



Society for Experimental Biology Annual Main Meeting 28th June – 1st July 2009, Glasgow, UK

C6 – GENERAL THERMAL BIOLOGY

C6.1

09:00 Wednesday 1st July 2009

Physiological responses of Mediterranean corals to temperature and pH perturbations

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Understanding coral responses to environmental change is critical to predicting their health and future distribution. While tropical and subtropical corals generally experience limited environmental changes, temperate corals undergo pronounced seasonal cycles in irradiance, temperature and nutrients. Their ability to cope with environmental changes makes temperate organisms an ideal model to investigate the effects of global change on coral physiology.

Using the two symbiotic Mediterranean corals, *Cladocora caespitosa* and *Oculina patagonica*, we studied the effects of natural changes in light and temperature on their physiological responses both in laboratory and in situ. Temperature was shown to be the major factor affecting coral metabolism. Photosynthetic and growth rates were maximal under normal summer temperatures up to a physiological threshold after which very high temperatures induced, in both coral species, a severe decrease in the rates of photosynthesis and growth. Coral response to high temperatures was species-specific, and highly dependent on the amplitude and length of the temperature stress. These results, together with the observations of recurrent mass-mortalities during recent summers suggest that endemic Mediterranean corals are living near their upper thermal limits. A second study assessed the effects of seasonality, thermal stress (+3 °C) and ocean acidification (700 μatm ; end-of-century prediction) on the coral *C. caespitosa*. Corals were collected at 30 m depth and maintained in aquaria over a one-year period under experimental conditions. Surprisingly, calcification and photosynthetic rates were not affected by the high $p\text{CO}_2$ conditions, while the seasonal change in temperature had significant effects.

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C6.2

09:20 Wednesday 1st July 2009

Physiological and shell microstructural responses of an intertidal periwinkle *Littorina littorea* (Linnaeus, 1758) to ocean acidification and elevated temperature

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Future changes in seawater temperature and pH could significantly affect marine biodiversity, yet there are still few studies that have addressed the combined influence of these environmental stressors. In this study, a laboratory experiment was used to investigate how the potential synergistic/additive effects of long-term exposure (30 days) to different levels of seawater pH (8.0, 7.8, 7.6, and 6.5) and temperature (ambient and +4 °C) on the physiology and shell construction of the intertidal gastropod, *Littorina littorea*. To determine effects on physiological function, concentrations of ATP, ADP, AMP, succinic and lactic acid were measured, as well as rates of respiration and water loss. In addition, vertical and horizontal sections through the shell were taken and fragments of approximately 5 mm in length assessed for the growth form (thickness) and structural layers. The aim of this study is to identify whether the combined exposure to ocean warming and acidification at the levels predicted for the year 2100 and 2250, and for CO_2 leakage from geological storage will exert a synergistic or additive effect on the fitness of this key intertidal grazing species as currently predicted under the simultaneous influence of both ocean acidification and temperature change.

Keywords: Biodiversity; Acidification; Temperature; ATP; ADP; AMP; Succinic acid; Lactic acid; Fitness

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C6.3**09:40 Wednesday 1st July 2009****Impacts of hypercapnia and temperature on physiological performance of marine invertebrates from the Baltic Sea**

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Anthropogenic CO₂ emissions cause rising ocean pCO₂ and decreased ocean pH. This progressing ocean acidification has been shown to compromise physiological performance of many marine benthic organisms. In this study, Baltic blue mussel *Mytilus edulis* and common starfish *Asterias rubens* from Kiel Fjord were exposed to 6 different hypercapnic levels between 0.04 and 0.41 kPa pCO₂ for 1–2 weeks, respectively, at 12 °C. The experiments revealed extracellular acidosis in both species with no active accretion of HCO₃⁻. Even at moderate pCO₂ levels (e.g. 0.08 kPa) pHe was significantly decreased. Although shell dissolution occurred in the highest pCO₂ treatment, no HCO₃⁻ or Ca²⁺ accumulation was observed in extracellular fluids. Gradients of pCO₂ between body fluids and ambient sea water were stable at lower pCO₂ levels and decreased at 0.41 kPa, which might indicate a metabolic depression. Ongoing metabolic rate and filtration rate determinations will resolve this issue. Calcification rates were only minorly impacted in the lower pCO₂ treatments and became negative at 0.41 kPa pCO₂. Field measurements conducted in Kiel Fjord revealed a large annual variability of surface pH and pCO₂. During winter and spring, surface pH averaged 8.1 but mean summer pH values were <7.8 and the highest measured pCO₂ value exceeded 0.2 kPa (ca 2000 µatm), thus even the maximum average pCO₂ values modelled for the surface ocean of the year 2300.

