

Paper II

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HORIZONS

Life in a warming ocean: thermal thresholds and metabolic balance of arctic zooplankton

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The magnitude and characteristics of the response of Arctic marine ecosystems to the challenges resulting from climate change are not known. Among the drivers of change, temperature plays a fundamental role, influencing biological processes from individual organisms to whole ecosystems, and sets the thresholds for species performance, abundance and distribution, and is responsible for massive shifts in ecosystem structure and function. The metabolic theory of ecology is generally invoked to ascertain the effects of global temperature changes on shifts in ecosystems, from individual size and species composition to global trophic status. However, as generally occurs with most scaling laws, there is a lively debate about its usefulness to predict something more than gross tendencies. In general, to explain variability is much more interesting than to predict average values. The successful performance of species and the trophic status of ecosystems are controlled by the balance between energy gains and losses. The temperature-induced mismatch between the positive and negative terms of the metabolic balance appears to depend on precise characteristics of their respective thermal windows, hardly identifiable by the averaging

predictions made by the metabolic theory. As a case study, we discuss the response to temperature changes of the balance between ingestion and respiration rates of the copepod *Calanus glacialis*, a fundamental component of Arctic pelagic food webs. We suggest using the response of the metabolic balance (at the organismal, community or ecosystem level) to temperature changes to identify thermal thresholds leading to tipping points and nonlinear ecosystem shifts.

KEYWORDS: global warming; metabolic balance; temperature response; ingestion; respiration; *Calanus glacialis*

INTRODUCTION

Anthropogenically derived climate change is the main source of environmental perturbations on a global scale, with an accelerated rate of temperature rise that exceeds many pessimistic forecasts. The effects of these perturbations are particularly intense in the Arctic, where temperatures have increased in the past decades at a rate of from 2- to 4-fold that of the global average (ACIA, 2004; Screen and Simmonds, 2012), and both ice cover (Comiso *et al.*, 2008) and thickness (Kwok and Rothrock, 2009) have experienced severe reductions. Some possible outcomes would include changes in primary production (Wassmann *et al.*, 2008), species composition (Olli *et al.*, 2007; Blachowiak-Samolyk *et al.*, 2008) and top-down trophic cascade effects (Smetacek and Nicol, 2005). However, whatever the nature of the changes experienced by the ecosystem, the response to smooth and sustained environmental changes will most likely include abrupt, nonlinear phase discontinuities (May, 1977) and regime shifts (Hare and Mantua, 2000; Weijerman *et al.*, 2005; Holding *et al.*, 2013) when environmental stressors reach certain thresholds and tipping points (Wassmann, 2011; Duarte *et al.*, 2012).

At present, the nature of the potential changes in Arctic plankton due to global climate change is not well known. Some predictions about global effects have been made using coupled physical–biological models (Slagstad *et al.*, 2011) and comparisons of the fundamental and realized niches for key zooplankton species and their potential vicariants (Helaouët *et al.*, 2011). Similarly, phenological studies have provided insights regarding possible mismatch mechanisms affecting the temporal onset of phytoplankton blooms and those of their consumers (Ji *et al.*, 2010; Varpe, 2012; Winder, 2012), which could significantly modify the characteristics of Arctic food webs. Changes in the predator–prey interactions have been also identified as responsible for structural changes of plankton communities, especially in high latitude systems (Smetacek and Nicol, 2005; Kaartvedt, 2008; Berge *et al.*, 2012), although some of these

approaches rely fundamentally on statistical models that are based on time series and affected by a high degree of interannual variability.

However, apart from the above-mentioned control mechanisms, temperature appears to be the main driver of ecosystem changes. Temperature influences processes at different hierarchical organization levels from molecular to cellular to systemic, and affects the global function of organisms (Hofmann and Todgham, 2010; Somero, 2010). Therefore, a better prediction of how species, communities and ecosystems will respond to the increasing temperatures is of paramount importance.

