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## HORIZONS

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

MIQUEL ALCARAZ<sup>1\*</sup>, JORGE FELIPE<sup>1</sup>, ULRIKE GROTE<sup>2</sup>, ELENA ARASHKEVICH<sup>3</sup> AND ANASTASIA NIKISHINA<sup>3</sup>

<sup>1</sup>INSTITUT DE CIÈNCIES DEL MAR, CONSEJO SUPERIOR DE INVESTIGACIONES CIENTÍFICAS, CSIC, 08003 BARCELONA, SPAIN, <sup>2</sup>DEPARTMENT OF ARCTIC AND MARINE BIOLOGY, UNIVERSITY OF TROMSØ, 9037 TROMSØ, NORWAY AND <sup>3</sup>SHIRSHOV INSTITUTE OF OCEANOLOGY RAS, 117997 MOSCOW, RUSSIA

\*CORRESPONDING AUTHOR: miquel@icm.csic.es

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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

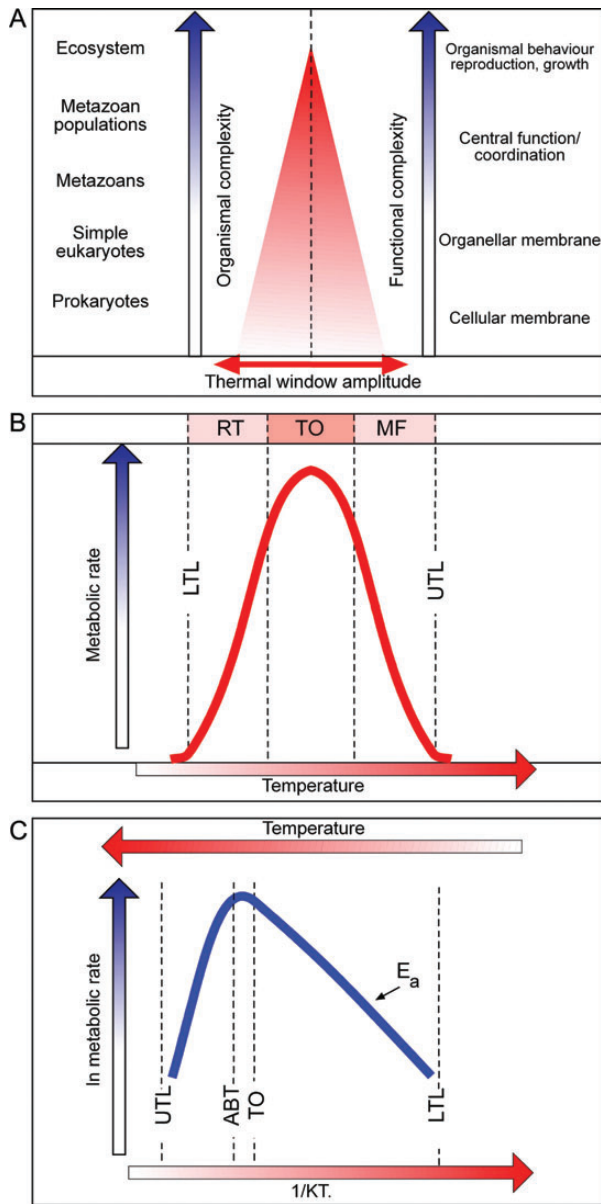
approaches rely fundamentally on statistical models that are based on time series and affected by a high degree of interannual variability.

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).  $\text{O}_2$  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 ( $C_{\text{cop}}$ ) 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  $2.5^\circ\text{C}$ , 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 ( $6^\circ\text{C}$ ) was higher than in the case of ingestion ( $C_I$ ). Like ingestion, respiration decreased as temperature increased above the TO (Fig. 2B). The

