



## SYMPOSIUM

# Impacts of Climate Variability and Change on (Marine) Animals: Physiological Underpinnings and Evolutionary Consequences

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**Synopsis** Understanding thermal ranges and limits of organisms becomes important in light of climate change and observed effects on ecosystems as reported by the IPCC (2014). Evolutionary adaptation to temperature is presently unable to keep animals and other organisms in place; if they can these rather follow the moving isotherms. These effects of climate change on aquatic and terrestrial ecosystems have brought into focus the mechanisms by which temperature and its oscillations shape the biogeography and survival of species. For animals, the integrative concept of oxygen and capacity limited thermal tolerance (OCLTT) has successfully characterized the sublethal limits to performance and the consequences of such limits for ecosystems. Recent models illustrate how routine energy demand defines the realized niche. Steady state temperature-dependent performance profiles thus trace the thermal window and indicate a key role for aerobic metabolism, and the resulting budget of available energy (power), in defining performance under routine conditions, from growth to exercise and reproduction. Differences in the performance and productivity of marine species across latitudes relate to changes in mitochondrial density, capacity, and other features of cellular design. Comparative studies indicate how and why such mechanisms underpinning OCLTT may have developed on evolutionary timescales in different climatic zones and contributed to shaping the functional characteristics and species richness of the respective fauna. A cause-and-effect understanding emerges from considering the relationships between fluctuations in body temperature, cellular design, and performance. Such principles may also have been involved in shaping the functional characteristics of survivors in mass extinction events during earth’s history; furthermore, they may provide access to understanding the evolution of endothermy in mammals and birds. Accordingly, an understanding is emerging how climate changes and variability throughout earth’s history have influenced animal evolution and co-defined their success or failure from a bio-energetic point of view. Deepening such understanding may further reduce uncertainty about projected impacts of anthropogenic climate variability and change on the distribution, productivity and last not least, survival of aquatic and terrestrial species.

## Introduction

### Mechanisms underpinning windows of thermal tolerance across organism domains

No ectothermal macro-organism with a body temperature close to ambient, neither plant nor animal, occurs over the widest temperature ranges possible across latitudes between polar and tropical areas. Complex multicellular ectotherms specialize on environmental temperature much more than do unicellular bacteria and algae (Pörtner 2002a; Clarke 2014; Storch et al. 2014). Accordingly, the positions and

widths of thermal tolerance windows of ectothermal animal species and their life stages are related to geographical distribution and associated seasonality (Fig. 1, cf. Huey and Hertz 1984; Huey and Kingsolver 1993; Gilchrist 1995; Pörtner 2001, 2002a, 2002b; Pörtner et al. 2014; Settele et al. 2014). Thermal ranges as well as the capability of species to acclimatize differ depending on latitude and temperature variability. Thermal specialization causes most marine organisms to follow the shifting isotherms in the oceans (Poloczanska et al. 2013, 2014; Settele et al. 2014). Functional consequences

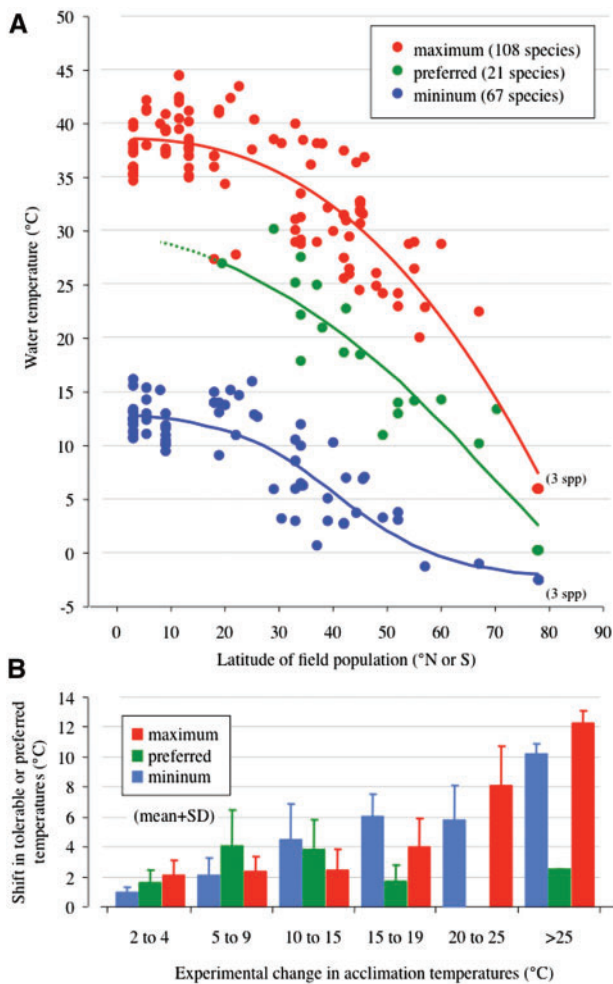
of thermal adaptation or acclimatization become visible when ectotherms specialized on various temperature regimes and their tissues are compared. On a global scale, the marine realm offers clearly defined thermal niches and, thus, an ideal basis for such comparisons. Marine animals of the high Antarctic, for example, rely on constant water temperatures; many of them are permanent stenotherms and sustain the complete set of life functions required for species survival and fitness at temperatures below 3°C to 6°C (Peck et al. 2014). In contrast, eurytherms tolerate wider temperature fluctuations and, in temperate to sub-polar zones, are able to dynamically shift or change the widths of tolerance

windows between summer and winter temperature regimes. However, no animal has been found that lives long term beyond body temperatures of 45°C to 47°C. The thermal specialization of animals and other creatures was hypothesized to be domain-specific, causing upper thermal limits to decrease with rising structural and functional complexities (Storch et al. 2014). Compared to animals, multicellular plants are similarly complex and have long-term upper thermal limits to performance close to those of metazoans (Larcher 2001; Storch et al. 2014; cf. Figure S1 in Supplementary Material).