TEMPERATURE AND PHYSIOLOGICAL RATES

The temperature conditions at which ectothermic organisms thrive set the upper and lower limits of the thermal window for different physiological processes (Pörtner *et al.*, 2000). The amplitude of these thermal windows is in general inversely related to the complexity of the organism and of the physiological process considered. Prokaryotes exhibit higher and lower temperature limits than metazoans; similarly, pure physiological survival and short-term tolerance have broader thermal limits than long-term, successful maintenance (Fig. 1A). Although environmental variables other than temperature contribute to define the limits of the ecological niche for ectothermic organisms (Hutchinson, 1957; Levins, 1968), the fundamental (precompetitive) thermal niche and its limits are of paramount physiological importance (Shelford, 1931; Pörtner, 2002; Hoffmann and Todgham, 2010).

The quantitative response of different biological process to temperature changes is unimodal within the limits of functional integrity (Fig. 1B) and displays an increasing pattern when temperature increases, until reaching a temperature optimum (TO) at which the velocity of the process is maximal. Further temperature increases lead to the critical thermal maximum (CT_{max} , Somero, 2010) and

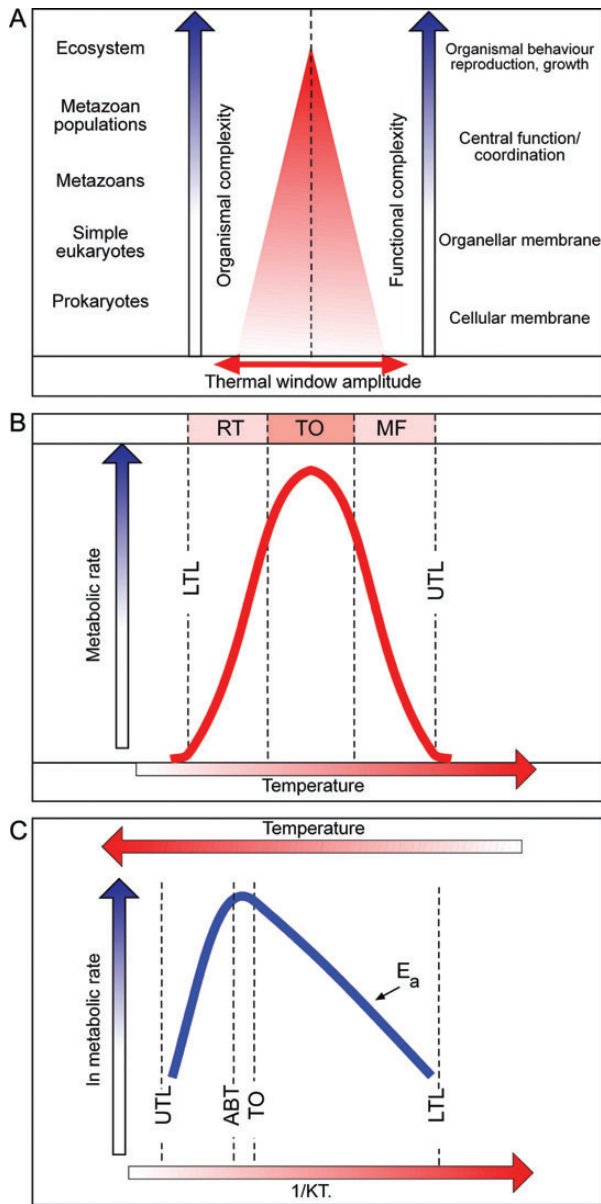


Fig. 1. (A) Thermal window amplitude in relation to organismal and functional complexity modified from Pörtner (2002). The thermal window for functional integrity narrows from protists to higher organizational levels and from cellular membrane function to organismal behaviour, growth and reproduction. (B) Relationship between temperature and metabolic rate modified after Frederich and Pörtner (2000). From the lower thermal limit compatible with functional integrity (LTL), the rate increases with temperature (rising trait, RT) until reaching the temperature optimum (TO). Further warming leads to a monotonic fall (MF) and the upper thermal limit (UTL) compatible with functional integrity. (C) Arrhenius plot modified after Marshall *et al.* (2011) showing the relationship between the natural log of the metabolic rate and the reciprocal of the absolute temperature (KT). ABT is the Arrhenius breakpoint temperature. E_a (the mean activation energy) corresponds with the slope of the rising trait in the Arrhenius plot. See online supplementary data for a colour version of this figure.