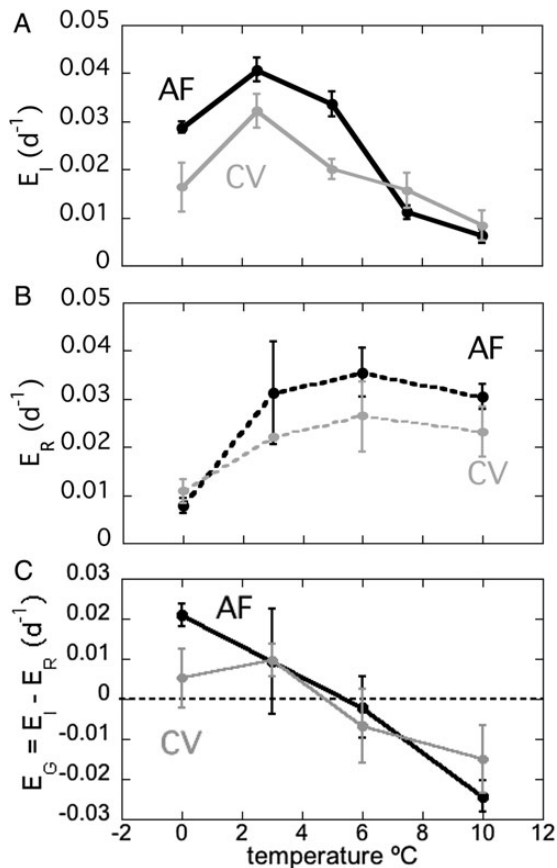
uncoupling between the TO values of the two metabolic rates, with  $C_I$  decreasing above  $2.5^\circ\text{C}$ , but  $C_R$  still increasing until  $6^\circ\text{C}$ , with further decrease above this temperature, resulted in a gradient of  $E_G$  values between the thermal limits of organismal survival. The continuous decrease of the  $E_G$  as the temperature increased resulted in a continuous loss of performance until approximately  $5^\circ\text{C}$ , 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* ( $6^\circ\text{C}$ ) 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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### REFERENCES

ACIA (Arctic Climate Impact Assessment). (2004) Impacts of a warming Arctic Scientific Report. In Walsh, J. E. (ed.), *Arctic Climate Impact and Assessment*. Cambridge University Press, Cambridge, pp. 141.

Alcaraz, M. (1988) Summer zooplankton metabolism and its relation to primary production in the western Mediterranean. *Oceanol. Acta*, **9**, 185–191.

Alcaraz, M., Almeda, R., Calbet, A. et al. (2010) The role of arctic zooplankton in biogeochemical cycles: respiration and excretion of ammonia and phosphate during summer. *Polar Biol.*, **33**, 1719–1731.

