Editorial

Life and applications of extremophiles

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The Earth contains a plethora of environments that, from an anthropocentric perspective, might be classified as extreme. Relative to the typical standard conditions of temperature, pressure, humidity, air quality, light, nutrient supply, shelter, lack of predation, etc. that many humans encounter in everyday life, almost all other forms of life live under more constrained conditions. From this perspective, the world is clearly full of extremes – temperature, salinity and pH being the abiotic factors that first to spring to mind. Even environments that represent large portions of the biosphere, such as cold environments (e.g. > 80% of the Earth's biosphere is permanently below 5°C), are considered extreme – clearly not because they are extreme to the large number of organisms that can survive there, but because the extreme cold greatly restricts human colonization (e.g. the cold deep ocean).

Still, even with this concept of extreme not aptly reflecting the 'viewpoint' of many life-forms on the planet, by recognizing what are anthropocentric extremes and pondering how life prevails in such environments, strong lines of scientific research have been generated that have resulted in important discoveries being made about the resident 'extremophiles' and life on Earth as a whole. Breakthroughs have provided completely new levels of understanding about biological mechanisms of adaptation, informed us about the evolution of life on Earth, expanded the repertoire of locations suitable for searching for extra-terrestrial life, and provided a boon for biotechnology and related commercial industries.

With regard to the concept of extremophiles and what has been learned about them, there is value in further considering what constitutes an extreme environment and what defines an extremophile – in particular, the match between the organism and the specific environmental extreme, and the mechanisms that lead to survival and in some cases ecological dominance. Consider for example, that many microorganisms found in hot acidic environments require low pH and high temperature for growth – at low temperature or alkaline pH the same organisms cease growth and/or lyse and die. In this regard it is straightforward to consider the microorganisms as thermoacidophiles, where 'phile' denotes 'love' or in essence, a 'requirement' for those conditions. Consistent with this line of reasoning, in the case of halophiles, there is an obligate requirement for high levels of salt in the growth medium. However, radically different mechanisms have evolved to achieve 'halo' extremophily, with obligate extreme halophiles from the domains *Archaea* and *Bacteria* accumulating very high concentrations of salt in the cell, whereas moderate halophiles or halotolerant microbes adopt a more flexible strategy, largely excluding salt and synthesizing instead compatible organic solutes to maintain osmotic balance.

It is interesting to consider other types of extremophiles, such as radiation resistant *Deinococcus radiodurans* (bacteria), *Methanosarcina* species (archaea) from permafrost and *Pyrococcus furiosus* (archaea) from hydrothermal vents – all are highly resistant to γ-radiation, yet none have evolved to 'love' or even tolerate extremely high levels of radiation. Instead, extreme radiation resistance is a result of cross protection having arisen from selection pressure to repair damaged DNA caused by dehydration or thermal injury. In one further example, many microorganisms from naturally cold environments display a relatively slow rate of growth when cultivated at *in situ* temperatures compared with higher temperatures. While at first glance this may appear to indicate that these psychrophiles are poorly adapted to the cold, temperature-dependent growth rate is in fact a very poor indicator of fitness for psychrophiles. Studies of psychrophilic bacteria and archaea have demonstrated both physiological adaptation and ecological competitiveness at *in situ* temperatures – responses that do not occur at relatively high temperatures such as T_{opt} (the temperature at which microorganisms grow the fastest).

As a result of the awareness about the diversity of extreme environments (often involving multiple types of extremes), the range of evolutionary paths that have led to individual microorganisms becoming extremophiles, and the overall lack of understanding about the adaptive mechanisms of individual extremophiles and whole microbial communities, knowledge in the field has been most effectively gained through studies that have incorporated a thorough evaluation of the particular environmental extreme. This combined with letting empirical determination (and not preconception) guide the work, and keeping a wise eye open to the capacity of discovery to surprise has allowed the successful augmentation of this important knowledge base.