the Arrhenius breakpoint temperature (Weinstein and Somero, 1998; Marshall *et al.*, 2011) before a monotonic drop in the velocity of the process (Frederich and Pörtner, 2000; Deutsch *et al.*, 2008; Dell *et al.*, 2011). Unimodal responses in relation to temperature had been described by Loosanoff (Loosanoff, 1958) for oyster metabolism, Bernard (Bernard, 1970) for the hatching time of copepod eggs and Thebault (Thebault, 1985) for ingestion in planktonic copepods. Tande (Tande, 1988) and Hirche (Hirche, 1987) have observed a similar response for respiration in *C. glacialis*, and more recently, Møller *et al.* (Møller *et al.*, 2012) identified different temperature optima for the clearance rates of *C. finmarchicus* and *C. helgolandicus*, and Kjellerup *et al.* (Kjellerup *et al.*, 2012) observed an increase in faecal pellet production in *C. glacialis* up to 7.5°C, with a decrease at higher temperatures.

For the temperature range over which the biological processes increase with increasing temperature, the response rates follow the Boltzmann–Arrhenius model (Loosanoff, 1958; Kordas *et al.*, 2011) defined in equation (1).

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

where V is the physiological rate, V_0 is a constant in the same units as V , E_a is the mean activation energy coefficient related to the temperature sensitivity of the corresponding metabolic function, R is the universal gas constant and T is the absolute temperature (Fig. 1C).

Although the metabolic theory of ecology (Gillooly *et al.*, 2001; Brown *et al.*, 2004) predicts equivalent thermal responses (i.e. similar E_a , and therefore similar thermal windows) for all biological functions, the experimental evidence does not support this hypothesis. In fact, the examples of differences in the activation energy E_a , or the mismatch in optimal temperature TO (Fig. 1C) for closely related metabolic processes seem to be the rule. Harder (Harder, 1925, cited in Margalef, 1974) observed that the rate of respiration increased faster than that of photosynthesis with increasing temperature in aquatic mosses. More recently, similar phenomena have been mentioned for marine (Vona *et al.*, 2004) and terrestrial environments (forests of *Pseudotsuga-Tsuga*, Harmon *et al.*, 2004). Haemolymph O_2 tension, ventilation rate and heart rate also show significant differences in E_a and TO in the decapod crustacean *Maja squinado* (Pörtner, 2002), as occur for respiration and excretion rates in mixed zooplankton or single copepod species (Alcaraz *et al.*, 2013; Ikeda, 2013).

TEMPERATURE, THERMAL WINDOWS AND ORGANISMAL FITNESS

The successful performance of organisms and ecosystems is strongly dependent on the balance between the two terms of the metabolism shown in the following equation:

$$E_G = E_I - E_R \quad (2)$$

where E_G is the energy allocable to growth and reproduction, once the costs of maintenance, E_R (respiration that accounts for the losses, from physiological homeostasis and basal metabolism to movement) have been deducted from the energy gains, E_I . When there is a mismatch in the quantitative responses of E_I and E_R to similar temperature changes, the temperature at which losses equal gains will set a threshold or tipping point. If losses increase faster than gains with further temperatures changes, the organism (or the ecosystem) falls beyond the limits of functional integrity. The response of E_G (fitness) to temperature changes should thus provide insights into organisms, communities or ecosystems regarding the proportion of extra energy allocable to biological processes that are related to growth, development or trophic status and therefore about the temperature limits for their future performance. When temperature increases occur below the optimum temperature, TO , for both gain and loss processes (Fig. 1B), the positive or negative tendency of E_G (equation 2) depends on the relative values of E_a . When temperature rises above TO , the resulting positive or negative E_G tendency depends, apart from the relative values of the activation energy coefficients (E_a), on the match–mismatch in the corresponding TO for E_I and E_R (equation 2), and on the respective decreasing rates after the temperature rises beyond the beginning of the monotonic fall (MF; Fig. 1C).