- Alcaraz, M., Almeda, R., Saiz, E. *et al.* (2013) Effects of temperature on the metabolic stoichiometry of Arctic zooplankton. *Biogeosciences*, **10**, 689–697.
- Alcaraz, M., Saiz, E., Calbet, A. *et al.* (2003) Estimating zooplankton biomass through image analysis. *Mar. Biol.*, **143**, 307–315.
- Alcaraz, M., Saiz, E., Fernandez, J. A. *et al.* (1998) Antarctic zooplankton metabolism: carbon requirements and ammonium excretion of salps and crustacean zooplankton in the vicinity of the Bransfield Strait during January 1994. *J. Mar. Syst.*, **17**, 347–359.
- Almeda, R., Alcaraz, M., Calbet, A. *et al.* (2011) Metabolic rates and carbon budget of early developmental stages of the marine cyclopoid copepod *Oithona davisae*. *Limnol. Oceanogr.*, **56**, 403–414.
- Arashkevich, E., Wassmann, P., Pasternak, A. *et al.* (2002) Seasonal variation in zooplankton abundance in the marginal ice zone and the central Barents Sea. *J. Mar. Syst.*, **38**, 189–204.
- Barthel, K. G. (1988) Feeding of three *Calanus* species on different phytoplankton assemblages in the Greenland Sea. *Meeresforschung*, **32**, 92–106.
- Beaugrand, G., Luczak, C. and Edwards, M. (2009) Rapid biogeographical plankton shifts in the North Atlantic Ocean. *Global Change Biol.*, **15**, 1790–1803.
- Berge, J., Gabrielsen, T. M., Moline, M. *et al.* (2012) Evolution of the Arctic *Calanus* complex: an Arctic marine advocado?. *J. Plankton Res.*, **34**, 191–195.
- Bernard, S. (1970) Quelques aspects de la biologie du copépode pélagique *Temora stylifera* en Méditerranée. *Pelagos*, **11**, 1–196.
- Blachowiak-Samolyk, K., Soreide, J. E., Kwasniewski, S. *et al.* (2008) Hydrodynamic control of mesozooplankton abundance and biomass in the northern Svalbard waters (79–81°N). *Deep Sea Res. II*, **55**, 2210–2224.
- Brown, J. H., Gillooly, J. F., Allen, A. P. *et al.* (2004) Towards a metabolic theory of ecology. *Ecology*, **85**, 1771–1789.
- Campbell, R. G., Sherr, E. B., Ashjian, C. J. *et al.* (2009) Mesozooplankton prey preference and grazing impact in the western Arctic Ocean. *Deep Sea Res. II*, **56**, 1274–1289.
- Carstensen, J., Weidmann, A., Olszewska, A. *et al.* (2012) Effects of environmental conditions on the biomass of *Calanus* spp. in the Nordic Seas. *J. Plankton Res.*, **34**, 951–966.
- Clarke, A. (1993) Seasonal acclimatization and latitudinal compensation in metabolism: do they exist?. *Funct. Ecol.*, **7**, 139–149.
- Clarke, A. (2003) Costs and consequences of evolutionary temperature adaptation. *Trends Ecol. Evol.*, **18**, 573–581.
- Comiso, J. C., Parkinson, C. L., Gersten, R. *et al.* (2008) Accelerated decline in the Arctic sea ice cover. *Geophys. Res. Lett.*, **35**, L01703.
- Dagg, M. J. and Walser, W. E. (1987) Ingestion, gut passage and egestion by the copepod *Neocalanus plumchrus* in the laboratory and in the sub-arctic Pacific Ocean. *Limnol. Oceanogr.*, **32**, 178–188.
- Dell, A., Pawar, S. and Savage, V. M. (2011) Systematic variation in the temperature dependence of physiological and ecological traits. *Proc. Natl Acad. Sci. USA*, **108**, 10591–10596.
- Deutsch, C. A., Tweksbury, J. J., Huey, R. B. *et al.* (2008) Impacts of climate warming on terrestrial ectotherms across latitude. *Proc. Natl Acad. Sci. USA*, **105**, 666–6672.
- Duarte, C. M., Agustí, S., Wasmann, P. *et al.* (2012) Tipping elements in the Arctic marine ecosystem. *AMBIO*, **41**, 44–55.
- Falk-Petersen, S., Mayzaud, P., Kattner, G. *et al.* (2009) Lipids and life strategy of Arctic *Calanus*, a review. *Mar. Biol. Res.*, **5**, 18–39.