Experiments will be repeated at summer temperatures of 18–22 °C in June 2009 to clarify if thermal extremes increase the species' sensitivity towards hypercapnia.

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C6.4**10:30 Wednesday 1st July 2009****Synergistic effect of ocean acidification and elevated temperature on the physiological ecology of the intertidal crab *Porcellana platycheles***

Piero Calosi (University of Plymouth), Penelope Donohue (University of Plymouth), Stefanie Alber (University of Konstanz and University of Plymouth), John I. Spicer (University of Plymouth)

Ongoing global environmental changes pose an unprecedented threat to global biodiversity; in particular increasing environmental temperatures and decreasing ocean pH (Ocean Acidification or OA, as a result of increased seawater pCO₂). The extent to which these two drivers will act synergistically, reducing the thermal tolerance window of individual species, and so potentially affect their large-scale distribution, is only beginning to be understood. Here we present a formal test on the potential synergistic effect of elevated temperatures and hypercapnic sea water on the rate of O₂ uptake (as a proxy for metabolism), tolerance to heat, and the degree of exoskeleton calcification in the intertidal porcellanid crab *Porcellana platycheles*. Eighty individuals crabs were haphazardly assigned to one of four treatments, and kept for 40 days at either 15.0 °C (seasonal ambient) or 20.0 °C (+5 °C), and at either pH 8.0 (seasonal ambient) or 7.4. In *Porcellana platycheles* metabolic activity and tolerance to heat were positively affected by increasing temperature, whilst the degree of exoskeleton calcification was negatively affected. No

effect of pH was detectable. It is therefore suggested that *P. platycheles* may not be affected by medium-term exposure to the predicted level of OA, but that acclimation to elevated temperatures may result in improved tolerance of high temperatures despite an increase in metabolic costs and a decrease of calcification. Our results are discussed within a broader ecological and evolutionary context, with particular emphasis on the idea that intertidal species may be to some extent adapted to hypercapnic exposure.

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C6.5**10:50 Wednesday 1st July 2009****Oxygen deficiency under elevated temperatures: a mechanism connecting the response of stream ectotherms to global warming?**

Wilco C.E.P. Verberk (University of Plymouth, University of Nijmegen), David T. Bilton (University of Plymouth)

There are few demonstrated cases of causal links between global warming and changes in the species composition of communities, and the structure and functioning of ecosystems. Changes in growth, fecundity or the seasonal timing of biological events reduce a species' fitness and competitive ability, which may ultimately result in shifts in the species composition.

Oxygen deficiency may provide an example of a direct temperature-mediated causal link. Stream invertebrates display a range of adaptations related to respiration, and oxygen is considered a key factor structuring species assemblages. Furthermore, as water temperatures rise, aquatic ectotherms face the double problem of reduced oxygen concentrations and increased oxygen demand. Therefore, oxygen deficiency may be an important mechanism setting limits to thermal optima, thus explaining many of the effects of global warming. In marine ecosystems, a mismatch between oxygen demand and oxygen supply to tissues appears to be the first mechanism to restrict survival at thermal extremes.

Here we present evidence suggesting that climate-driven oxygen deficiency may occur in aquatic stream invertebrates. Not all species will be equally at risk, depending on their physiology (metabolic rate, thermal limits) and other traits (e.g. body size, type of respiration). Integrating information on a species' physiological and biological traits may yield a comprehensive mechanistic understanding of its thermal sensitivity.