As mentioned above, differences between the thermal responses of different metabolic processes seem to be the rule, affecting processes directly related to the rate of energetic gains (i.e. photosynthesis, E_I) and losses (respiration, E_R). For the whole metabolic balance of the pelagic system of the Arctic Ocean, the higher thermal sensitivity of respiration when compared with photosynthesis allows prediction of a two-fold increased rate of respiration above primary production for an expected temperature rise of 6°C (Vaquer-Sunyer *et al.*, 2010), and this result can be extended to the global ocean (Regaudie-de Gioux and Duarte, 2012; Duarte *et al.* 2012; Holding *et al.*, 2013). Regarding heterotrophic ectotherms, Lemoine and Burkepile (Lemoine and Burkepile, 2012) have also described similar unbalanced responses of metabolic gains and losses to temperature changes. In general, for a similar temperature rise, metabolic losses tend to increase faster

than gains. Therefore, we suggest exploring the feasibility of using the response to temperature changes of the metabolic balance, as a descriptor of physiological fitness (at the organismal, community or ecosystem level), to identify thermal thresholds and limits leading to tipping points and nonlinear shifts in ecosystems.

TEMPERATURE RESPONSES BY ARCTIC ZOOPLANKTON: A CASE STUDY

Forecasting the response of pelagic marine ecosystems to temperature increases requires a better understanding of the thermal windows and performances for their key components and biological processes. Zooplankton are a fundamental component in the web of transfer of matter and energy in the Arctic, for they not only shape the structure and function of micro-, auto- and heterotrophs by grazing (Hirche *et al.*, 1991; Møller *et al.*, 2006) and transfer matter and energy from primary producers to upper consumers (Hjort, 1914; Tande and Båmstedt, 1985; Falk-Petersen *et al.*, 2009; Mountain and Kane, 2010), but they also contribute to the re-supply nutrients available for phytoplankton via excretion (Sterner 1990; Alcaraz *et al.*, 2010). Large copepods of the genus *Calanus* account for up to 80% of zooplankton carbon and are the main drivers of the Arctic and sub-Arctic, lipid-based food webs (Klungsoyr *et al.* 1989; Arashkevich *et al.* 2002).

At the predicted rate of temperature rise, the development of adaptive strategies, that is, the capacity of maintaining metabolic rates in spite of temperature changes, will be severely reduced for the relatively long-lived Arctic zooplankton (Clarke, 1993, 2003; Peck and Conway, 2000). Therefore, studies concerning their response to acute temperature changes (acclimation) could provide suitable insights into the thermal thresholds for the different life conditions that will face Arctic organisms, from just survival to optimal thriving.

As an example of the effects of rising temperature on the balance between metabolic gains and losses (E_I and E_R , respectively; in equation 2) for Arctic zooplankton, we present preliminary data concerning the copepod, *Calanus glacialis*. The study was conducted within the framework of the ATP project (EU226248), whose objective was to improve our understanding of environmental thresholds and tipping points in Arctic marine ecosystems. The proxies for metabolic gains (E_I) and losses (E_R) were the carbon-specific ingestion rates, C_I , and the carbon-specific respiration, C_R . The experiments were carried out during early summer (15–29 June 2009) on board the R/V ‘Jan

Mayen' at a series of stations around the Svalbard archipelago.

C_I were estimated for adult females (AF) and copepodites V (CV) by incubation experiments at five experimental temperatures (0, 2.5, 5, 7.5 and 10°C). The ingestion rates were assessed from gut fluorescence contents and gut clearance rates (Holm-Hansen and Riemann, 1978; Dagg and Walser, 1987). Chlorophyll ingestion was converted to C ingestion using C/Chl *a* ratios of 45.9 and 125 for the stations sampled during bloom and post bloom periods, respectively (Arashkevich, personal observation). We included the contribution of heterotrophic microplankton C to the copepod diet (Kleppel 1993; Ohman and Runge 1994) using the percentages given in Barthel (Barthel, 1988), Levinsen *et al.* (Levinsen *et al.*, 2000) and Campbell *et al.* (Campbell *et al.*, 2009). The inclusion of microheterotrophs in the copepod diet was considered the most realistic approach to total C ingestion considering the omnivorous diet of most copepods (Saiz and Calbet, 2011). The C-specific ingestion rates, C_I , were expressed as $\mu\text{g C } \mu\text{g C}_{\text{cop}}^{-1} \text{ day}^{-1} (\text{d}^{-1})$.

