The interaction among age, thermal acclimation and growth rate in determining muscle metabolic capacities and tissue masses in the threespine stickleback, *Gasterosteus aculeatus*

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**Abstract**

Thermal acclimation may directly modify muscle metabolic capacities, or may modify them indirectly via effects upon physiological processes such as growth, reproduction or senescence. To evaluate these interacting effects, we examined the influence of thermal acclimation and acclimatization upon muscle metabolic capacities and tissue masses in 1+ stickleback, *Gasterosteus aculeatus*, in which confounding interactions between temperature and senescence should be absent. Furthermore, we examined the influence of thermal acclimation upon individual growth rate, muscle enzyme levels and tissue masses in 2+ stickleback sampled at the beginning of their final reproductive season. For 1+ stickleback, cold acclimation more than doubles mitochondrial enzyme levels in the axial muscle. Thermal acclimation did not change the condition of 1+ stickleback at feeding levels which could not maintain the condition of 2+ stickleback. Compensatory metabolic responses to temperature were not apparent in field acclimatized 1+ stickleback. The growth rate of 2+ stickleback was markedly affected by temperature: warm-acclimated fish generally lost mass even at very high levels of feeding (up to 78 enchytraid worms per day) while cold-acclimated fish gained mass. This suggests that warm temperatures accelerate the senescence of 2+ stickleback. Generally, muscle enzyme activities increased with growth rate. In axial muscle, the relationships between CS activity and growth rate differed with acclimation temperature. Independent of the influence of growth rate, CS activities were consistently higher in cold- than warm-acclimated 2+ stickleback, suggesting compensatory increases of CS activity with cold acclimation.

**Introduction**

Whereas the general capacities of muscle found in a given species are determined by adaptation for specific locomotory or feeding strategies, the phenotype of muscle can be adjusted according to the conditions in which individuals are found. In mammals and fish, exercise training and growth rates are major factors which modify muscle performance capacities. In ectotherms, the influence of thermal acclimation upon the metabolic capacities of muscle has also been well demonstrated, in particular for temperate zone species, such as goldfish, *Carassius auratus* and striped bass, *Morone saxatilis*. In such species, cold acclimation enhances the aerobic capacity of muscle, both by increasing the proportion of red fibers and by increasing the percentage of fiber volume occupied by mitochondria in white

Corresponding author; This paper is dedicated to the memory of Gerry J. FitzGerald who passed away on March 14, 1994.
and red fibers (Johnston and Dunn 1987; Guderley and Blier 1988; Sidell and Moerland 1989). This increased aerobic capacity enhances the sustained swimming capacity at low temperatures and is presumably adaptive for cold-active species (Rome et al. 1984; Sisson and Sidell 1987). Temperature may influence muscle metabolic capabilities of fish by modifying growth rates which can independently modify enzyme levels (Pelletier et al. 1993a, b).

The anadromous form of the threespine stickleback, *Gasterosteus aculeatus*, migrates from the ocean into shallow tidal pools and rivers in which they reproduce. On the south shore of the St. Lawrence Estuary, sticklebacks migrate into salt marsh pools in early May (seawater temperatures ~ 4°C). Reproduction occurs during the following six to eight weeks at temperatures which can reach 30°C (Reebs et al. 1984). Since it is unlikely that one metabolic profile suffices over such a wide thermal range (Guderley 1990), the maintenance of locomotion suggests the occurrence of thermal compensation of muscle aerobic capacity. Laboratory acclimation of two year old (2+) stickleback to 4 and 20°C revealed compensatory responses of muscle aerobic capacity, but only at maximal feeding levels (Vézina and Guderley 1991). Under these conditions, mitochondrial enzyme levels were two-fold higher in the muscles of cold- than warm-acclimated individuals. On the breeding grounds, the condition factor (mass/length$^3$) of 2+ males captured in late June (mean temperatures approximately 20°C) is considerably worse than that of males captured in early May (mean temperatures < 10°C). Enzyme levels in both the pectoral and axial muscle decline markedly with this decrease in condition. Females change less than males (Vézina and Guderley 1991). During the reproductive season, the territorial and reproductive activities of the males may hinder feeding. These data suggest that the metabolic capacities of stickleback may be influenced more by growth rates than by temperature.

An alternative interpretation is that as 2+ sticklebacks are in their final reproductive season (Picard et al. 1990), their decrease in physical condition during the reproductive season may be a senescent decay which can be delayed when reproduction is prevented (as in the laboratory), when temperatures are low or at high levels of feeding. Cold acclimation would thus delay senescence and concomitant declines in condition and muscle metabolic capacities. Since 1+ stickleback may reproduce during a second year, confounding interactions between temperature and senescence should be absent and compensatory increases in aerobic capacity should be evident in response to cold acclimation and natural cold acclimatization.

Our objectives in this study were twofold. First, to examine whether compensatory increases in aerobic capacity occur in the absence of confounding interactions between temperature and senescence, we examined, in 1+ stickleback, the changes in tissue masses and enzymatic activities in response to thermal acclimation and acclimatization. Stickleback (1+) were sampled in the salt marsh pools in early May when temperatures were low, other 1+ stickleback were acclimated to 6°C and 22.5°C for six weeks and finally 1+ stickleback were sampled at the end of June when temperatures in the salt marsh pools were high. Six weeks acclimation is sufficient to complete compensatory changes in enzyme activities (Sidell 1983). Determination of the tissue masses and enzymatic properties of these stickleback followed Vézina and Guderley (1991). Second, we examined the influence of acclimation temperature and individual growth rate upon muscle metabolic capacities and tissue masses in 2+ male sticklebacks. Fish were individually housed to minimize the aggressive interactions which can lead to feeding hierarchies and to facilitate measurement of individual growth rates. Muscle metabolic capacity was assessed by measuring the activities of lactate dehydrogenase and citrate synthase in the pectoral and axial muscles. Lactate dehydrogenase is specific to glycolysis whereas citrate synthase activity mirrors mitochondrial abundance. To evaluate the anatomic response to growth rate and temperature, the masses of the pectoral and axial muscles, liver, heart, gonad and kidney were monitored.