = 0.66$).

Discussion

This analysis indicates that exposure to cold temperatures leads to increasing nutrient content of poikilothermic organisms. The pattern was apparent whether the currency used was protein and RNA or N and P, thus supporting the idea that these alternative currencies reflect a common, underlying, catalytic currency. Moreover, the pattern remained when the data set was partitioned along taxonomic lines. Bacteria were the primary exception to the overall pattern: as a group, bacteria showed strong increases in RNA, but no change in the amount of protein, following cold exposure. In *Escherichia coli*, the contents of both total and functioning ribosomes increase during cold exposure (Yun, Hong & Lim 1996), perhaps explaining observed disproportionate increases in RNA and P. However, it remains unclear why proteins do not respond when catalytic RNAs do. The importance of bacteria to

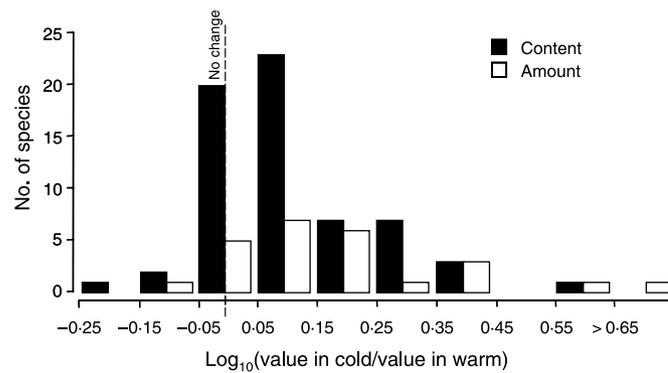


Fig. 4. Effects of acclimation to different temperatures on species from studies in which data were expressed as contents or amounts. Data on N- and P-containing compounds were averaged within species. The mean values of both groups were significantly greater than zero, but the mean value of data expressed as amounts was significantly higher than the mean value of data expressed as contents.

regional and global elemental cycles (Rivkin & Legendre 2001; Hoppe *et al.* 2002) suggests that additional work on temperature and bacterial stoichiometry should be a high priority.

Shifts in composition were unrelated to the magnitude of the temperature treatment (Fig. 3). At least two kinds of explanations may account for this result. First, a positive relationship may exist, but the data are noisy enough (e.g. owing to different methods and acclimation times among studies) to obscure it. A second, more likely, explanation is that the biological meaning of temperature change varies from species to species – for example, if stenothermal species respond physiologically to small temperature changes as strongly as eurythermal species respond to large temperature changes (e.g. van Dijk *et al.* 1999). Insufficient data are available to evaluate the relative eurythermality of species in the survey. Logically, the magnitude of the effect must fall to zero as the temperature shift approaches zero. Indeed, species subjected to temperature shifts of about 5 °C exhibited small shifts in composition. Additional examination of the literature on global warming showed that the effect disappears at low temperature shifts. In several studies of plants (difference between temperature treatments 2–5 °C), the average decrease in nutrient content at the higher temperature was about 3% for both N and P (Chapin *et al.* 1995; Michelsen *et al.* 1996; Kandeler *et al.* 1998; Dury *et al.* 1998; Fritschi *et al.* 1999; Williams, Norby & Lincoln 2000).

Our findings are relevant to a number of current efforts to understand the relationship between temperature, body size and composition. Recently, Gillooly *et al.* (2002) showed that a single, general model incorporating both body size and temperature could explain variation in developmental times across essentially all taxonomic groups. Interestingly, most of the residual unexplained variation in development time was subsequently explained by incorporating biomass C : P ratios into the model. Our results show, however, that temperature itself can cause shifts in C : P ratios. Thus, the two factors are not independent, suggesting that

such models may be improved by understanding and incorporating their interaction.

