The metabolic costs of osmoregulation in a euryhaline fish, hogchoker (*Trinectes maculates*)

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Abstract

Fish that live in euryhaline environments in which the salinity varies substantially, such as estuaries, are required to regulate water and ions in their body through osmoregulation in order to combat passive diffusion across their cell membranes. This process involves the active transport of ions across cell membranes and requires energy, but the actual metabolic cost remains unclear. Estimates from previous studies range widely from 1.5% to 27% of the total energy budget of the fish. The purpose of this study was to attempt to determine the actual energetic costs of osmoregulation in a euryhaline fish, hogchoker (*Trinectes maculates*). Eighty-two fish were acclimated to either hypo-, iso-, or hyperosmotic conditions (0, 10, 30 ppt respectively) and their metabolic rates measured through static respirometry. There was a no significant difference in metabolic costs in any treatment; however, the activity of the active transport enzymes Na^+/K^+-ATPase and citrate synthase were both significantly elevated in the hyperosmotic treatment. The results suggest that while increased environmental salinity does present a challenge to the fish, the energetic costs of the physiological response are quite low at the whole organism level.

Introduction

The presence and movement of ions within a body play a critical role in how cells function in both terrestrial and marine habitats, affecting the overall performance of the organism. Varying levels of salts within the body, including Na^+, K^+, Cl^-, and Ca^{2+}, affect hydration, blood pH, and function and ability of muscles and nerves (Laurent and Perry, 1990). Due to the polar properties of water, ions are highly soluble. The majority of aquatic organisms have limited ability to control this passive movement of ions and are isosmotic, living in equilibrium with their respective environments. Vertebrates such as fish are able to regulate the amount of solutes, including ions, that are in their bodies. Freshwater fishes tend to lose ions and gain water because the potential gradient has a higher concentration of ions within the body than in the external environment. Saltwater fishes are the opposite, losing water and gaining ions because the salts in the external environment are at a much higher concentration than found inside the body. Most organisms are stenohaline – restricted to a narrow range of salinity – and the direction of ion movement varies depending on whether it is a freshwater or seawater species. However, some fishes are euryhaline and are capable of thriving across a range of salinity, which requires them to have the capability to maintain homeostasis at both lower and higher levels of ions.

When ion differences such as these occur, ions enter and exit the body through diffusion across two types of gradients: concentration and electrical. In concentration gradients ions diffuse passively from areas of high concentration to areas of low concentration until equilibrium is reached. In electrical gradients, ions actively move between areas of positive and negative electrical charge until the charge is neutral. Organisms seeking to regulate internal ion content must therefore have mechanisms to counteract these passive movements and maintain homeostasis.

In terrestrial environments, much of the burden of osmoregulation is carried by the kidney. Water is retained and excess ions are removed from the blood stream via diffusion across gradients, to be transported out of the body in a concentrated urine. In fishes, however, the gills are the main osmoregulatory organ for monovalent ions and the kidneys and intestines handle movements of divalent ions and water (McCormick et al. 1989).

Oxygen dissolves poorly in water, and because the primary function for which gills evolved was gas exchange for respiration, the gill structures are exceedingly thin in order to allow the oxygen to diffuse rapidly into the blood. This tremendous efficiency at gas exchange poses a problem when ion gradients are present between the organism and the environment, since ions and water are also able to rapidly diffuse across the membranes (McCormick *et al.*, 1989). The sites of osmoregulatory action in the gills are ionocytes – cells which facilitate the movement of ions using a number of transporter and channel proteins such as Na^+/K^+-ATPase (NKA) to create concentration and electrical gradients (McCormick *et al.*, 1989; Laurent and Perry 1990; Wood and Marshall 1994). Much of this process, including the role of NKA, involves active transport, using energy in the form of adenosine triphosphate (ATP) to pump ions against gradients. ATP is the basic unit of molecular energy. It is primarily created when glucose is broken down to pyruvate and then enters the complex series of aerobic enzyme reactions known as the citric acid cycle. One of the key enzymes in that process is citrate synthase; the presence of elevated levels of this enzyme can be used as an indicator of the presence of oxidative metabolism (McCormick *et al.*, 1989).

It has long been argued that osmoregulation must be metabolically demanding since it requires cellular energy reserves. Some authors have argued that this cost can affect the growth and fitness of teleost fish (e.g. Beouf and Payan, 2001; Wood and Marshall, 1994). Theoretical calculations place the cost of ion transport at 0.5-1% of resting metabolic rate (McCormick *et al.*, 1989). Previous authors have attempted to experimentally measure the metabolic costs of

osmoregulation in fishes; however, direct measurement of these costs has been extremely difficult to achieve. The results to date have been confounding, as high as 27% in some studies (e.g. Rao, 1968).

The observed values of the metabolic cost of osmoregulation likely differ greatly from theoretical calculations because of methodological difficulties. Different methods have been used in this pursuit: some authors have measured the growth rate of fishes in various salinities (Peterson-Curtis 1997), some have measured dissolved oxygen consumption (Febry and Lutz 1987; McCormick et al. 1989; Peterson-Curtis 1997; Boeuf and Payan 2001), and some have measured the activities of chemicals and hormones within the body (McCormick 1989). One issue with the study of growth rate is that it is not solely determined by the metabolic costs; other factors include food intake and utilization or hormonal control.

from analysis because it was difficult to precisely measure MO_2 in such small fish in the respirometers used in this study. All statistical analyses were conducted on the remaining 63 fish (Table 1). There was no mortality in any of the treatments. Metabolic rate (Fig. 3) and tissue water content (Fig. 4) were not significantly different among any treatment. There was a significant difference between the activity of both Na^+/K^+-ATPase and citrate synthase in the 30 ppt treatment compared to the other treatments (Fig. 5 A and B); however, 0 ppt and 10 ppt were not significantly different from each other.

energetically costly brackish water. The results of this study do not support that finding. While there was a slight trend to lower MO_2 from 0 ppt to 10 ppt, the magnitude was small and not significant. Additionally, there was no difference in