'Life and Applications of Extremophiles' is the focus of special issues in *Environmental Microbiology* and *Environmental Microbiology Reports* and a thematic issue in *Microbial Biotechnology*. Reflecting the broad coverage of the journals, the thirty-plus papers cover diverse topics about a wide range of extremophiles. Several papers arose out of the MicroPerm Workshop held 8–10 November 2010 in Potsdam, Germany – the first workshop aimed at bringing together microbiologists working on Arctic and Antarctic permafrost environments.

All life requires water for growth. Lithotrophs living on or just below rock surfaces, survive for long periods with low water activity. Bjelland and colleagues (2011) used molecular phylogenetic analyses to characterize lichen–rock-associated microbial metacommunities from areas of Norway. Their work revealed that lichens are much more than a symbiosis between algae and fungi but additionally house a diverse mix of bacteria and archaea, with an apparent association between community composition and species of lichen that may account for the specific rock weathering characteristics observed with different species of lichen. Perfumo and colleagues (2011) used both molecular phylogenetic and cultivation-dependent techniques to study the microbial communities associated with ferromagnetic sand from an arid coastal mine area in Italy. Similar to the lithotrophs studied by Bjelland and colleagues (2011), microbial communities are exposed to dehydration and UV, but in this case the ferromagnetic sand communities are also exposed to high temperature and very high iron content. Reflecting some of the common selection pressures, some microbial groups (*e.g. Deinococcus*) were detected in both studies. A related story that speaks to survival by avoiding extremes, is the report by Reeb and colleagues (2011) on the microbial communities present within buffalo bones found in a high altitude region of Yellowstone National Park. Members of the *Stichococcus* clade of green algae were found to be abundant, and the authors speculated that similar to endolithic communities in Antarctic soil, they might proliferate in the bone due to protection from high UV radiation

and desiccation, as well as protection against toxic metals in the environment.

A number of reports and reviews highlight the development of methodology for advancing studies of extremophiles: the use of proteomics for studying extremophiles (Burg *et al.*, 2011), RNA stable isotope probing for studying methanotrophic communities (Graef *et al.*, 2011), quantitative PCR to measure the abundance of syntrophic acetate-oxidizing microorganisms in ammonia-stressed biogas reactors (Westerholm *et al.*, 2011) and high temperature petroleum reservoirs (Mayumi *et al.*, 2011), metagenomics for studying viruses from hypersaline lakes (Sime-Ngando *et al.*, 2011), a multiplex approach for quantification of fine-scale temperature-induced changes in the proteome (Williams *et al.*, 2011) and a microarray for gene regulation studies (Campanaro *et al.*, 2011) of a psychrophilic archaeon, and development of gene transfer systems for manipulating halophiles (Calo *et al.*, 2011 and Köcher *et al.*, 2011a,b), psychrophiles (Cavicchioli *et al.*, 2011) and thermophiles (Taylor *et al.*, 2011).

The development of tractable genetic systems has paved the way for breakthroughs in both discovery science and commercially orientated research of many biological systems. For extremophiles, developing a suitable system can be complicated by the challenges imposed by the extreme cultivation and plating conditions. Taylor and colleagues (2011) review gene transfer systems developed for (hyper) thermophilic archaea and bacteria, focusing on the value of genetic systems for learning about cellular physiology, and particularly for whole cell conversion of lignocellulose to alcohols. Kobayashi and colleagues (2011) demonstrated a role for the σ^{32}-mediated heat-shock response in organic-solvent tolerance in *Pseudomonas putida*. Calo and colleagues (2011) developed a system for enabling glycoproteins to be synthesized in haloarchaea. The study flows from previous studies that defined the pathway for synthesis of novel N-linked glycans in *Haloferax volcanii*. In their article in Environ. Microbiol., Köcher *et al.* (2011a) describe the development of a markerless mutagenesis gene deletion system for the moderately halophilic bacterium, *Halobacillus halophilus*, and demonstrate its use for deleting the *proHJA* operon. In their accompanying study in EMI Reports, Köcher *et al.* (2011b) examine the regulation of proline synthesis in response to physiological perturbation, rationalizing the role of proline as a carbon and energy source, and as a compatible solute.