However, compartments and mechanisms contributing to complexity likely differ between domains. For example, unicellular eukaryotic phytoplankton as well as macroscopic plants host both mitochondria and chloroplasts in one cell, are more complex at the cellular level than heterotrophic unicells and animals. Thermal limits being similarly low in phytoplankton, plants and animals, and higher in unicellular (eukaryotic) heterotrophs than in animals, suggests that cellular complexity is more relevant in setting thermal tolerance low in plants, whereas systemic complexity may be more relevant in animals (Storch et al. 2014; for the highest complexity mechanisms in animals see below). This illustrates that analyses of the mechanisms setting domain-specific thermal constraints are timely, as they will support a cause-and-effect understanding of thermal habitat and observed impacts of climate change on natural systems (Jensen 2003; Parmesan and Yohe 2003).

Here we project these lines of thought further back into earth's history. Over that history, large climate oscillations have contributed to mass extinctions (Stanley 1987). They have generated room for evolving higher levels of organismic complexity and performance. Temperature-dependent constraints may have played a key role (Stanley 1987) as they do today (see Supplementary Material).

The present article considers the key trade-offs and constraints in thermal adaptation shaping the characteristics of eurytherms versus stenotherms as end points on a continuum of thermal window width (Fig. 1). It considers recent progress in the field of thermal physiology, which ranges from an advanced understanding of thermal tolerance windows and of mechanisms of thermal adaptation (Johnston and Bennett 1996; Pörtner 2002a; Pörtner et al. 2012) to an evaluation of the trade-offs in thermal specialization focusing on the energetic benefits of constant versus fluctuating body temperatures. Comparing marine animals from polar and non-polar environments with constant versus fluctuating temperatures in both hemispheres



**Fig. 1** (A) Schematic depiction of the thermal tolerance ranges in marine fish in a latitudinal cline. Thresholds largely reflect classical determinations during short-term heating or cooling protocols, beyond thresholds of physiological functioning (i.e., peius and critical temperatures of Figure 3). The diagram ignores the difference between climate regimes in Northern and Southern hemispheres. (B) Shifts of preferred temperatures and tolerance windows can occur depending on the acclimation protocol (adopted from Pörtner and Peck 2010).

reveals unifying principles of temperature-dependent cellular design and thereby supports conclusions with respect to whole animal survival and performance. These mechanistic principles provide insight into (1) the selective forces, trade-offs and constraints that may have driven animal evolution toward high performance at high complexity. They are also interpreted in the context of (2) recent meta-analyses considering the role of compartmental and functional complexity in the thermal biology of organisms (Pörtner 2002a; Storch et al. 2014), of (3) the role of high temperature extremes in driving the transition to air-breathing in warm-water crustaceans (Giomi et al. 2014), and of (4) how the principles of thermal adaptation and evolutionary change observed in stenothermal versus eurythermal marine fauna may apply to terrestrial environments and may explain the evolution of animal endotherms and their high modes of energy demand (Pörtner 2004; Clarke and Pörtner 2010).

We hypothesize that oxygen supply versus demand may thus be the highest complexity function linking most compartments in animals, and the one experiencing the first line of thermal limitation to the whole organism (Storch et al. 2014), following a systemic to molecular hierarchy of tolerance limits (Pörtner 2002a). Accordingly, the upper limit of heat tolerance of all animals, which is much lower than that found in bacteria and still lower than in unicellular eukaryotes, fell in parallel to the gain in structural and functional complexity between pro- and eukaryotes and between unicellular organisms and metazoans (Pörtner 2002a; Storch et al. 2014). This line of thought suggests a common principle explaining the diversity of thermal biology across domains—a principle, however, that remains largely unexplored.

### **A systems view: oxygen and capacity limitation of thermal tolerance in animals (OCLTT)**

In animals, evidence has accumulated that, at the highest levels of complexity, the limits of thermal tolerance (Figure S1 in Supplementary Material) match the limited capacity and functional co-ordination of oxygen supply mechanisms to cover oxygen demand. Thermal and oxygen constraints to routine metabolic scope thus relate to large-scale biogeographical distribution of animal ectotherms in the oceans (Deutsch et al. 2015).

Associated with the gain in complexity toward metazoans is an increase in metabolic rate (Hemmingsen 1960; Banse 1982; Schmidt-Nielsen 1997); both may occur at the expense of decreasing

heat tolerance limits. The stepwise rise in performance capacity seen between prokaryotes and unicellular eukaryotes as well, later in evolution, between simple eukaryotes and metazoa may have been enabled by rising atmospheric oxygen levels (despite maintaining low internal oxygen tensions, see above).

The onset of a mismatch between oxygen delivery capacity and the oxygen demand of the organism is indicating the first limit of long-term warm or cold tolerance in animals (Pörtner 2001, 2002a; see Supplementary Material). The question immediately arises what are the trade-offs determining and linking these upper and lower tolerance thresholds and what are the mechanisms shaping the width of thermal window in eurytherms versus stenotherms? Cellular mechanisms identified to play a role in temperature adaptation provide a clue. These mechanisms have predominantly been documented in muscle (for review see Pörtner 2002b) and in brain (e.g., Kawall et al. 2002). They are likely common to all tissues, depending on their specific energy demand, including those responsible for ventilatory and circulatory capacity (which again involve muscular tissues) as well as their potential links to nervous tissue functioning. In general, the integration of molecular and cellular components into the larger units and the cellular design constraints involved are seen as crucial in shaping whole organism functioning, thermal tolerance windows, and temperature-dependent performance. Design constraints relate to cellular trade-offs, e.g. whether space is used for contractile fibers or mitochondria when adjusting functional capacity of tissues and organism to the required thermal tolerance window. All of these elements are subject to acclimation/adaptation with whole organism consequences. An understudied area is how the integration of molecular components into tissue and whole organism leads to e.g. thermal constraints that set in at whole organism level first (Pörtner 2002a, 2002c).