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C6.6**11:10 Wednesday 1st July 2009****Thermal dependence of inducible defences in mosquito larvae**

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Temperature profoundly influences the reaction rates and efficiency of all physiological systems. During predator–prey interactions we often expect temperature to directly influence the locomotor capabilities of both predator and prey, and thus alter the dynamics of the system. However, predation is seldom just a simple game of 'cat and mouse'. Prey can induce behavioural and morphological defenses that increase their

chances of escape and survival. Prey can commonly achieve this by reducing their activity and making themselves less conspicuous to predators. However, reducing activity constrains total foraging time and can lead to substantial energetic costs. For ectothermic prey, increases in temperature could magnify these costs by increasing total metabolic demands. We tested this idea by examining the effect of temperature on the costs of behavioural responses to predators in mosquito larvae. Larvae of the urban mosquito *Aedes notoscriptus* avoid predation by reducing activity. Our previous research has shown that the response is indeed costly, retarding growth and development and manifesting smaller adults that have a shorter lifespan when not fed. We expect these costs to be exacerbated in larvae reared at higher temperatures or, larvae will trade-off the increased costs by limiting their behavioural response. This study provides an examination of the influence of temperature on the costs of inducible defences in prey and provides insight into the subtle effects of the thermal environment on ecosystem dynamics.

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C6.7

11:30 Wednesday 1st July 2009

Variation in the physiological responses of multiple marine gastropod species in relation to the various thermal regimes of the intertidal region

Samuel D. Clayman (University of Sydney), Frank Seebacher (University of Sydney), Michael B. Thompson (University of Sydney)

The intertidal region experiences a high degree of thermal variability at daily and seasonal scales. The capacity of marine gastropods, which occur from subtidal to supratidal habitats, for aerobic and anaerobic metabolism may differ with increasing shore height. We first quantified the thermal variability of various height intervals on a rock platform near Sydney, Australia, then compared five gastropod species to quantify physiological responses to the varying thermal regimes along the shore gradient. Whole-animal rate of oxygen consumption (VO_2) was measured in summer- and winter-acclimatized snails in both air and water, across a test temperature range of 10–35 °C. Aerobic and anaerobic enzyme activity was measured at 10°, 20° and 30 °C. VO_2 in intertidal species was up to three times higher than sub- or supra-tidal species at most temperatures in water in both seasons, with the same pattern occurring in aerial VO_2 during winter but not in summer. Respiratory ratios (aerial VO_2 :aquatic VO_2) increased 1.21–4.22 fold in all species in winter, suggesting an opportunistic seasonal increase in metabolic activity while thermal stress is low. Only the high-intertidal species compensated both aerobic and anaerobic enzyme activities when tested at 20 °C in summer compared to 10 °C in winter. Differences in the use and regulation of physiological parameters such as VO_2 and enzyme activities are related to position on the shore, which likely represent changes caused by the selective pressures of variation in temperature regimes.

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C6.8

11:50 Wednesday 1st July 2009

Understanding physiological tolerance through thermal limits of three amphipod species

Colette Mesher (University of Plymouth), Andy Foggo (University of Plymouth), John I. Spicer (University of Plymouth)

In order to make predictions about the persistence of species in their present habitats in a changing climate, it is important to consider not just their physiological performance under current environmental conditions, but also their absolute tolerances, as determinants of their thermal niche. Critical thermal maximum (CT_{max}) as well as critical thermal minimum (CT_{min}) are both parameters which have the potential to be key limiting factors in a species' distribution. We investigated the effects of biotic (mass) and environmental (temperature and salinity) factors on the plasticity of these physiological tolerances for three species of amphipod from the Avon estuary, *Gammarus marinus*, *G. chevreuxi* and *Corophium volutator*. Preliminary data indicate that when individuals were acclimated to winter temperatures (10 °C), CT_{mins} were lower, conversely when individuals were summer acclimated (20 °C), CT_{max} increased. All species had similar temperature ranges (CT_{max}–CT_{min}), but their upper and lower tolerances differed. *C. volutator* showed the greatest upper thermal tolerance (CT_{max} = 41 °C) and *G. marinus* showed the greatest tolerance of low temperatures (CT_{min} = –2 °C). The effects of salinity on thermal tolerance appear to be minimal. Mass did not influence maximal temperature tolerance but larger individuals did appear to have a lower CT_{min} than smaller ones. The thermal tolerance work will be discussed in detail along with the implications of present and future geographical distribution of these animals. Additionally, how this work forms part of the physiological component of a generic model for amphipod distribution will be briefly discussed.