The role of compatible solutes in archaea and bacteria is discussed in several reports (Schwibbert *et al.*, 2011; Empadinhas and Costa, 2011; Oren, 2011). Empadinhas and Costa describe the role of sugar glycerates, in particular mannosylglycerate and glucosylglycerate in stress adaptation by functioning as osmolytes, as protectors

against thermal stress or as precursors to larger macro-molecules in bacteria and archaea, including (hyper) thermophiles and halophiles. The extensive review covers physiological responses, biosynthetic pathways and biotechnological/medical applications. Schwibbert and colleagues (2011) describe the complete genome sequence of *Halomonas elongata* DSM 2581^T, and genomic and experimental analyses leading to a comprehensive view of the entire ectoine metabolism pathways, including the development of a metabolic flux model for ectoine metabolism. The model was used for not only learning about the ways in which *H. elongata* survives salt stress, but also for improving industrial production of ectoine. Oren (2011) provides an analysis of the bioenergetics surrounding growth and survival in hypersaline environments. By reflecting on principles of thermodynamics he explains that the limits to various biogeochemical processes in hypersaline environments can be explained by whether the relevant halophilic microbes have evolved the energy-demanding compatible-solute strategy or the less energy expensive salt-in-cell strategy to cope with high salt concentrations. In so doing he highlights areas where knowledge is lacking, providing important foci for future studies. Indeed, the study by Lazar and colleagues (2011) extends the known salinity limit of one such process, acetoclastic methanogenesis.

The types of minerals in hypersaline environments can vary a great deal depending on the origin of the water basins. Soda lakes are rich in carbonate and sodium and as a result have a high pH. Lefèvre and colleagues (2011) studied a number of alkaline sites in California and isolated microorganisms that were not only alkaliphiles, but were anaerobic, sulfate reducing, magnetotactic bacteria that produced bullet-shaped, magnetite-containing magnetosomes. In contrast to soda lakes, deep-sea anoxic brines arise in areas characterized by diverse tectonic activity where evaporitic deposits are dissolved or expelled as interstitial brine producing a range of hypersaline environments that differ in temperature, pH and chemical composition. Antunes and colleagues (2011) review these systems describing, for example, the microbiology of Atlantis II Deep in the Red Sea which is ~ 2200 m deep basin that contains a 200 m thick brine with a pH 5.3 and a temperature up to 68°C. While the logistics of studying these environments is challenging, Antunes and colleagues (2011) describe the advances being made in understanding the ecology of the diverse archaea and bacteria that have been identified, as well as some interesting findings about eucaryotes and viruses.

Although the ability to fix atmospheric nitrogen offers a selective advantage to microbes living in nitrogen-depleted environments it requires significant input of energy. In many extreme environments a higher proportion of the microbes' resources are directed towards main-taining a functional cellular environment, therefore the study by Hamilton and colleagues (2011) was interesting in providing the first evidence of thermoacidophilic nitrogen fixation in hot and acid geothermal springs in Yellowstone National Park. The freshwater of Yellowstone Lake supports fish that are pivotal to the ecology of the park's larger and enigmatic fauna; however, Clingenpeel and colleagues (2011) show that, while dominated by typical freshwater-lake bacteria, chemolithotrophs, fuelled by underwater hydrothermal vents, are also likely to contribute to the lake's ecology, together with the cyanobacterium, *Prochlorococcus*, more typical of marine environments. Le Fourn and colleagues (2011) report on the role of horizontal gene transfer in providing the ability of diverse clades of anaerobic (hyper)thermophiles to withstand exposure to oxygen. By defining pathways of oxygen consumption in the bacterium *Thermotoga maritima*, and performing phylogenetic analyses of the genes involved, the authors inferred that gene exchange between (hyper)thermophilic members of the *Bacteria* (*Thermotogales*) occurred with members of the *Archaea* (*Thermococcales*) – selection pressure for the gene exchange events arising from the need to cope with fluctuating environmental oxidative conditions.