From a systems point of view, it does not appear surprising that convincing evidence for a primary role of individual tissues, such as nervous tissue in thermal limitation has not been provided (see Supplementary Material). Also from a systems point of view, the focus should be on the earliest sublethal thermal limits to the whole organism and their ecosystem level consequences. This view also supports the present emphasis on sublethal limits in a climate change context, e.g. in endotherms such as humans. In (routinely active) humans and other mammals, the onset of dangerous thermal imbalance over time occurs at a wet bulb temperature of 35 °C (measured by covering a standard

thermometer bulb with a wetted cloth and fully ventilating it) which may characterize the beginning inability of thermal regulation to fully dissipate metabolic heat in rising ambient humidity (Sherwood and Huber 2010).

### **OCLTT: low cost of stenothermal versus high cost of eurythermal cold adaptation**

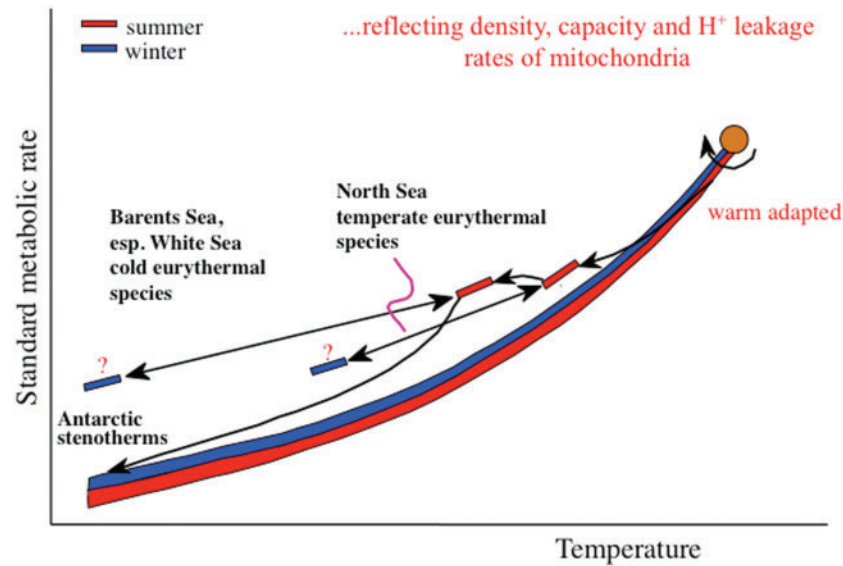
On evolutionary time scales, marine ectotherms at high latitudes, especially around Antarctica, experienced the lowest mean temperatures of marine habitats. These Antarctic taxa display very narrow windows of thermal tolerance, possibly as a consequence of cold adaptation at minimized metabolic costs (Pörtner 2006). However, despite almost constant water temperatures between  $-1.9^{\circ}\text{C}$  at the continental margin and  $+1^{\circ}\text{C}$  off Signy Island, tolerance windows are not identical for all Antarctic species. The narrowest windows are found in species with low resting or standard metabolic rates (SMRs) and correlate with reduced aerobic scope, which goes hand in hand with lower capacities of ventilation and circulation and lower activity levels (for review see Pörtner et al. 2000; Pörtner 2002a; Peck et al. 2009).

In contrast, the variable and much younger thermal history of Arctic compared to Antarctic organisms, associated with a lower degree of isolation of the Arctic from adjacent seas, may not allow for the degree of stenothermy found in the Antarctic. While animals in the Antarctic have developed features of permanent cold adaptation over millions of years, some species or species subpopulations in the Arctic may still be found in transition to life in the permanent cold. Animals in the sub-Arctic even need to compensate for large diurnal and seasonal temperature fluctuations. Accordingly, elevated standard metabolic rates are observed in cold adapted populations of sub-Arctic eurythermal animals (e.g., Sommer and Pörtner 2002; Pörtner 2006). These high SMRs extend to elevated capacities of ventilation and circulation as a precondition for widened windows of thermal tolerance, and, as a consequence, they support cold compensated metabolic scopes and activity levels (Fig. 2, Pörtner et al. 2000; Pörtner 2002b).

Elevated metabolic rates due to cold adaptation have also been seen in terrestrial eurytherms such as insects (e.g., Williams et al. 2016). Daily cold exposure during nighttime in intertidal or terrestrial environments requires permanent extreme eurythermy, while seasonal acclimatization to winter cold allows for a parallel shift of tolerance limits

(e.g., van Dijk et al. 1999; Wittmann et al. 2008). The following text will investigate our present knowledge of the metabolic features and cellular consequences involved in these different patterns of thermal adaptation as well as their wider evolutionary implications.

In aquatic and some terrestrial animals, the kinetic depression of performance and aerobic capacity by cold temperature is compensated for at the cellular level by mitochondrial proliferation and associated molecular and membrane adjustments (Pörtner 2002b). This includes thermal modification of contractile proteins and membrane excitability for the maintenance of muscle function as well as enhanced mitochondrial densities. For example, in Antarctic pelagic notothenioids, mitochondrial densities are the highest known for vertebrates (Johnston 1987; Dunn et al. 1989; Johnston et al. 1998) and are associated with an emphasis on aerobic metabolism. Such emphasis goes in parallel with a reduction of anaerobic scope, rapid recovery from exhaustive exercise and enhanced lipid stores, as well as preference for lipid catabolism which is characterized by high energy efficiency at high ambient oxygen supply (for review see Pörtner 2002b, 2006). The basic insight is that for two species with the same moderate performance level, the one with the colder body temperature would need more mitochondria and more mitochondrial enzymes for the same level of aerobic capacity and performance. But high densities of mitochondria limit cellular space available for other components of muscle, including contractile fibers, such that Antarctic fish can produce only relatively small maximal forces. At the same time, despite an over-proportional build-up of low capacity mitochondria for producing aerobic energy, narrowing the thermal window enables SMR to be minimized in polar stenotherms (Fig. 2 and caption, Pörtner 2006). Since aerobic metabolic rate can only be increased to a limited extent above the level of standard metabolism, maximum performance levels in cold-adapted stenotherms remain far below those reached with the same volume of mitochondria in warm-adapted organisms (cf. Pörtner 2002b). These trade-offs and limitations emphasize the loss of aerobic and anaerobic exercise performance toward cold temperatures, likely for the sake of freeing energy for growth and reproduction (e.g., Heilmayer et al. 2004) and exploiting cold-compensated capacity for protein synthesis (Storch et al. 2005). Available data suggest that a larger proportion of metabolic energy of Antarctic ectotherms is indeed channeled into protein synthesis (Fraser et al. 2002). At the same time, the over-proportional reduction in



