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Review

Metabolic restructuring during energy-limited states: Insights from *Artemia franciscana* embryos and other animals

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Abstract

Many life history stages of animals that experience environmental insults enter developmental arrested states that are characterized by reduced cellular proliferation, with or without a concurrent reduction in overall metabolism. In the case of the most profound metabolic arrest reported in invertebrates, i.e., anaerobic quiescence in *Artemia franciscana* embryos, acidification of the intracellular milieu is a major factor governing catabolic and anabolic downregulation. Release of ions from intracellular compartments is the source for approximately 50% of the proton equivalents needed for the 1.5 unit acidification that is observed. Recovery from the metabolic arrest requires re-sequestration of the protons with a vacuolar-type ATPase (V-ATPase). The remarkable facet of this mechanism is the ability of embryonic cells to survive the

dissipation of intracellular ion gradients. Across many diapause-like states, the metabolic reduction and subsequent matching of energy demand is accomplished by shifting energy metabolism from oxidative phosphorylation to aerobic glycolysis. Molecular pathways that are activated to induce these resilient hypometabolic states include stimulation of the AMP-activated protein kinase (AMPK) and insulin signaling via suite of *daf* (dauer formation) genes for diapause-like states in nematodes and insects. Contributing factors for other metabolically depressed states involve hypoxia-inducible factor-1 and downregulation of the pyruvate dehydrogenase complex. Metabolic similarities between natural states of stasis and some cancer phenotypes are noteworthy. Reduction of flux through oxidative phosphorylation helps prevent cell death in certain cancer types, similar to the way it increases viability of dauer stages in *Caenorhabditis elegans*. Mechanisms that underlie natural stasis are being used to pre-condition mammalian cells prior to cell biostabilization and storage.

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Keywords

Metabolic depression; Diapause; Anoxia; Vacuolar-ATPase; Intracellular pH; Metabolic preconditioning; Glycolysis; Oxidative phosphorylation; Hypoxia inducible factor-1

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