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Active ion transport mechanisms and their role for past, present and future life in marine systems

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Homoeostatic regulation of biological compartments was a critical step in the evolution of life on earth. Only in a confined space with controlled abiotic conditions, can chemical processes take place in a reproducible manner, leading to the origin of biochemical interactions between lipids, enzymes and nucleic acids. Some hypotheses identify that proton translocating proteins were among the first transporters in the evolution of the cell by using environmental ion and pH gradients to generate phosphate-based energy equivalents (Weiss *et al*., 2016). This central importance of proton translocating mechanisms is reflected in the ubiquitous existence of V- and F-type ATPases in all organisms on earth, ranging from eukaryotes to bacteria and archaea (Mulkijjanian *et al*., 2007; Grüber *et al*., 2014). Due to the necessity to optimally regulate biological compartments for the functioning of enzymes, a wide range of ion-transporting proteins have evolved to regulate intra- and extra-cellular homoeostasis. In addition, primary active ion transport by ATPases is not only capable of generating ion concentration differences but are mostly associated with a net flux of electrical charges, leading to the generation of an electrical potential across biological membranes. This electrical potential is responsible for the excitability of cells (e.g. nerve and muscle cells), and together with the chemical gradient driving all secondary active transport processes, essential for ionic homoeostasis and nutrition.

Comparative approaches through studying organisms from different positions in the tree of life can provide insights into the evolutionary diversity as well as the common origin of ion-transport mechanisms. Here molecular advances providing genomes and transcriptomes have opened new venues for the identification of ion pumps in animals, plants and microbes. However, besides this access to genetic information, allowing reconstructions of evolutionary processes, mechanistic knowledge regarding the physiological function of these ion pumps remains of fundamental importance. This becomes particularly evident given the fact that selection acts on the functionality (e.g. salinity and pH tolerance, water homoeostasis) of an organism in a particular environment, leading to changes in the genetic material and not vice versa. Thus, understanding the mechanisms underlying homoeostatic regulation represents fundamental information that, together with genomic approaches can lead to a holistic understanding of the function and evolution of membrane transport processes. Along these lines, the *Journal of the Marine Biological Association of the United Kingdom* (JMBA) has promoted research in the field of ion-transport and homoeostatic regulation in marine organisms since the first issue in 1889 that included an article on the function of the electrical organ of skates (Sanderson & Gotch, 1889). Electrical organs are found in several fish species and are believed to serve communication and feeding purposes, representing a prime example of cellular ion transport. Electrical organs are capable of generating high voltages based on the same electrophysiological principles as found in the action potential of nerve and muscle cells using the electrochemical gradients provided by the Na^+/K^+-ATPase (Bennett, 1970). Over the last century JMBA has published a large number of studies addressing the ion-transport physiology of aquatic organisms including crustaceans (Panikkar, 1941; Wheatly, 1997), molluscs (Stallworthy, 1970; Clarke *et al*., 1979) and fish (Wood & Shuttleworth, 1996), to name just a few.

Studying membrane transport processes for the regulation of intracellular and extracellular homoeostasis is a core discipline in environmental physiology. In the marine environment homoeostatic regulation plays a pivotal role in allowing organisms to occupy ecological niches in diverse marine habitats ranging from the poles to the tropics and from coastal areas to the deep sea, including the hydrothermal vent systems of mid ocean ridges (Somero *et al*., 2017). Here ion-regulatory mechanisms represent a key trait that allowed marine organisms to survive in environments with strong fluctuations in salinity or pH, such as coastal areas and estuaries. The characterization of these physiological adaptations helps to illuminate adaptive strategies to specific environments and also provides a glimpse into the future as to how animals may respond to changes in marine systems (Melzner *et al*., 2020). In the context of climate change, the physiology of homoeostatic regulation in marine organisms has received considerable attention from the research community. Changes in seawater salinity and pH are key factors driven by the global phenomenon of climate change that directly challenges homoeostatic regulation of marine species. In particular, pH regulatory systems have been identified as an important physiological trait associated with a range of important functions in marine organisms including blood-gas transport, digestion and biomineralization (Stumpp *et al*., 2012, 2013; Hu *et al*., 2014). The importance of ion-regulatory processes in the resilience of marine species to changes in seawater pH has been underlined by studies addressing the potential of organisms to evolutionarily adapt to near-future ocean acidification. These studies demonstrate an increased selection pressure, seen in higher single nucleotide polymorphisms (SNPs), on genes coding for ion-regulatory and metabolic proteins in sea urchin larvae raised under near-future ocean acidification conditions (Pespeni *et al*., 2013).

Homoeostatic regulation in organisms is a foundation for life that has led to the evolution of an enormous diversity of ion pumps, transporters and channels. Based on phylogenetic position, a higher or lower complexity of these membrane proteins work in concert to secure homoeostasis in organisms allowing them to occupy different ecological niches. Thus, to generate a holistic understanding of the fundamental process of homoeostatic regulation in organisms, an integrative approach, including ecology, physiology and molecular biology is necessary. In this way, connecting the concept of homoeostasis from the ecosystem through to the molecular level will help in understanding the role of ion-regulatory strategies in organisms of past, present and future oceans.

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