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C6.9

13:30 Wednesday 1st July 2009

Energy consumption and expenditure in gammarid amphipods across a natural thermal gradient

Samuel S. Rastrick (Bangor University), Nia M. Whiteley (Bangor University)

Whole-animal rates of oxygen uptake and protein synthesis were determined in four gammarid species distributed along the coastal fringes of the north Atlantic and Arctic Oceans. Whole-animal rates of oxygen uptake and protein synthesis, measured in individuals collected from a wide range of latitudes (79–36°N) and at the temperatures at which they were collected, were scaled to a standard body mass of 1 g. Rates of oxygen uptake in the arctic/boreal species decreased with latitude accompanied by a similar decline in fractional rates of protein synthesis. Consequently, polar populations at 5 °C were characterised by relatively low rates of energy consumption and expenditure. In contrast, the warm-temperate and temperate/boreal species compensated for the natural decline in habitat temperature with latitude. As a result both rates of oxygen uptake and protein synthesis were maintained at a specific level despite changes in latitude. The warm-temperate species, however, maintained higher levels of protein synthesis than the temperate/boreal species indicating differing levels of energy expenditure. Phylogenetic studies revealed that the species with the relatively high rates of protein synthesis occupied the same clade as Mediterranean gammarids and the two species characterised by low rates of protein synthesis grouped with cold-water species. Consequently gammarid amphipods show a range of species-specific physiological responses to latitude which are linked to thermal histories and ancestral origins. Interestingly, the species with the greatest tolerance to temperature change compensated for latitudinal changes in temperature, but maintained low rates of energy expenditure throughout its latitudinal range.

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C6.10

13:50 Wednesday 1st July 2009

AMP-activated protein kinase: Function as cellular energy gauge during the development of endothermy in birds (*Gallus gallus*)?

Isabel Walter (University of Sydney), Frank Seebacher (University of Sydney), Bronwyn Hegarty (Garvan Institute of Medical Research, Sydney)

Endothermy is characterised by high metabolic rates. During embryogenesis endotherms cannot regulate their body temperature metabolically and are therefore similar to ectotherms. The transition from ectothermy to endothermy occurs by the increase of metabolic capacity coupled to increasing energy demands, so that the cellular energy balance has to be adjusted during this developmental process. Molecular mechanisms coordinate, control and adjust metabolic pathways to maintain a stable cellular energy status. AMP-activated protein kinase (AMPK) is a key player in controlling energy metabolism in mammals by sensing cellular energy status (AMP/ATP ratio). AMPK phosphorylates a variety of targets that regulate down stream processes, including mitochondrial biogenesis mediated by an increased abundance of the transcriptional coactivator PGC-1 α . In earlier research we showed that PGC-1 α is an important component for the development of endothermy. Therefore, the aims of this study were to determine, firstly, to what extent development of endothermy in a bird (*Gallus gallus*) is associated with an increase in AMPK expression and activity. Secondly, we tested the hypothesis that chronic activation of AMPK with AICAR induces an increase in mitochondrial biogenesis, which leads to an increase in thermogenic capacity. Thirdly, we investigated whether thyroid hormones link AMPK activity to increases in thermogenic capacity. Our preliminary results show an increase in AMPK activity 3 days before and after hatching compared to 1 day before hatching. Reduced thyroid hormone levels also cause elevated AMPK activity. Our findings suggest that AMPK play an important role to establish endothermy in birds.

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C6.11

14:10 Wednesday 1st July 2009

Thermal acclimation causes changes in exercise performance and body temperature but not in tissue metabolic capacity of a small endotherm (*Rattus fuscipes*)

Elsa J. Glanville (University of Sydney), Frank Seebacher (University of Sydney)

Cold environments demand increased heat production for endotherms to maintain a stable body temperature (T_b). Small mammals are particularly susceptible to decreases in environmental temperature (T_a), and can respond by increasing metabolic heat production capacity. Concurrent decreases in T_b may offset the increased cost of life in the cold. We aimed to determine how thermal acclimation affects T_b , running performance and metabolic capacity of a wild rat (*Rattus fuscipes*). Rats were acclimated to warm (WA: 24 °C, $n = 10$) or cold (CA: 12 °C, $n = 10$) temperatures for four weeks. Mean T_b of CA rats (36.56 °C \pm 0.11) was significantly lower than that of WA rats