A number of non-exclusive hypotheses have been proposed to explain the effect of temperature on composition:

- i Temperature may have differential effects on the synthesis and degradation of macromolecules (Das & Prosser 1967; Haschemeyer 1968; Sidell 1977; Kanda *et al.* 1994; Pinedo *et al.* 2000). Analogously, if temperature affects N and P contents (in any biochemical form) at the level of whole organism, it must do so by altering relative rates of N or P intake and loss – at least transiently. Eventually, a new steady-state nutrient content may be reached at which rates of nutrient gain and loss assume their former values.
- ii Temperature may have differential effects on growth and on N and P accumulation. This hypothesis is related to the one above but considers simultaneously the effects of temperature on N and P accumulation and *on growth* (Körner & Larcher 1988) – in particular, at higher temperatures higher rates of growth and development may dilute nutrient pools (Dury *et al.* 1998; Jonasson *et al.* 1999).
- iii Increasing levels of RNA and protein in cold-exposed tissues may be mechanisms for offsetting reduced rates of biochemical reactions. This idea, especially with respect to metabolic enzymes, has been a well-established feature of the literature on thermal acclimation for at least 40 years (Precht 1958; Prosser 1962; Hazel & Prosser 1974; Hochachka & Somero 1984) and appears in numerous more recent incarnations (e.g. Guy 1990).
- iv In 1949, Siminovitch and Briggs proposed that increases in soluble protein content protected cells against intracellular freezing. Their paper led to considerable work on cold hardiness and freezing resistance in plants in the intervening 50 years, reviewed by Brown (1978), Kacperska-Palacz (1978), Tseng & Li (1987). Johnson-Flanagan & Singh (1988), Guy (1990) and Hällgren & Öquist (1990).

Accumulation of antifreeze proteins, now identified in fish, terrestrial arthropods and plants, may be an important component of cold protection in a variety of ectotherms (Cheng 1998; Duman 2001).

These ideas fall into two classes: those based on temperature's effects on underlying biochemical mechanisms (i, ii) and those based on evolutionary or adaptive explanations (iii, iv). These classes are not exclusive and, in many instances, may be different views of the same phenomenon, e.g. an organism may exhibit higher tissue concentrations of protein and RNA following cold exposure as a means of maintaining rates of biosynthesis (an adaptive hypothesis); and the shift may be manifest because rates of ribosome degradation are more sensitive to temperature than are rates of ribosome synthesis (a mechanistic hypothesis). In individual studies it may be worth explicitly considering the whole range of hypotheses, at present an uncommon occurrence.

CHANGE IN COMPOSITION VERSUS CHANGE IN SIZE

Most poikilothermic organisms are larger when they develop in or acclimate to cold temperatures, compared with conspecifics exposed to warm temperatures (Ray 1960; von Bertalanffy 1960; Körner & Larcher 1988; Atkinson 1994). Furthermore, the cellular basis of these changes often appears to be alterations in cell size rather than number (Partridge *et al.* 1994; Van Voorhies 1996; Azevedo, French & Partridge 2002). Evaluating whether size changes played an important role in our findings is difficult, as the surveyed literature generally did not report size. Nonetheless, several lines of evidence suggest that increased size due to cold exposure can account for some of the overall result (Fig. 1).

First, survey data expressed as amounts showed larger increases during cold exposure than did data expressed as contents (Fig. 4), despite similar average temperature treatments between groups. This effect almost surely arises because *amount* is a more general unit: amounts increase if contents increase but also if contents stay the same and *size* (of cells, organs or whole organisms) increases. Second, individual survey studies showing equivocal effects of temperature on chemical content often showed strong effects of temperature when they were reanalysed in terms of amounts – in the few cases where sufficient data were available. For example, Burr & Hunter (1969) reared several species of *Drosophila* at 15 and 25 °C. For protein N content, the ratios were 1.06, 0.96, 0.92 and 1.01, respectively, suggesting that protein content was invariant with temperature. Likewise the ratios of RNA content were 0.84, 1.33, 1.04, 1.02, also suggesting no systematic pattern. However, Burr and Hunter's data also showed that cold-reared flies were systematically larger than warm-reared conspecifics. From their

data (their Tables 1–3) we calculated total N and RNA amounts *per fly* at the two temperatures. The ratios of total N per fly in the cold to in the warm were 1.44, 1.01, 1.17 and 1.16. The ratios of RNA per fly were 1.20, 1.35, 1.19 and 1.18. Thus, for both biochemical components, flies showed no increases in *content* at colder temperatures but did show increases in *total amount*. Similar conclusions emerge from reanalysis of data on phytoplankton (Jørgensen 1968; Goldman & Mann 1980) and plants (Siminovitch & Briggs 1949; Siminovitch 1963; Siminovitch, Rheume, & Sachar 1967; Siminovitch *et al.* 1968).