**Fig. 2** The “hub” of metabolic temperature adaptation during seasonal and permanent cold (modified after Pörtner et al. 2000), arrows showing the metabolic rate transitions for stenothermal and eurythermal marine ectotherms between summer and winter and as a consequence of cold adaptation. Eurythermal cold adaptation causes standard metabolic rate to rise (cf. Figure 4) in relation to the degree of ambient temperature fluctuations, the cold compensation of mitochondrial aerobic capacity and proton leakage and the requirement to maintain function at both low and high temperatures. This trend is maximized when aerobic metabolism and scope are maintained at low body temperatures, at small body sizes, and during rapid temperature transitions. This contrasts the picture for Antarctic marine stenotherms. For further explanations see text.

functional capacity (including that of oxygen supply or of ATP synthesis capacity in mitochondria) and associated energy demand (including that of mitochondrial proton leakage, Figure S4 in Supplementary Material) in Antarctic ectotherms reduces oxygen demand and alleviates the constraint of oxygen limitation on cold tolerance (Pörtner et al. 2013).

In contrast to metabolic down regulation seen in Antarctic marine stenotherms (or in temperate zone winter stenotherms; Wittmann et al. 2008), both seasonal cold acclimatization (activity maintained) and eurythermal cold adaptation lead to a rise in organismal oxygen demand (standard metabolic rate) when compared to warm acclimated specimens at the same temperatures (Fig. 2, Pörtner 2006). Eurythermy also appears as a trait resulting from high mitochondrial densities (at high ATP synthesis capacities) in the smaller individuals of a species, a trait related to the cost associated with enhanced body surface to volume ratio of smaller individuals. Eurythermy and/or body size thus need to be considered when analyzing the mechanisms underpinning the co- or counter-gradient variation of functional traits in a latitudinal cline (Conover and Schultz 1995).

If both, stenotherms and eurytherms have elevated mitochondrial densities in the cold, the question

arises why different levels of oxygen demand result? A straightforward explanation for a rise in metabolic costs in the cold would include the high mitochondrial densities, which are, in principle, associated with enhanced levels of mitochondrial proton ( $H^+$ ) leakage (Figure S4 in Supplementary Material). However, during eurythermal cold adaptation, not only mitochondrial density rises as seen in sub-Arctic White Sea fish and invertebrates compared to their temperate North Sea conspecifics (e.g., Sommer and Pörtner 2002, 2004; Fischer 2002; Lannig et al. 2003) and in other northern hemisphere species (Fangue et al. 2009). In addition, the ATP synthesis capacity per mg mitochondrial protein rises by a factor of about two, hand in hand with an increment in proton leakage (e.g., Tschischka et al. 2000; Sommer and Pörtner 2002). The available data suggest that cold adapted eurytherms do not reach the mitochondrial densities found in Antarctic stenotherms, but still reach higher metabolic rates due to higher mitochondrial capacities. Shifts in mitochondrial functional properties also occur during shorter-term acclimation of individual fish (Guderley and Johnston 1996; Kraffe et al. 2007; O’Brien 2011; Strobel et al. 2013; Chung and Schulte 2015). On short timescales the capacity to acclimate to cold seems more expressed in Northern than in southern populations of Northern hemisphere fish

(Lucassen et al. 2006; Dhillon and Schulte 2011; for further discussion of the mechanisms involved in setting energy demand differently in stenotherms versus eurytherms, see Supplementary Material).

Temperate eurytherms may undergo shifts in thermal windows and their widths between seasons. This leads to adjustments of baseline maintenance costs and thus rates, from low cost during winter stenothermy, to high cost during spring cold eurythermy and lower cost in the summer when cold temperatures are excluded from the thermal range (Wittmann et al. 2008). Due to losing tolerance to cold temperatures summer energy turnover may involve minimizing baseline cost and enhancing mitochondrial cost efficiency at low mitochondrial densities. Excess energy then allows eurytherms to shift most of their growth to the warmer part of the year. Animals permanently in warmer climates may also benefit from such enhanced energy efficiency, especially if hypometabolic; however, they live at the expense of enhanced climate sensitivity (Deutsch et al. 2008).

Furthermore, the level of membrane leakiness and associated cost of ion (including acid-base) regulation may be enhanced in eurytherms compared to stenotherms, thereby maintaining functional flexibility at the expense of further costs (see Supplementary Material). An analysis of the mechanisms and cost of acid-base regulation showed that in temperate eurytherms temperature-dependent changes in intracellular pH occur by active ion transport and at a higher cost than in cold adapted polar stenotherms where high passive buffering mechanisms defend pH<sub>i</sub> values (Pörtner and Sartoris 1999). These relationships need to be investigated further by comparing lipid compositions and densities of functional proteins in membranes in stenothermal and eurythermal ectotherms from various climate zones.

