Netherlands Journal of Zoology
36(3): 322-343 (1986)

METABOLIC ADAPTATIONS TO ENVIRONMENTAL ANOXIA IN THE INTERTIDAL BIVALVE MOLLUSC *MYTILUS EDULIS* L.

by

D. I. ZANDEE, D. A. HOLWERDA, J. H. KLUYTMANS & A. DE ZWAAN

(*Department of Experimental Zoology, State University of Utrecht, 8 Padualaan, NL-3584 CH Utrecht, The Netherlands*)

SUMMARY

Many invertebrate species are able to withstand periods with interrupted oxygen supply that may extend over days. These so-called euryoxic organisms show metabolic adaptations different from those found in temporarily anoxic vertebrate tissues. It has been the authors' field of research over more than 15 years to investigate metabolic pathways and their regulation in euryoxic marine and freshwater molluscs, especially of the sea mussel *Mytilus edulis* L. This paper intends to provide, in a more or less chronological way, a survey of metabolic routes and regulation points through which sufficient metabolic energy is released without exhaustion of the available energy stores. It will be shown that reduction of energy demand and activation of highly efficient fermentation processes are the most important elements for survival. Finally, attention will be paid to the processes involved in the return from anoxic to normoxic conditions.

INTRODUCTION

The physiological responses of the sessile bivalve mollusc *Mytilus edulis* L. to changing intertidal conditions have been investigated extensively for more than 15 years (see DE ZWAAN, 1971; BAYNE *et al.*, 1976; GABBOTT, 1976; WIJSMAN, 1976; DE ZWAAN *et al.*, 1976; DE ZWAAN, 1977; EBBERINK, 1980; ZANDEE *et al.*, 1980a; ZANDEE *et al.*, 1980b; ZURBURG, 1981; DE ZWAAN, 1983; SCHULZ, 1983; DE ZWAAN & PUTZER, 1985; DE ZWAAN & VAN DEN THILLART, 1985).

The intertidal habitat is characterized by large fluctuations in temperature, salinity, food and oxygen availability. Maintenance in such an environment requires a great adaptability of the inhabitants. One of the most striking physiological adaptations of intertidal bivalve molluscs has been found on the level of energy metabolism.

At low tide, the sea mussel may become exposed to air and responds to this condition by closing the valves in order to prevent desiccation of the tissues. Although, depending on air humidity, a small valve gap may remain through which O_2 can diffuse into the mantle cavity, the animal's tissues will progressively get deprived of oxygen. Littoral bivalves do not possess morphological adaptations for aerial respiration. The lack of an oxygen carrying pigment together with a poor, open circulatory system makes oxygen storage and transportation to the tissues impossibe (GHIRETTI & GHIRETTI-MAGALDI, 1972). Eventually, a state of complete anoxia will be attained. Sustained shell closure in response to salinity or pollutant stress also will result in anoxia. All of the fore-mentioned changes of environmental condition, therefore, will induce, sooner or later, an anaerobic type of energy metabolism.

This review will present, more or less chronologically, our contributions to the study of anaerobic metabolism and its regulation in the sea mussel *Mytilus edulis* L.

In our laboratory, the investigation of anaerobic energy metabolism in the bivalve mollusc *Mytilus edulis* L. started at the end of the sixties. *M. edulis* belongs to the facultative anaerobes or euryoxic organisms. Among the marine invertebrates, *M. edulis* shows a high tolerance to anoxia, being able to survive without oxygen for several weeks (fig. 1).

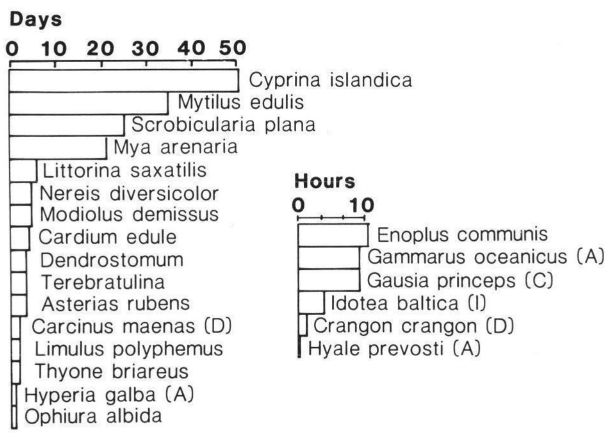

Fig. 1. Survival time of different marine invertebrates under conditions of anoxia or extreme hypoxia. Most values are LT_{50}, but some are maximum survival times (after HAMMEN, 1976).

Euryoxic marine animals generally contain large amounts of glycogen. In normoxic conditions they have the possibility of using carbohydrates, lipids and amino acids as an energy fuel. In *M. edulis* and other marine bivalves a large pool of free amino acids is found (CAMPBELL & BISHOP, 1970; SCHOFFENIELS & GILLES, 1972). Besides their role in osmoregulation (SCHOFFENIELS, 1976; GILLES, 1979) amino acids also function in anaerobic energy metabolism (COLLICUTT & HOCHACHKA, 1977; DE ZWAAN, 1977; ZANDEE *et al.*, 1980b;