(37.34 °C \pm 0.10). Resting metabolic rate was not affected by acclimation. However, maximal metabolic rate during exercise was greater in CA rats at low temperatures (7 °C and 12 °C), resulting in greater metabolic scope. Cold acclimation resulted in significant increases in sustained running performance at low test temperatures. ADP stimulated (SIII) mitochondrial respiration increased significantly in CA heart muscle but there was no change in SIII or uncoupled (SIV) mitochondrial respiration in any other tissue (skeletal muscle, liver or brown adipose tissue). Cold acclimation did not increase UCP1 mRNA concentration in BAT and had no effect on tissue specific metabolic enzyme activity (cytochrome c oxidase, citrate synthase, lactate dehydrogenase). Both wild and captive bush rats reduce the increased energetic cost of living in cooler T_a s by reducing T_b . However, the increased metabolic heat production capacity that accompanies the seasonally lower T_b in winter acclimatized rats does not occur in cold acclimated rats.

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C6.12

Poster Session – Tuesday 30th June 2009

Function of Photosystems I and II during coral bleaching

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Reef-building corals thrive in shallow waters due to their symbiosis with photosynthetic dinoflagellates (zooxanthellae). When seawater temperatures are anomalously high this symbiosis breaks down and corals 'bleach', that is they lose their symbionts and/or pigmentation. Previous research using chlorophyll-fluorescence techniques has shown that bleaching is initiated by damage to Photosystem II, whose function is impaired at high temperatures. However, Photosystem II is only one component of the photosynthetic machinery, and for corals little is known about the effects of temperature on the activity of Photosystem I nor on the major carbon fixation enzyme Ribulose-bisphosphate carboxylase/oxygenase (RuBisCO). In this study we simultaneously measured the activities of Photosystems II and I in two tropical coral species exposed to 'normal' (26 °C) and 'high' (32 °C) temperatures and under different heterotrophic feeding regimes (fed and unfed). In addition, the amounts of Photosystems II, I and RuBisCO in the experimental colonies were quantified using protein immunoblot assays. Results showed that the capacity for non-photochemical quenching of Photosystem II was higher for fed colonies and at normal temperatures. Unfed colonies suffered electron acceptor-limitation of Photosystem I whereas electron donor-limitation of Photosystem I was more intense at high temperature. These results confirm that Photosystem II function is restricted at high temperature, while analyses of Photosystem I activity provided significant additional information about temperature and feeding effects on photochemistry.

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C6.13

Poster Session – Tuesday 30th June 2009

Dispersal responses and tolerance to temperature and salinity in two hydraenid beetles from hypersaline inland waters

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Saline inland waters are interesting due to their halotolerant/halophilic biota. These habitats harbour a high number of endemic species, which often have restricted geographical ranges, as well as taxa of wider distribution. These differences in geographical range size occur often among sister species. Moreover, in many cases closely related species occupy exclusively in either lentic or lotic saline waters, characterised by important differences in thermal and salinity stability. Here we investigate the dispersal response (emersion and flight) and tolerance (immobility and mortality) to water temperature and salinity in two very closely related species of hypersaline waters with distinct biogeographies (*Ochthebius glaber* and *O. notabilis*). Both species are typical inhabitants of some Mediterranean saline habitats, but while *O. glaber* is endemic to Southeast Iberian Peninsula and is restricted to running waters, *O. notabilis* is found across the Iberian Peninsula and Northern Africa and inhabits saline lagoons.

Our results suggests that adult *O. glaber* and *O. notabilis* are not affected by salinity over the wide range tested and only the combination of extreme high temperatures and salinities represent a threat to individual survival. Nevertheless, *O. glaber*, the species with the most restricted geographical distribution and inhabiting lotic water bodies, displayed dispersal response at lower stress level as well as lower tolerance than *O. notabilis*, which occupies habitats with greater thermal variability. Our findings agree with previous work carried out on diving beetles, and suggest a relationship between thermal tolerance, habitat occupancy and geographical range in these inland saline water invertebrates.