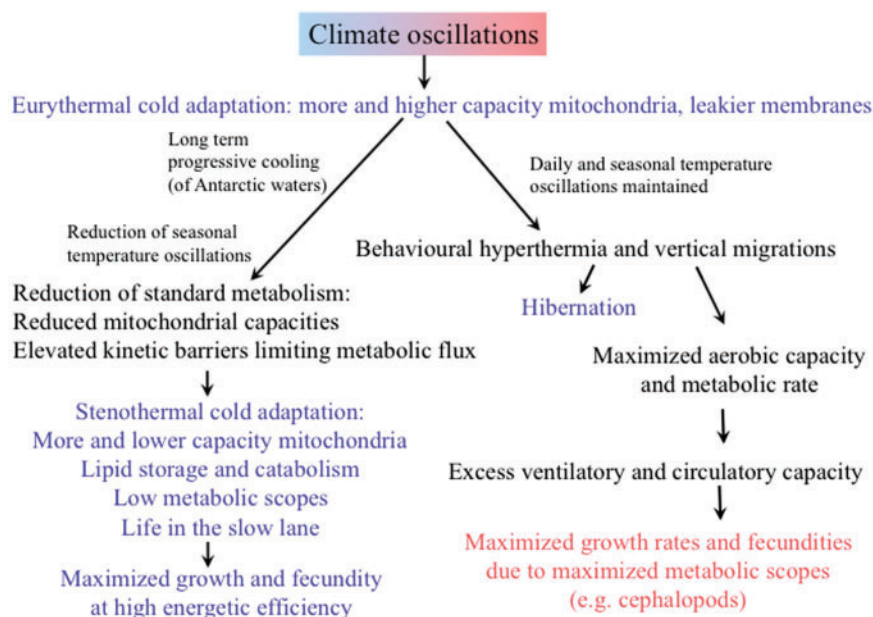
As a corollary, the treatment of thermal adaptation needs to distinguish stenotherms from eurytherms, ectotherms from endotherms and their respective temperature ranges in various climate zones. It also needs to consider the different time scales involved, from short term to evolutionary.

### **A role for climate-dependent eurythermy in evolution?**

Adaptation to stable versus variable climates may have played a key role in evolutionary history. The contrasting energetic patterns of cold stenothermy versus cold eurythermy may represent two extremes of a range of pathways for evolving cold-adapted lifestyles and associated energy expenditures

(Fig. 3). The hypometabolic pathway in Antarctic stenotherms supports growth (see above) but occurs at the expense of low net aerobic scope, limited ventilatory and circulatory capacities, a mismatch of oxygen demand versus supply setting in at lower temperatures during warming and, in consequence, expressed stenothermy (Pörtner 2001, 2002a). If growth is compensated for at the expense of reduced metabolic rate and scope this may exclude the most active lifestyles from permanently cold waters and explain why there are no high performance fish like scombrids (tuna) or sharks permanently living in high polar areas (Clarke 1998; Pörtner 2002a, 2002b). Furthermore, high mitochondrial densities not only characterize cold adapted tissue but also tissue in small, e.g. larval compared to large specimens (Wieser 1995). Therefore, cold adaptation constraints are felt especially in small early lifestages (Pörtner 2006). This may contribute to why active pelagic larvae represent a disadvantage to the respective fauna at high latitudes (see Supplementary Material). This said, even Antarctic ectotherms display some inverse variability in growth and metabolic cost, e.g., in pelagic (i.e., more active) Antarctic fishes standard metabolism is elevated at lower growth (cf. Pörtner et al. 2005a) and supports wider thermal windows (Peck et al. 2009).

In contrast, exposure to variable including cold temperature appears as a major driving force of enhanced functional capacities, supported by a higher cost, capacity and density of mitochondria, and a higher capacity and flexibility of ventilation and circulation (Figs. 4 and 5). However, thermal flexibility is not the only benefit resulting from being eurythermal. The moderate increase in mitochondrial volume densities at more variable cold temperatures reflects the same tissue design as required for elevated levels of aerobic motor activity (cf. Pörtner 2002b). Nonetheless, cold compensation of aerobic performance remains incomplete. However, if as expected in a permanent eurytherm, the cold induced maximization of aerobic capacity is not fully reversed during acclimation to warmer periods, excess energy availability remains for maximized aerobic metabolic rates and net scopes at warmer temperatures (Fig. 4). Such a trend toward permanent but costly eurythermy is observed in sub-Arctic populations of temperate fish and invertebrate species (e.g., Sommer and Pörtner 2002, 2004). Despite similar summer temperatures at White Sea and North Sea locations, metabolic rates of White Sea animals remain enhanced. Maintenance of elevated exercise capacity at higher temperatures may be favored by



**Fig. 3** Energetic consequences of cold stenothermy versus eurythermy in evolution. Animals are suggested to follow two principal, contrasting pathways of energy turnover. Energy savings are supported by constant low temperatures of the Antarctic, whereas high energy turnover modes of life results from an exploitation of eurythermal tissue design. If maximally exploited both pathways can support maximized rates of growth and reproduction in relation to baseline metabolic energy turnover (see text).

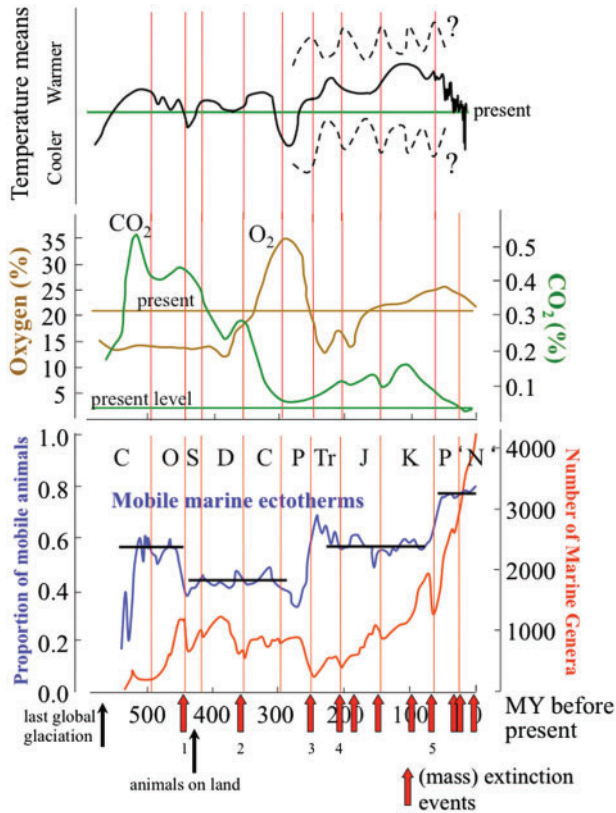
the use of permanently cold adapted eurythermal cellular membranes with a higher capacity for ion exchange to balance ion leakage (cf. Pörtner 2004). Such a trend toward a higher energy turnover mode of life requires maximized oxygen availability which is supported by a high capacity of oxygen supply mechanisms.