The effects of rising temperature on C_R as an indicator of E_R were estimated for *C. glacialis* AF and CV in incubation experiments at 0, 3, 6 and $10 \pm 0.1^\circ\text{C}$ following the method described in Alcaraz *et al.* (Alcaraz *et al.*, 1998, 2010) and Almeda *et al.* (Almeda *et al.*, 2011). O_2 consumption rates were converted to respiratory C losses using a respiratory quotient of 0.97 (Omori and Ikeda, 1984).

The biomass of the experimental individuals as organic C (C_{cop}) was calculated from the zooplankton biovolume (BV) using the conversion factor given in Alcaraz *et al.* (Alcaraz *et al.*, 2003, 2010), namely, $1 \text{ mm}^3 \text{ BV} = 0.008 \text{ mg C}_{\text{cop}}$. The biovolume of the experimental organisms was estimated by image analysis according to Alcaraz *et al.* (Alcaraz *et al.*, 2003, 2013) and Saiz *et al.* (Saiz *et al.*, 2012). The carbon-specific respiration rates (C_R) were calculated as the quotient between respiration rates ($\mu\text{mol } C_R \text{ day}^{-1} \text{ experiment}^{-1}$) and organismal biomass in the experiments ($\mu\text{mol } C_{\text{cop}} \text{ experiment}^{-1}$) and expressed as $\mu\text{g } C_R \mu\text{m } C_{\text{cop}}^{-1} \text{ day}^{-1} (\text{day}^{-1})$. The gross metabolic balance was estimated as the difference between C_I (the proxy for energy gains, E_I) and C_R (the proxy for losses, E_R), which can be considered a conservative estimate of the total energetic demand (Alcaraz, 1988; Alcaraz *et al.*, 1998).

Specific ingestion rates (C_I) increased until a thermal optimum (TO) of 2.5°C , where the maximum values were recorded for both developmental stages. Further temperature increases resulted in a decrease of C_I (Fig. 2A). Respiration (C_R) also increased consistently with temperature, but the TO (6°C) was higher than in the case of ingestion (C_I). Like ingestion, respiration decreased as temperature increased above the TO (Fig. 2B). The

uncoupling between the TO values of the two metabolic rates, with C_I decreasing above 2.5°C , but C_R still increasing until 6°C , with further decrease above this temperature, resulted in a gradient of E_G values between the thermal limits of organismal survival. The continuous decrease of the E_G as the temperature increased resulted in a continuous loss of performance until approximately 5°C , where E_G values = 0 ($E_G = C_I - C_R$, Fig. 2C). This is the theoretical E_G limit allowing just survival, and above which, C_I could not fulfil the minimum C_R requirements for either the CV or the AF.

CONCLUSIONS AND FUTURE DIRECTIONS

The geographic range and abundance of species strongly depend on the temperature tolerance of organisms (thermal window). Climate change, with the predicted temperature rise will be, and is actually, responsible for drastic changes in ecological distributions (Beaugrand *et al.*, 2009). Although predicting the response of organisms to global climate changes must include not only thermal sensitivity (i.e. synergistic factors like ocean acidification and ecological competition with vicariant species must be also considered), the responses to temperature changes of estimators of energetic gains and losses appear as valuable indicators to better understand potential effects of global warming. Although predicting precise changes in geographic ranges, species-specific substitutions or ecological shifts due to temperature increase are hardly possible by simple thermal physiology, estimations of the thermal metabolic vulnerability of key components of marine food webs should help elucidate possible tendencies in the shifts of ecosystem structure and function.