It thus appears that organisms respond to cold in one or both of two qualitatively distinct ways: (i) by increasing the contents of synthetic and catalytic components; or (ii) by increasing size. The first scheme is implicit in traditional views of metabolic compensation (e.g. Eckert & Randall 1983). However, we note that both responses provide more total catalytic capacity in the cold (Kent, Koban & Prosser 1988). In many circumstances, total catalytic capacity of tissues or organs may be more important to performance or fitness than is the tissue-specific catalytic capacity. Such a view unifies changes in content and size into a common functional framework. Future work on temperature acclimation should partition these effects more carefully and should pursue mechanistic explanations for why particular organisms may exhibit one kind of change over the other.

ECOLOGICAL IMPLICATIONS

The last decade has seen renewed interest in scaling across levels of biological organization, from molecules and cells to ecology (Ehleringer & Field 1993; Jones & Lawton 1995; Brown & West 2000; Elser *et al.* 2000b; Gillooly *et al.* 2001; Gillooly *et al.* 2002). A prerequisite for such efforts is a currency recognizable across levels. The empirical analysis above provides strong correlational support for a connection between protein and RNA as forms of biochemical currency and N and P as a corresponding elemental currency. An implication is that biochemical shifts by cells or tissues, occurring in response to temperature-driven alteration in fundamental chemical and physical events, may ultimately appear as nutrient (N and P) signals important in ecological patterns and processes.

How specifically might these connections appear? Consider three broad areas of current interest:

1. Cold-induced responses of individuals may be involved in latitudinal and altitudinal patterns of nutrient content. High-altitude plants, for example, usually exhibit higher N content than low-altitude conspecifics (Körner 1989). Likewise, plants from arctic areas often have higher N and P contents than related plants from temperate areas (Chapin, Van Cleve & Tieszen 1975; Chapin & Oechel 1983). Our analysis suggests that geographical patterns in

nutrient content may be driven at least in part by temperature-driven biochemical shifts in the cells and tissues of individual organisms.

2. Temperature effects on nutrient content likely have important ramifications for understanding biogeochemical cycling and trophic dynamics in environments with strong temperature gradients (Cotner & Biddanda 2002). For example, higher nutrient contents in plant litter in cold environments might partially offset reductions in rates of decomposition imposed by cold temperatures. Similarly, herbivores constrained by low nutrient content of plant biomass (Elser *et al.* 2000a) might adopt a strategy of feeding on plant biomass growing in particularly cool micro-environments (to obtain a more nutrient-rich diet).
3. Recent theory and empirical work has suggested that the degree of stoichiometric imbalance between resources and consumers affects species coexistence. Under conditions where stoichiometric imbalance is strong (food quality is poor), herbivores may not be in competition with each other, but rather may be involved in intra- and interspecific facilitation because their collective nutrient recycling tends to raise the nutrient content of their food base (empirical data: Urabe *et al.* 2002; theoretical findings: I. Loladze *et al.* personal communication). Thus, stoichiometric imbalance may enhance species coexistence by reducing the tendency for competitive exclusion.

This raises the possibility that the effects of temperature on biomass stoichiometry that we document here impinge on biodiversity. For example, stoichiometric imbalance between herbivores and their food might become particularly pronounced in situations where herbivores are forced by other ecological pressures (e.g. predation) to adopt a strategy of living in the cold (tending to raise herbivore nutrient content) but feeding in warm microhabitats (which will tend to produce lower-quality food). An example is vertically migrating zooplankton such as *Daphnia* (Enright 1977; Pearre 1979), which avoid visual predators by spending much of the day in cold dark layers of the lake (Zaret 1976) but venture by night to the surface to feed on algae in the surface mixed layer. Such a situation may impose chronic food quality limitation on consumers, weakening competition and maintaining unexpectedly high levels of biodiversity. To our knowledge no experiments have yet examined whether temperature heterogeneity affects species coexistence via stoichiometric mechanisms.