The high baseline cost of cold adaptation in eurytherms may draw on energy required for other processes, with the exception of aerobic exercise, which benefits, e.g. from enhanced capacities of aerobic metabolism and ion exchange (Pörtner 2002b). The cost of cold adaptation may in fact explain why growth performance and fecundity is lower in cold adapted cod (*Gadus morhua*) populations at high latitudes than in their warm adapted conspecifics when measured at the same temperatures (Pörtner et al. 2001, 2008).

During metazoan evolutionary history, two contrasting evolutionary strategies emerge to overcome energetic constraints on growth depending on the ambient climate regime (Figure S3 in Supplementary Material). In Antarctic species, constant cold temperatures enable permanent energy savings and thereby maximize the fraction of growth in the energy budget. In climates with variable temperatures such strategy is not possible. Energy savings can only be time-limited, e.g. when eurythermal animals enter metabolic depression at

cold temperatures during winter dormancy (hibernation, see above, cf. Wittmann et al. 2008), a period when they also suspend growth and reproduction. In the marine realm, energy savings may also be associated with vertical migrations to the stable cold of the deep ocean as observed in Arctic copepods (Hirche 1998). Interestingly, such strategies are much more widespread in copepod zooplankton of the Arctic where ocean surface temperatures are more variable than in the Antarctic (Schnack-Schiel 2001). During dormancy, animal eurytherms may thus transiently escape from the elevated metabolic costs associated with maintaining activity levels at cold temperature.

An alternative strategy available to cold eurytherms in variable climates would be to exploit the energetic stimulation associated with eurythermal tissue design, overcome existing constraints in energy allocation to growth, progressively enhance energy expenditure and thereby maximize energy availability to growth and a high energy turnover mode of life. This may in fact have happened in evolutionary history during periods of extreme climate variability and associated mass extinction events (Bambach et al. 2002; Pörtner et al. 2005b). This is also conceivable in today's ocean when repeated vertical migrations from warm surface waters to the cold deep, e.g. during feeding, enhance the eurythermal stimulus. As an example, ambient temperature oscillations are



**Fig. 4** Correlated changes in mean global temperatures, atmospheric oxygen and CO<sub>2</sub> levels compared to present atmospheric levels and the evolution of marine fauna (figure adopted from Pörtner et al. 2005; modified after Dudley 1998; Berner and Kothavala 2001; Huch et al. 2001; Bambach et al. 2002). High CO<sub>2</sub> levels and low oxygen levels are interpreted to favor hypometabolic life forms. Once ambient O<sub>2</sub> levels were high and CO<sub>2</sub> levels low a stepwise evolutionary shift to more mobile animal forms starting with the Permian Triassic mass extinction events appear as a consequence of (climate induced) evolutionary crises. Predominant survival of animals with high energy turnover lifestyles and elevated capacities of circulatory and ventilatory structures was favored by excessive climate oscillations, consistent with the “cost of eurythermy” hypothesis. During more stable climate periods, the resulting upward shift of performance levels and enhanced diversification of energy turnovers may have supported the exponential rise in the number of marine genera over the last 55 to 65 MY (see text, bottom numbers 1–5 indicate key mass extinction events).

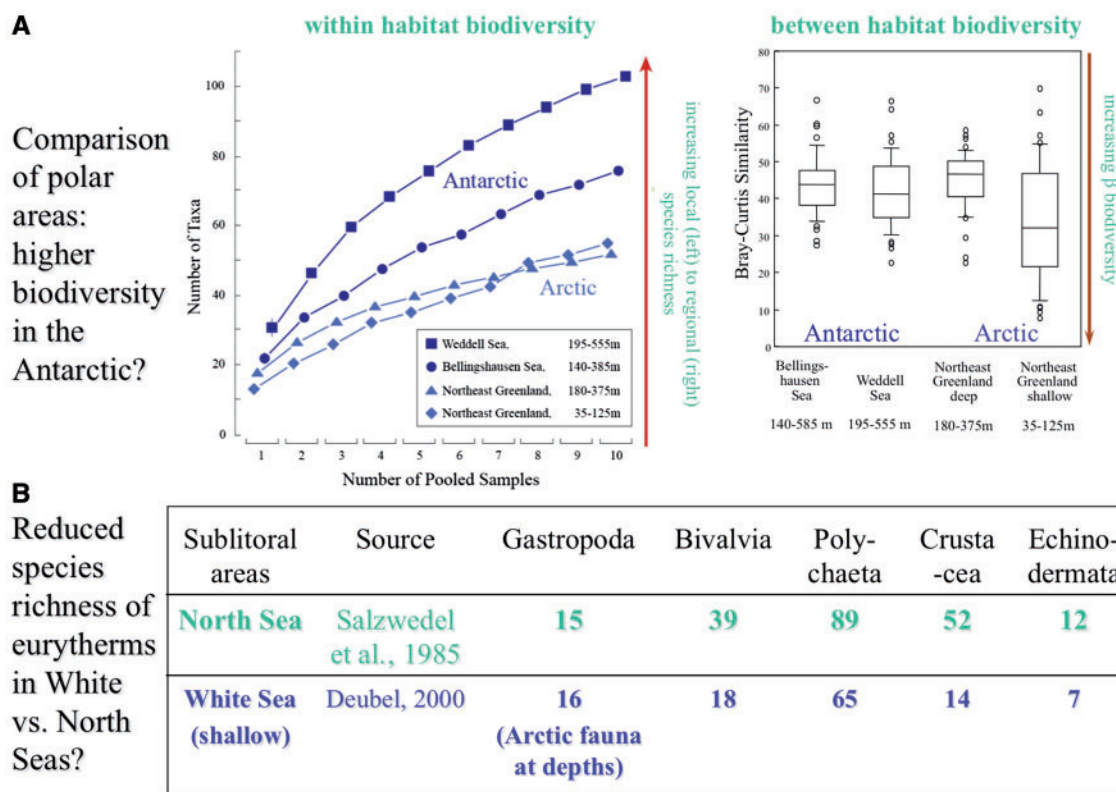
both environmentally and behaviorally induced in tuna (Block 1991), and may have supported the evolution of its high energy turnover mode of life, associated with eurythermal tissue design (Fudge et al. 1998). The resulting capacities of energy providers (e.g., mitochondria) and users (e.g., ion exchange) support performances and behaviors which then have ecosystem level consequences (Nagelkerken and Munday 2015). Maximized energy turnover and performance also supports the capacity to