The metabolic theory of ecology is frequently invoked to interpret and predict changes at multiple levels, from intracellular physiology to community dynamics. However, substantial aspects of the theory, like the value of the scaling factors, are subjected to a lively discussion (Horn, 2004). One of the problems of the theory in relation to the detection of thermal thresholds is the inability to detect differences in the responses to temperature changes of different metabolic processes, as the residuals from the regressions obtained by the average scaling factors range by a factor of about 20 (Brown *et al.*, 2004).

Interestingly, the temperature increase that sets the upper limit for a positive balance between ingestion and respiration in *C. glacialis* (6°C) is not only the same as that for the balance between photosynthesis and respiration in the whole Arctic plankton ecosystem (Vaquer-Sunyer

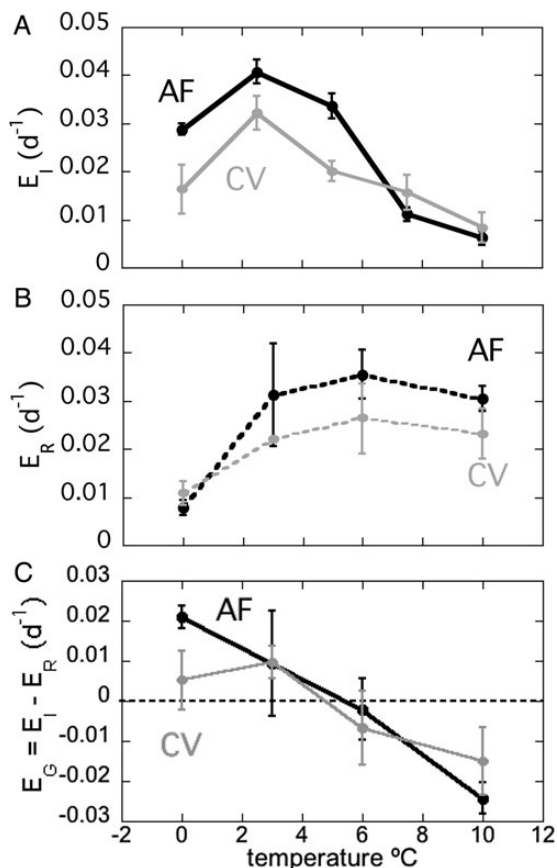


Fig. 2. Response to temperature changes by ingestion (A), respiration (B) and the balance between ingestion and respiration (C) in *C. glacialis* adult females (AF) and copepodites V (CV). Bars are standard errors.

et al., 2010), but also coincides with the temperature threshold for the presence of *C. glacialis* (Carstensen et al., 2012). Thus, the existence of a temperature threshold close to 6°C defining the upper limit of the fundamental thermal niche (in the sense of Hutchinson, 1957 and Levins, 1968) for *C. glacialis* and most likely for the majority of the Arctic planktonic species (Helaouët and Beaugrand, 2007; Helaouët et al., 2011) seems to be confirmed. Warming beyond this temperature limit could lead to a dramatic shift (a tipping point) in the structure and function of marine Arctic ecosystems.

According to the metabolic pattern that emerged from the study on *C. glacialis*, the significant changes observed in their physiological performance could be extrapolated to other components of the ecosystem. It can be argued that this study on the effects of sudden temperature rise on copepod's metabolic balance cannot be compared with similar, albeit slower, increases in Arctic Ocean temperatures as molecular adaptations (Gracey et al., 2004) or other evolutionary mechanisms could modify the copepod's thermal window. However, the energetic cost of molecular adaptation would be too high (Clarke, 2003). Given the

rate at which the Arctic climate is now changing, and the comparatively low turnover rate of Arctic zooplankton, the existence of a temperature threshold that sets the limit for a sustainable metabolic balance in the present community of Arctic copepods should not be ignored. Although it is difficult to predict exact geographic ranges by simple thermal physiology, specific-species substitution or ecological shifts, we suggest estimating the changes in the metabolic balance for key components of the ecosystem in relation to temperature as a tool to estimate their potential capacity to tolerate temperature changes and the capacity of species, communities or ecosystems to cope with the increasing costs of living in a warming world.

SUPPLEMENTARY DATA

Supplementary data can be found online at <http://plankton.oxfordjournals.org>.

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