In conclusion, our results show that across diverse taxa, cold exposure leads to significant increases in nutrient content and amount. These findings complement recent general ideas about the relationships between temperature and size (Atkinson 1994; Gillooly *et al.* 2001; Gillooly *et al.* 2002) and provide motivation for connecting stoichiometric (Sternner & Elser

2002) and scaling (Brown & West 2000) theory. Future work should extend these findings inward to cellular and molecular levels and outward to ecological levels of organization. We propose here several initial ideas – that changes in nutrient content and size may alternative means of maintaining catalytic capacity in the cold, and that temperature-driven shifts in chemical composition are likely to resonate in diverse ecological patterns and processes.

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Appendix

List of species in literature survey

Algae

<i>Asterionella formosa</i>	<i>Laminaria saccharina</i>
<i>Chaetoceros calcitrans</i>	<i>Monochrysis lutheri</i>
<i>Chaetoceros gracilis</i>	<i>Pavlova lutheri</i>
<i>Chaetoceros simplex</i>	<i>Phaeodactylum tricoratum</i>
<i>Chilomonas paramecium</i>	<i>Scenedesmus abundans</i>
<i>Chlorella sorokiniana</i>	<i>Scenedesmus</i> sp.
<i>Dunaliella tertiolecta</i>	<i>Skeletonema costatum</i>
<i>Euglena gracilis</i>	<i>Thalassiosira alleni</i>
<i>Gracilaria tikvahiae</i>	<i>Thalassiosira nordenskiöldii</i>
<i>Isochrysis galbana</i>	<i>Thalassiosira pseudonana</i>

Yeast

Candida utilis

Animals

<i>Anguilla anguilla</i>	<i>Ictalurus punctatus</i>
<i>Bufo boreas</i>	<i>Lamellidens marginalis</i>
<i>Carassius auratus</i>	<i>Lampito mauritii</i>
<i>Carassius carassius</i>	<i>Lepomis cyanellus</i>
<i>Cryptolestes ferrugineus</i>	<i>Leuciscus idus</i>
<i>Cyprinus carpio</i>	<i>Onychiurus arcticus</i>
<i>Daphnia magna</i>	<i>Ophicephalus punctatus</i>
<i>Drosophila melanogaster</i>	<i>Opsanus tau</i>
<i>Drosophila pseudoobscura</i>	<i>Osmoderma eremicola</i>
<i>Drosophila viracochi</i>	<i>Salmo gairdneri</i>
<i>Drosophila willistoni</i>	<i>Sitophilus granarius</i>
<i>Gadus morhua</i>	<i>Tegenaria atrica</i>
<i>Hemipteris americanus</i>	

Bacteria

<i>Aerobacter aerogenes</i>	<i>Micrococcus cryophilus</i>
<i>Bacillus subtilis</i>	<i>Pseudomonas</i> sp.
<i>Escherichia coli</i>	<i>Salmonella typhimurium</i>
Marine planktonic bacteria	<i>Vibrio</i> AF-1

Plants

<i>Abutilon theophrasti</i>	<i>Pyrus malus</i>
<i>Albizia julibrissin</i>	<i>Robinia pseudoacacia</i>
<i>Amaranthus retroflexus</i>	<i>Secale cereale</i>
<i>Buxus microphylla</i>	<i>Solanum acaule</i>
<i>Capsicum annuum</i>	<i>Solanum commersoni</i>
<i>Cucumis sativus</i>	<i>Solanum tuberosum</i>
<i>Cucurbita ficifolia</i>	<i>Spinacia oleracea</i>
<i>Medicago sativa</i>	<i>Thuja occidentalis</i>
<i>Melilotus indica</i>	<i>Trifolium pratense</i>
Mixed	<i>Triticum aestivum</i>
<i>Pinus resinosa</i>	

To view the raw data set, see http://cluster6.biosci.utexas.edu/IB/faculty/woods/survey_data.htm.