compete for resources and the respective ecological niche. For example, coleoid cephalopods like squid have maximized performance and energy turnover allowing them to successfully compete with vertebrates. As a spin-off they display extremely high, similar to mammalian, growth rates (Lee 1994). As a corollary, both high energy efficiency at low energy turnover in cold stenothermy (Heilmayer et al. 2004) and maximized energy turnover in cold eurythermy support elevated growth and fecundity at either very low or very high baseline metabolic costs (Fig. 3). This dichotomy indicates the trade-offs involved in specialization to narrow versus wide temperature ranges.

The physiology of stenothermy versus eurythermy may thus advance our understanding of some unifying physiological principles behind the forces and patterns of evolution (Pörtner et al. 2005b). Large oscillations in palaeo-climates not only triggered mass extinction events due to limited thermal tolerance (Stanley 1987; Crowley and North 1988) but they may also have contributed to shaping the functional properties of surviving species, e.g. enhanced activity levels as a consequence of selection for enhanced eurythermy. Similar to the effects of present climate change (Poloczanska et al. 2013, 2014) past climate changes also caused shifts, contractions, and expansions of biogeographical ranges as well as habitat heterogeneity. Plate tectonics and the rearrangements of continents especially at higher latitudes determined the patterns of long term or seasonal climate oscillations. During the Permian, strong climatic gradients developed when Pangaea covered all latitudes from North to South. At the same time, a global selective trigger of extinctions was potentially provided by extreme oscillations between warm and cold periods (cf. Knoll et al. 1996). These oscillations may have contributed to the wave-like progressive mass extinction events in marine and terrestrial, especially tropical environments in the late Permian as well as Triassic to Jurassic periods. Even the equatorial Tethys Sea as the last refuge for tropical life forms was affected. Similar events may have been involved in other mass extinction events (Fig. 4). The potential interaction with reduced aquatic oxygen and elevated CO<sub>2</sub> concentrations (ocean acidification) may have narrowed thermal windows and thereby pushed even more for the survival of eurythermal survivors as has been developed elsewhere (Pörtner et al. 2005b; Pörtner 2010).

During the late Permian mass extinction events, hypometabolic sessile marine animals (articulates, echinoderms, bryozoans, cnidarians) were those affected most, whereas others with more sophisticated





**Fig. 5** (A) Local (left) to regional (right) species richness in similar Antarctic versus Arctic marine ecosystems. The difference in depth strata (shallow and deeper shelf) between the Arctic and Antarctic is due to the different average shelf depths. Lower levels of biodiversity result in Arctic waters (after Starman and Gutt 2002) presumably due to lower climate stability. (B) Lower species numbers in the sub-polar White Sea than the North Sea (after Salzwedel et al. 1985; Deubel 2000) go hand in hand with lower temperature means at the White Sea and with maintained or even wider ambient temperature windows.

circulatory and ventilatory functions survived to a larger extent (molluscs, arthropods, chordates). It has been suggested that rapid changes in aquatic CO<sub>2</sub> concentrations were key to such evolutionary crises in the marine realm as CO<sub>2</sub> restricts animal performance (Knoll et al. 1996). However, temperature oscillations combined with aquatic hypoxia may have played an equally important role, because of limited tolerance to persistent climate oscillations in less active species (see above). In light of the (cold) eurythermy hypothesis developed here, hypometabolic animals adapted to warmer climates would in fact be most sensitive to cold exposure, especially when thermal tolerance windows are narrowed by concomitant hypoxia associated with CO<sub>2</sub> fluctuations (Pörtner 2010). Conversely, extant more mobile Antarctic marine ectotherms with a higher metabolic rate and larger metabolic scope, due to their larger circulatory (and ventilatory) capacities, are more eurythermal than sessile hypometabolic species (Pörtner et al. 2000; Peck et al. 2009). As a consequence, some evolutionary crises were predominantly survived by eurythermal animal groups,

which for the same reasons reached wider ranges of geographical distribution (Stanley 1987).

