lower activities of mitochondrial enzymes following anoxic periods (267, 311). Acclimation of turtles to 3°C with access to air resulted in a decrease in heart levels of ATP and an increase in CP with respect to warm-acclimated animals (234). The decrease in temperature probably resulted in an increase in pH_i, which in turn would shift the equilibrium of the CK reaction in favor of CP. There was no difference in the expression of heart LDH isozymes between cold- and warm-acclimated turtles (25).

C. Low-Temperature Exposure of Freeze-Tolerant Frogs

At least four species of terrestrial frogs (*R. sylvatica, Hyla versicolor, Hyla crucifer, Pseudacris triseriata maculata*) survive freezing at temperatures of about −3 to −7°C. The heart does not beat in the frozen state and appears pale probably because of withdrawal of blood into distended large vessels above the heart (330). The exceptional ability of the wood frog (*R. sylvatica*) to maintain heart performance was evident by continued spontaneous contractility of isolated hearts down to −2°C and in intact animals the maintenance of amplitude of the QRS wave of the electrocardiogram between 15 and 0°C, conditions under which the QRS of the bullfrog deteriorated (230).

In some species, intracellular glucose accumulates and appears to act as a cryoprotectant and metabolic fuel. Acute transitions of intact wood frogs to −2.5°C resulted in an increase in intracellular glucose from ~0 to ~150 μmol/g. Heart glucose was derived from the plasma as glycogen levels remained constant. Under frozen conditions, oxygen delivery to the heart by diffusion alone must be very low, and lactate accumulates. Freeze-thaw cycles of 96 h resulted in oscillations in glucose levels such that glucose decreased when temperature was elevated and increased again in response to freezing. Lactate takes longer to clear than glucose, and levels as high as 70 μmol/g were noted after three cycles (329). Ventricle strips from wood frog survived freezing in vitro, in the presence of high levels of glucose, and could be stimulated to contract upon thawing. Hearts from grass frogs (*R. pipiens*) did not tolerate freezing in keeping with freeze intolerance at the whole animal level (54).

D. Conclusions

Isolated preparations from ectothermic myocardia reveal that an acute decrease in temperature usually results in decreases in heart performance associated with lower rates of contraction, longer time to peak tension, longer time to relaxation, a lengthening of the action potential, and a decrease in oxygen consumption. The effect of a decrease in temperature on contractility represents a compromise of two tendencies. Force development tends to fall due to a decrease in actin-myosin interactions at a given state of activation. This is counteracted by an increase in both the amount and time of activator Ca^{2+}. Decreases in temperature usually result in an impairment of maximal in vitro levels of enzyme activities, although the Q_{10} for CS in particular may be very low. Energy metabolism is not the limiting factor in performance following acute thermal decrease; however, in some species there may be marked decreases in fatty acid catabolism.

Some nonpolar fish species exhibit positive thermal compensation in response to seasonal low temperatures. This is evident by increases in rates of contraction and ability to maintain force development at elevated frequencies. One component of this response is a decrease in time to relaxation. An increase in heart mass is a frequent response to low temperature. Both increases in maximal contraction frequency and heart size could contribute to enhanced maximal cardiac output. In some species there is an increase in metabolic potential due to elevated levels of some enzymes of energy metabolism. Most frequently observed are increases in mitochondrial enzymes necessary for aerobic fatty acid catabolism. In Antarctic species that live their entire life cycles at temperatures close to 0°C, there are higher concentrations of enzymes necessary for a fatty acid-based aerobic metabolism relative to other fish species.

In contrast to those fish that exhibit positive thermal compensation, cardiac performance in amphibians that do not freeze appears to be decreased following a period of low-temperature acclimation. This is based on rates of contraction, electrical properties, and tension development. A reduction in contractility is consistent with whole animal responsiveness and cardiac demands. In amphibians there is a shift in fuel preference from a carbohydrate- to a lipid-based metabolism as occurs in some fish species.

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