- Frederich, M. and Pörtner, H. A. (2000) Oxygen limitation of thermal tolerance defined by cardiac and ventilator performance in spider crab, *Maja squinado*. *Am. J. Physiol. Integr. Comp. Physiol.*, **279**, 1531–1538.
- Gillooly, J. F., Brown, J. H., West, G. B. *et al.* (2001) Effects of size and temperature on metabolic rate. *Science*, **293**, 2248–2251.
- Gracey, A. Y., Fraser, E. J., Fang, Li W. *et al.* (2004) Coping with cold: and integrative multitissue analysis of the transcriptome of a poikilothermic vertebrate. *Proc. Natl Acad. Sci. USA*, **101**, 16970–16975.
- Hare, S. R. and Mantua, N. J. (2000) Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Prog. Oceanogr.*, **47**, 103–145.
- Harmon, K. B., Ryan, M. G., Shaw, D. C. *et al.* (2004) Production, respiration and overall carbon balance in an old-grown *Pseudotsuga-Tsuga* forest ecosystem. *Ecosystems*, **7**, 498–512.
- Helaouët, P. and Beaugrand, G. (2007) Macroecology of *Calanus finmarchicus* and *C. helgolandicus* in the North Atlantic Ocean and adjacent seas. *Mar. Ecol. Prog. Ser.*, **345**, 147–165.
- Helaouët, P., Beaugrand, G. and Reid, P. C. (2011) Macrophysiology of *Calanus finmarchicus* in the North Atlantic Ocean. *Prog. Oceanogr.*, **91**, 217–228.
- Hirche, H. J. (1987) Temperature and plankton. II. Respiration and swimming activity of copepods from the Greenland Sea at different temperatures. *Mar. Biol.*, **94**, 347–356.
- Hirche, H. J., Baumann, M. E. M., Kattner, G. *et al.* (1991) Plankton distribution and the impact of copepod grazing on primary production in Fram strait, Greenland Sea. *J. Mar. Syst.*, **2**, 447–494.
- Hjort, J. (1914) Fluctuations in the great fisheries viewed in the light of biological research. *Rep. Process.*, **20**, 1–13.
- Hofmann, G. E. and Todgham, A. E. (2010) Living in the now: physiological mechanisms to tolerate a rapidly changing environment. *Annu. Rev. Physiol.*, **72**, 127–145.
- Holding, J. M., Duarte, C. M., Arrieta, J. M. *et al.* (2013) Experimentally determined temperature thresholds for Arctic plankton community metabolism. *Biogeosciences*, **10**, 357–370.
- Holm-Hansen, O. and Riemann, B. (1978) Chlorophyll a determination—improvements in methodology. *Oikos*, **30**, 439–447.
- Horn, H. S. (2004) Commentary on Brown *et al.*'s 'Toward a metabolic theory of ecology'. *Ecology*, **85**, 1816–1818.
- Hutchinson, G. E. (1957) Concluding remarks. *Cold Spring Harb. Symp.*, **22**, 415–427.
- Ikeda, T. (2013) Respiration and ammonia excretion of euphausiid crustaceans: synthesis toward a global-bathymetric model. *Mar. Biol.*, **160**, 251–262.
- Ji, R., Edwards, M., Mackas, D. L. *et al.* (2010) Marine plankton phenology in a changing climate: current research and future directions. *J. Plankton Res.*, **32**, 1355–1368.
- Kaartvedt, S. (2008) Photoperiod may constrain the effect of global warming in Arctic marine systems. *J. Plankton Res.*, **30**, 1203–1206.
- Kjellerup, S., Dünweber, M., Swalethorp, R. *et al.* (2012) Effects of a future warmer ocean on the coexisting copepods *Calanus finmarchicus* and *C. glacialis* in Disko Bay, western Greenland. *Mar. Ecol. Prog. Ser.*, **447**, 87–108.
- Kleppel, G. S. (1993) On the diets of calanoid copepods. *Mar. Ecol. Prog. Ser.*, **99**, 183–195.
- Klungsoyr, J., Tillet, S., Wilhelmsen, S. *et al.* (1989) Fatty acid composition as indicator of food intake in cod larvae *Gadus morhua* from Lofoten, North Norway. *Mar. Biol.*, **102**, 183–188.