### Eurythermy, speciation, and biodiversity: an evolutionary perspective

An overall trend becomes visible that within mass extinction events cold eurythermal species were selected, which at the same time meant a selection and shift toward higher activity, high energy turnover life forms. In fact, this becomes visible as a stepwise trend through the later phases of animal evolution when CO<sub>2</sub> levels had decreased and more mobile animal forms were favored by mass extinction events (Bambach et al. 2002, Fig. 4). At the same time, ectotherms with a small body size are more eurythermal than large animals (Pörtner 2002c; Pörtner et al. 2008; see above). This matches the observation that according to the fossil record, small animals survived mass extinctions in the first place (Stanley 1987). As a corollary, the hypothesis emerges that oxygen and capacity limitation at extreme temperatures, the cost of eurythermy and the interdependent evolution of enhanced eurythermy

and performance levels with climate change may have been important mechanistic principles effective during evolution of marine species. Along the same line of thought, large climate oscillations may in fact represent the missing trigger for the rapid Cambrian proliferation of animal life (Kerr 2002), involving the exploitation of enhanced oxygen availability. Similar trends may have been effective in terrestrial environments and contributed to the evolution of high-energy life forms and finally endothermy in mammals and birds (Pörtner 2004; Clarke and Pörtner 2010). Integrated studies of climate responses in extant fauna and climate-dependent changes in the fossil record are needed to further test these hypotheses.

Between mass extinctions speciation did not change the fraction of mobile animals among marine fauna (Fig. 4) but diversification of species, lifestyles and thus energy turnover may have occurred within and across those fractions. Competition between the surviving, more active species may have supported the establishment of even more powerful ventilatory, circulatory, and locomotory systems as well as more complex, energetically costly behaviors. Conversely, more stable climates may have allowed a variable number of species to “return” to the slow lane during progressive evolutionary transitions, especially in the permanent Antarctic cold or in tropical latitudes, where specialization on narrowing thermal windows resulted in reductions of energy turnover. Overall, the survival of eurytherms after climatically induced mass extinction events appears as a key trigger for consecutive improvements in performance capacity and mobility.

As a corollary, the course of metazoan evolution may have involved the stepwise enhancement of performance levels in situations of faunal instability, followed by a progressive differentiation of performances. Climate changes may thus have stimulated the evolution of an elevated energetic, functional and performance potential, supported by the availability of high atmospheric (and accordingly, aquatic) oxygen levels (Table S1 and Figure S4 in Supplementary Material). Some species would exploit the high energy turnover “lanes” that became available and others would evolve to live in the slow lane in subsequent less variable climates. This would have allowed for increasing functional biodiversity, an associated increase in the number of marine genera, and a reorganization of ecosystems between mass extinction events (Fig. 4, Figure S5 in Supplementary Material). During protracted (more moderate) climate oscillations and the establishment of climate gradients, speciation was supported

through an “enhanced diversity pump” resulting from climate-dependent shifts, range contractions, expansions, and temporary isolation (Crame 1993; Clarke 1996) as well as the recolonization of niches emptied during previous crises. Accordingly, the progressively enhanced bioenergetic potential for enhanced performances and the consecutive increase in functional diversity resulting from extreme and then more moderate climate oscillations may have contributed to the progressive increase in the degree of speciation observed especially during the last 55 to 65 MY (Fig. 4) and thus be a key mechanism involved. Such speciation, however, may be restricted to periods of more stable climates after mass extinctions when returning to the slow lane was possible at the expense of enhanced thermal sensitivity (Figure S5 in Supplementary Material).

In an ecosystem with higher temperature variability where all species display elevated energy turnover, species richness should be less than in a similarly structured ecosystem with similar resource availability and composed of low energy turnover stenotherms. Conversely, all species being more or less stenothermal and energy efficient may support enhanced species diversity. For the same reason and again, across structurally similar systems only, eurythermy is possibly linked to shorter food chain length (cf. Post 2002). When comparing systems with similar (nutritional) energy availability in constant versus variable temperatures, higher degrees of eurythermy may thus limit species richness to lower levels. Furthermore, enhanced activity and roaming ranges associated with eurythermy (Pörtner 2002b) may enhance the chances to find food but this effect enhances energy demand and may not fully compensate for constraints on species numbers. There is some but limited support available for these hypotheses: A lower level of biodiversity was in fact found in the thermally more variable Arctic than in a Southern Ocean ecosystem at more invariant temperatures, at the same level of between habitat biodiversity (Gutt and Starman 2002, Fig. 5). Similarly, when comparing marine ecosystems in a latitudinal cline, species richness among several phyla (Mollusca, Polychaeta, Echinodermata, Crustacea) was found lower in the sublittoral, subpolar waters of the White Sea than in similar biotopes of the southern North Sea (Salzwedel et al. 1985; Deubel 2000, Fig. 5). At similar temperature variability the White Sea system is characterized by lower mean temperatures and extended winter periods. Energy demand of populations of the same species in these systems has been compared and is higher in cold eurythermal White Sea invertebrates than in

temperate eurythermal North Sea ones (e.g., Sommer and Pörtner 2002, 2004). More field examples combined with physiological studies are needed to test for a role of these suggested principles. All of these considerations are in line with the conjecture that maximum species numbers in similar ecosystems under different temperature regimes is related to energy (food) availability and demand (see above). In general, such observations would underline the general importance of understanding eurythermal versus stenothermal adaptations to temperature and their macro-ecological consequences.

For a more detailed picture and, finally, quantitative understanding of the mechanisms and pathways of evolutionary temperature adaptation, the underlying molecular, cellular, and whole organism mechanisms need to be investigated in various climates (cf. Johnston and Bennett 1996; Pörtner et al. 2000; Pörtner 2002a, 2002b, 2002c; Criddle et al. 2003). The recently developed “Community Temperature Index” (CTI) may be suitable to test relevant hypotheses as it tracks changes in thermal specialization of biological communities across time and space (Stuart-Smith et al. 2015). CTI uses the global distributions of species to define their thermal niches, and takes the temperature in the middle of the geographical range of the species, weighted by their abundance or presence in a community of  $n$  species, to analyze the contributions of e.g. eurytherms or stenotherms to a community. It also needs to be elaborated how the evolutionary principles discussed here operate and may differ in extant ecosystems. As a perspective, such knowledge would also support a deeper understanding of how the physiology of thermal limitation and adaptation contribute to shaping the responses of extant fauna to anthropogenic climate change.

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## Supplementary data

Supplementary data available at ICB online.

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