Two studies serve to further blur the distinction between geosphere and biosphere, including discussions of the role of terrestrial subsurface communities in seeding geothermal spring environments (Tin *et al.*, 2011), and the long-term survival of haloarchaea in subterranean halite from the Salar Grande in Chile (Gramain *et al.*, 2011). By comparing the microbial community composition of a cold, acidic, metal-rich pyrite mine in Wales with previous studies of acid-mine drainage in warmer environments, Kimura and colleagues (2011) were able to infer the importance of iron-oxidizing acidithiobacilli in generating acid in the colder mines.

The pelagic and subsurface reaches of the deep sea are cold, high pressure, oligotrophic environments that are technically challenging to study. Three reports cover different aspects of the deep sea and its sediments: Kawamoto and Kurihara (2011) elucidate a role for the cytoplasmic membrane polyunsaturated fatty acid, eicosapentaenoic acid, in facilitating cell division under high pressure in *Shewanella violacea*; Eloe and colleagues (2011) describe the microbial composition of particle-associated and free-living *Archaea, Bacteria* and *Eucarya* from the 6000 m deep Puerto Rico Trench in the Atlantic Ocean; and Engelhardt and colleagues (2011) report on the role of phage in structuring microbial community composition within sediment (up to 420 m deep) at depths of up to 5000 m below the surface of the Pacific Ocean. These reports offer base-line information about abyssal microorganisms, highlighting the lack of data for comparison. Interestingly, a different level of incomplete

understanding was described by Bouman and colleagues (2011) for subtropical upper ocean communities. Focusing on phytoplankton, they described the stratification of cyanobacterial versus eucaryotic microbial communities, noting the effect of genomic streamlining on *Prochlorococcus* species to facilitate growth in highly stable, oligotrophic systems, but only within zones that were subject to dynamic mixing.

Two reports focus on the cycling of C1 compounds through methanogenic and methanotrophic pathways in distinct cold environments. Lazar and colleagues (2011) describe the methanogenic diversity and activity in hypersaline sediments collected from the centre of the Napoli mud volcano at 1940 m of water depth in the Eastern Mediterranean Sea, and Graef and colleagues (2011) describe communities from the upper soil layers in the high Arctic Svalbard wetlands. Graef and colleagues (2011) determined that the diversity of methanotrophs was relatively low, inferring that Arctic communities may therefore be vulnerable to ecosystem change, and so compromise the effectiveness of microbial capture of the greenhouse gas, methane.

A number of studies revolve around the use of model extremophiles. These include, the psychrophilic archaeon *Methanococcoides burtonii* (Campanaro *et al.*, 2011; De Francisci *et al.*, 2011; Pilak *et al.*, 2011; Williams *et al.*, 2011), the ectoine-producing halophile *H. elongata* (Schwibbert *et al.*, 2011; Köcher *et al.*, 2011a,b), and N-glycosylation in the haloarchaeon *H. volcanii* (Calo *et al.*, 2011). While the studies on *M. burtonii* focused on the roles of RNA polymerase subunits E and F, chaperonins, and global gene regulation and expression on thermal adaptation, they also shed light on fundamental aspects of transcription (both the transcription machinery and operon structure) and protein folding (including the first crystal structure of a protein from a psychrophilic archaeon). The review by Piette and colleagues (2011) describe the present state of knowledge about protein folding in the cold. An important aspect of the review was highlighting the value of having studies available for numerous model psychrophilic systems so that principles versus specific features of adaptation could be inferred. For the same reasons, this rationale can be applied to studies of all types of extremophiles. The thirty-plus papers presented in this series make an important contribution to the vibrant field of extremophile research.

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