- Kordas, R. L., Helley, C. D. G. and O'Connor, M. I. (2011) Community ecology in a warming world: the influence of temperature on interspecific interactions in marine systems. *J. Exp. Mar. Biol. Ecol.*, **400**, 218–226.
- Kwok, R. and Rothrock, D. A. (2009) Decline in Arctic sea ice thickness from submarine and ICESat records: 1958–2008. *Geophys. Res. Lett.*, **36**, L15501, doi:10.29/2009GL039035.
- Lemoine, N. and Burkepile, D. (2012) Temperature-induced mismatches between consumption and metabolism reduce consumer fitness. *Ecology*, **93**, 2483–2489.
- Levins, R. (1968) *Evolution in Changing Environments. Some Theoretical Explorations*. Princeton University Press, pp. 132.
- Levinsen, H., Tuner, J. T., Nielsen, T. G. *et al.* (2000) On the trophic coupling between protists and copepods in arctic marine ecosystems. *Mar. Ecol. Prog. Ser.*, **204**, 65–77.
- Loosanoff, V. L. (1958) Some aspects of behaviour of oysters at different temperatures. *Biol. Bull.*, **114**, 57–70.
- Margalef, R. (1974) *Ecologia*. Omega, pp. 951.
- Marshall, D. J., McQuai, C. D. and Williams, G. A. (2011) Non-climatic thermal adaptation: implications for species' responses to climate warming. *Biol. Lett.*, **6**, 669–673.
- May, R. M. (1977) Thresholds and breakpoints in ecosystems with a multiplicity of stable states. *Nature*, **269**, 471–477.
- Møller, E. F., Maar, M., Jónasdóttir, S. H. *et al.* (2012) The effect of changes in temperature and food on the development of *Calanus finmarchicus* and *Calanus helgolandicus* populations. *Limnol. Oceanogr.*, **57**, 211–220.
- Møller, E. F., Nielsen, G. T. and Richardson, K. (2006) The zooplankton community in the Greenland Sea: composition and role in carbon turnover. *Deep-Sea Res. PT I*, **53**, 76–93.
- Mountain, D. G. and Kane, J. (2010) Major changes in the Georges Bank ecosystem, 1980s to the 1990s. *Mar. Ecol. Prog. Ser.*, **398**, 81–91.
- Ohman, M. D. and Runge, J. A. (1994) Sustained fecundity when phytoplankton resources are in short supply: omnivory by *Calanus finmarchicus* in the Gulf of St. Lawrence. *Limnol. Oceanogr.*, **39**, 21–36.
- Olli, K., Wassmann, P., Reigstad, M. *et al.* (2007) The fate of production in the central Arctic Ocean—top-down regulation by zooplankton expatriates?. *Prog. Oceanogr.*, **72**, 84–113.
- Omori, M. and Ikeda, T. (1984) *Methods in Zooplankton Ecology*. John Wiley, pp. 332.
- Peck, L. S. and Conway, L. Z. (2000) The myth of metabolic adaptation: oxygen consumption in stenothermal Antarctic bivalves. *Geol. Soc. Spec. Publ.*, **177**, 441–450.
- Pörtner, H. O. (2002) Climate variations and the physiological basis of temperature dependent biogeography: systemic to molecular hierarchy of thermal tolerance in animals. *Comp. Biochem. Physiol. A*, **132**, 739–761.
- Pörtner, H. O., Van Dijk, P. L. M. and Hardewig, I. (2000) Levels of metabolic cold adaptation: tradeoffs in eurythermal and stenothermal ectotherms. In: Davison, W. *et al.* (eds), *Antarctic Ecosystems: Models for Wider Ecological Understanding*. Caxton Press, NZ, pp. 332.
- Regaudie-de-Gioux, A. and Duarte, C. M. (2012) Temperature dependence of planktonic metabolism in the ocean. *Global Biogeochem. Cycles*, doi:10.1029/2010GB003907.
- Saiz, E. and Calbet, A. (2011) Copepod feeding in the ocean: scaling patterns, composition of their diet and the bias of estimates due to microzooplankton grazing during incubations. *Hydrobiologia*, **666**, 181–196.
- Saiz, E., Calbet, A., Isari, S. *et al.* (2012) Zooplankton distribution and feeding in the Arctic Ocean during a *Phaeocystis pouchettii* bloom. *Deep-Sea Res. I*, **72**, 17–33.
- Screen, J. A. and Simmonds, I. (2012) The central role of diminishing sea ice in recent Arctic temperature amplification. *Nature*, **464**, 1334–1337.
- Shelford, V. E. (1931) Some concepts of bioecology. *Ecology*, **XII**, 455–467.
- Slagstad, D., Ellingsen, I. H. and Wassmann, P. (2011) Evaluating primary and secondary production in an Arctic Ocean void of summer ice: an experimental simulation approach. *Prog. Oceanogr.*, **90**, 117–131.
- Smetacek, V. and Nicol, S. (2005) Polar ocean ecosystems in a changing world. *Nature*, **437**, 362–368.
- Somero, G. N. (2010) The physiology of climate change: how potentials for acclimatization and genetic adaptation will determine 'winners' and 'losers'. *J. Exp. Biol.*, **213**, 912–9220.
- Sterner, R. W. (1990) The ratio of nitrogen to phosphorus resupplied by herbivores: zooplankton and the algal arena. *Am. Nat.*, **136**, 209–229.
- Tande, K. S. (1988) The effects of temperature on metabolic rates of different life stages of *Calanus glacialis* in the Barents Sea. *Polar Biol.*, **8**, 457–461.
- Tande, K. S. and Båmstedt, U. (1985) Grazing rates of the copepods *Calanus glacialis* and *C. finmarchicus* in arctic waters of the Barents Sea. *Mar. Biol.*, **87**, 251–258.
- Thebault, J. M. (1985) Etude expérimentale de la nutrition d'un copépode commun (*Temora stylifera* Dana). Effets de la température et de la concentration de nourriture. *J. Exp. Mar. Biol. Ecol.*, **93**, 223–234.
- Vaquier-Sunyer, R., Duarte, C. M., Santiago, R. *et al.* (2010) Experimental evaluation of planktonic respiration response to warming in the European Arctic Sector. *Polar Biol.*, **33**, 1661–1671.
- Varpe, Ø. (2012) Fitness and phenology: annual routines and zooplankton adaptations to seasonal cycles. *J. Plankton Res.*, **34**, 267–343.
- Vona, V., Di Martino, V., Lobosco, O. *et al.* (2004) Temperature responses of growth, photosynthesis, respiration and NADH: nitrate reductase in cryophilic and mesophilic algae. *New Phytol.*, **163**, 325–331.
- Wassmann, P. (2011) Arctic marine ecosystems in an era of rapid climate change. *Prog. Oceanogr.*, **90**, 1–17.
- Wassmann, P., Carroll, J. and Bellerby, R. G. J. (2008) Carbon flux and ecosystem feedback in the northern Barents Sea in an era of climate change. *Deep-Sea Res. PT II*, **55**, 2143–2153.
- Weijerman, M., Lindeboom, H. and Zuur, A. F. (2005) Regime shifts in marine ecosystems of the North Sea and Wadden Sea. *Mar. Ecol. Prog. Ser.*, **298**, 21–39.
- Weinstein, R. B. and Somero, G. N. (1998) Effects of temperature on mitochondrial function in the Antarctic fish *Trematomus bernacchii*. *J. Comp. Physiol.*, **168**, 190–196.
- Winder, M., Berger, S. A., Lewandowska, A. *et al.* (2012) Spring phenological responses of marine and freshwater plankton to changing temperature and light conditions. *Mar. Biol.*, **159**, 2491–2501.