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C6.14

Poster Session – Tuesday 30th June 2009

Thermal biology of the interstitial polychaete species *Ophryotrocha labronica* (Polychaeta, Dorvilleidae)

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The gonochoric polychaete *Ophryotrocha labronica* is a widespread interstitial species commonly found in the fouling communities of harbour and lagoon environments. A number of manipulative experiments have revealed a strong influence of temperature on the life history and demography of this species. Furthermore, significantly different patterns in life-history and demographic traits have been demonstrated among populations inhabiting regions of the Mediterranean Sea with different climatic profiles. However, limited investigations have been carried out so far

on the thermal biology of this species. We have conducted an experimental characterisation of the thermal biology of *O. labronica*, and described mortality curves of individual male–female pairs kept at one of seven different temperatures, ranging between 5 and 35 °C. For each pair, life-history traits (size at first reproduction, growth and total egg production) were also characterised. In a separate experiment, the upper and lower thermal limits and relative acclimatory ability of individual polychaetes were determined using several sublethal end-points, as well as lethal limits. A series of trials were conducted to test the effect of acclimation temperature, duration of acclimation and temperature change rate during warming/cooling experiments. Results are discussed in the light of *O. labronica*'s ecology and life history.

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C6.15

Poster Session – Tuesday 30th June 2009

Effects of multiple stressors on energy metabolism in oysters

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Marine ectotherms including oysters are exposed to multiple stressors in estuaries, which may interactively affect their physiology. We have studied the effects of cadmium (Cd) on metabolic responses to elevated temperature and anoxia (during air exposure) in eastern oysters, *C. virginica*. Based on the concept of oxygen- and capacity-limited thermal tolerance in aquatic ectotherms (Pörtner, 2001), we show that Cd can have detrimental effects on metabolic performance during temperature rise. Thus, during acute warming from 20 to 28 °C (4 °C/48 h) Cd-exposed oysters showed a stronger temperature-dependent decrease in hemolymph oxygen partial pressures. The oxygen delivery systems could not provide enough oxygen to cover Cd-induced elevated metabolic demands at high temperatures. Interestingly, cardiac performance rose to a similar extent in control and Cd-exposed oysters with warming indicating that cardiac output was unable to compensate for elevated energy demand in Cd-exposed oysters. Cadmium also affected anaerobic metabolic capacity in oysters, as indicated by significantly lower rates of accumulation of anaerobic end products in Cd-exposed oysters than in controls during anoxia. This was accompanied by a significant decrease in ATP levels and ATP/ADP ratio during environmental anoxia in control and Cd-exposed groups. After 12 h of normoxic recovery, concentration of anaerobic end products and adenylates returned to the control levels in control but not in Cd-exposed oysters. These findings show that Cd exposure may partially inhibit the metabolic response to elevated temperature and anoxia stress and reduce stress tolerance in oysters. Supported by NSF CAREER (IBN-0347238) and Deutscher Akademischer Austauschdienst.

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C6.16**Poster Session – Tuesday 30th June 2009****Ambient media affect thermal response of cellular energy budget**

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Thermal windows differ between the performances of whole-organisms and isolated cells with the latter maintaining functions over a much wider temperature range. In the intact organism, as thermal limits are set by oxygen availability, temperature itself might cause shifts in cellular energy budget in vitro, thereby inflicting on whole-organism performance.

We investigated temperature-dependent oxygen consumption of cod hepatocytes (*Gadus morhua*) in the presence of specific inhibitors. Different media were used to investigate the impact of nutrient content on cellular temperature sensitivity (standard salt solution Hanks complemented with glucose vs. nutrient-enriched

Leibovitz L15-medium). Overall, cellular respiration was higher in L15-media. Chronic cold incubation (0 °C) reduced cell respiration without affecting thermal sensitivity as shown by similar Q10 values. A significant impact of media composition was found on thermal sensitivity of cellular energy budget. Prior to cold incubation measurements in both media revealed protein synthesis fractions higher at 23 °C than at 5 °C, associated with elevated fractions of ATP synthesis. Following cold exposure, ATP synthesis was found lower and proton leakage rates enhanced when assayed at 23 °C. Reduced ATP synthesis rates are associated with media-dependent changes in energy allocation in that way that Hanks-incubated cells showed reduced fractional rates of protein synthesis, whereas L15-incubated cells rather displayed reduced ion regulation via Na/K ATPase. Cold incubation had no effect on membrane properties and citrate synthase activity. The observed impact of media composition on thermal sensitivity of energy budget resulting in cold-induced limitation of different processes (protein synthesis vs. ion regulation) will be discussed.

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