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A capacity for long term survival without oxygen is well-developed among many invertebrate species as well as in selected ectothermic vertebrates. Anoxia tolerance has been particularly well-studied in various species of marine molluscs, including both bivalves (e.g. mussels, clams, oysters) and gastropods (e.g. littorine snails, whelks). These can encounter low environmental oxygen as a result of multiple factors: (1) gill-breathing intertidal species are deprived of oxygen when the waters retreat with every low tide, (2) high silt or toxin levels in the water as well as predator harassment can force shell valve closure, leading to substantial periods of "self-imposed" anoxia, (3) animals in small tidepools can be oxygen-limited when animal and plant respiration depletes oxygen supplies in the water, and (4) freeze-tolerant intertidal species face oxygen deprivation whenever their body fluids freeze. Life in the intertidal zone is particularly challenging since, in addition to the cyclic availability of oxygenated water (each tide cycle lasts 12.4 h), organisms can also be challenged with multiple other stresses including desiccation, changes in salinity, and changes in temperature, sometimes including freezing; all can potentially change rapidly over the course of a single tidal cycle of immersion and emmersion. For this reason, various residents of the intertidal zone have been used extensively as model systems of stress tolerance, the most widely studied species being the sessile bivalve, the blue mussel *Mytilus edulis* . Littoral snails that graze on rocks in the high intertidal zone are also an excellent model system for studies of both anoxia tolerance and freeze tolerance.

Marine invertebrates as a model system

Littorina littorea is one such gastropod mollusc that lives in the high intertidal zone. Snails are characterized by a soft body that can be divided into two main parts: 1) the head and foot region, responsible for neural activity and locomotion, respectively, and 2) the visceral mass, involved in digestion, respiration, excretion, and reproduction. Molluscan model systems have been widely used in a number of disciplines. For example, mollusc models have proven to be enormously successful in studies of nervous system function, especially gastropods and cephalopods. Several bivalve species have been extensively studies as models for the effects of pollution on marine habitats. Both bivalve and gastropod muscle and mantle tissues (and others) have also been widely used for studies of environmental stress effects on metabolism and tissue function (e.g. temperature, salinity, anoxia). The hepatopancreas, a voluminous structure that occupies the bulk of the visceral mass, performs a number of important functions in the mollusc, including protein synthesis, glycogenolysis, gluconeogenesis, as well as specific roles in both digestion and excretion. It has proven to be an excellent organ for metabolic studies at the molecular level, including both *in vivo* and *in vitro* research on gene expression profiling, protein synthesis and ribosomal analysis, and organ culture studies.

Anoxia, characterized by the complete absence of oxygen, is a state that many organisms experience infrequently. Although many organisms have retained some capacity for anaerobic metabolism, this strategy is usually just a short term one that deals with brief interruptions of oxygen delivery. Respiratory exchange for marine snails , which occurs during tidal immersion, can occur at a number of places through the skin of gastropods, but it is mainly sited at the surface of the ctenidium or gill. As inhabitants of the intertidal zone, *L. littorea* can be exposed to hypoxic or anoxic conditions twice daily for several hours at a time and, during aerial exposure, may arrive at a situation where tissue oxygen is fully depleted and cellular energy requirements can be met only by anaerobic metabolism.

For a review of anoxia studies in marine molluscs, please refer to the Elsevier book series "Cellular and Molecular Responses to Stress" Volume III, which contains a chapter entitled 'A profile of the metabolic responses to anoxia in marine invertebrates' authored by myself and Dr. Ken Storey.

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