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AN ANALYSIS OF ACID BASE, IONIC AND WATER BALANCE IN RAINBOW TROUT (*SALMO GAIRDNERI*) EXERCISED AT CRUISING SPEEDS

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Summary

Rainbow trout (Salmo gairdneri) *were exercised at cruising speeds for 5 hours. A slight but significant increase in dorsal aortic blood pH after 1 hour of exercise was accompanied by significant decreases in* PCO_2 *and total* CO_2 *content of blood. These changes were maintained throughout the exercise period of 5 hours. This respiratory alkalosis could be due to hyperventilation and/or the result of increased uptake of* Na^+ *and* Cl^- *which occurred along with the increase in plasma volume in order to maintain normal osmotic concentrations. The uptake of* Na^+ *and* Cl^- *occurred presumably via branchial* Na^+/H^+ *and* Cl^-/HCO_3^- *ion exchange mechanisms.*

Key words ; acid base balance, ionic balance, water balance, cruising speeds, trout.

1. Introduction

Although the nature of acid base disturbance has been studied extensively in fish exercised until exhaustion, this aspect has not been studied in detail in fish exercised at average cruising speeds. This is probably because it is generally assumed that in sustained exercise only slight respiratory and circulatory adjustments are necessary to meet the increased energy demands and still maintain the fish in a steady state condition.

The object of the present experiments is to make a detailed study of the nature of acid base disturbances and associated changes in ionic and water balance during sustained swimming and recovery from it; by monitoring blood pH, carbon dioxide content, lactate concentration, plasma ion concentrations and plasma volume.

2. Materials and Methods

Experimental procedures were identical to those previously described by Attygalle (1990) except that the fish were exercised at cruising speeds (3 fish lengths/sec.) for a duration of 5 hours instead of the fish being exercised until exhaustion. The dorsal aortic catheter was implanted as described by Smith and Bell (1964). After cannulation the fish were left undisturbed for at least

24 hours to recover (Hunn and Willford, 1970). Blood samples were taken at rest, after 30 min, 1h, 3h and 5 hours of exercise and after 1h, 2h, 3h and 19 hours of recovery. In one series of experiments (n = 6) approximately 200μl of blood was removed at each sampling time for measurement of pH, total CO_2 content and lactate concentrations. In the second series of experiments (n = 6) approximately 150μl of blood was removed at each sampling time for determination of blood volume, haematocrit and plasma Na^+, K^+ and Cl^- concentrations.

Total ion contents of plasma at each sampling time were obtained by calculation from the following relationship, ion content = plasma volume x ion concentration. Ion contents are presented as percentage changes from the resting values. When finding the changes, the resting values (A_o) were normalized to 100 and the values at various experimental times (A_i) were expressed as percentage changes from the resting values. Percentage change in ion content $= \frac{A_i}{A_o} \times 100$

Results are generally presented as mean ± standard error of the mean. Differences between the resting values and values at various experimental times were determined using the one tailed t-test for paired varieties. Each experimental sample is paired with the initial sample at rest, which serves as the control.

3. Results

A slight but significant increase (7.854 ± 0.037 to 7.913 ± 0.025, $p < 0.05$) in blood pH after 1 hour of sustained swimming was accompanied by significant decreases in P_{CO_2} (19.7%, $p < 0.05$) and total CO_2 content (5.5%, $p < 0.05$) of blood. These initial changes were maintained throughout the exercise period of 5 hours. Lactate concentration increased two fold ($p < 0.05$) after 30 min of exercise but decreased to values not significantly different from the resting value after 1 hour and these values were maintained until the end of the exercise period. During recovery the animals gradually approached resting values, and values not significantly different ($p < 0.05$) from the resting values were obtained after 24 hours (Fig. 1).

It is immediately clear from Fig 2b that the fish were well able to regulate plasma ion concentrations during sustained swimming. These ion concentrations were regulated by effecting marked changes in plasma ion contents (Fig. 3), which paralleled the marked changes in plasma volume (Fig. 2a). The pattern and magnitude of changes in Na^+ and Cl^- contents and plasma volume overlapped, while the increase in K^+ content was less. During exercise ion contents and plasma volume increased up to 3 hours, after which time they steadied until the end of exercise. During recovery ion contents and plasma volume decreased below the exercise levels, although at the end of 24 hours they were not corrected fully.

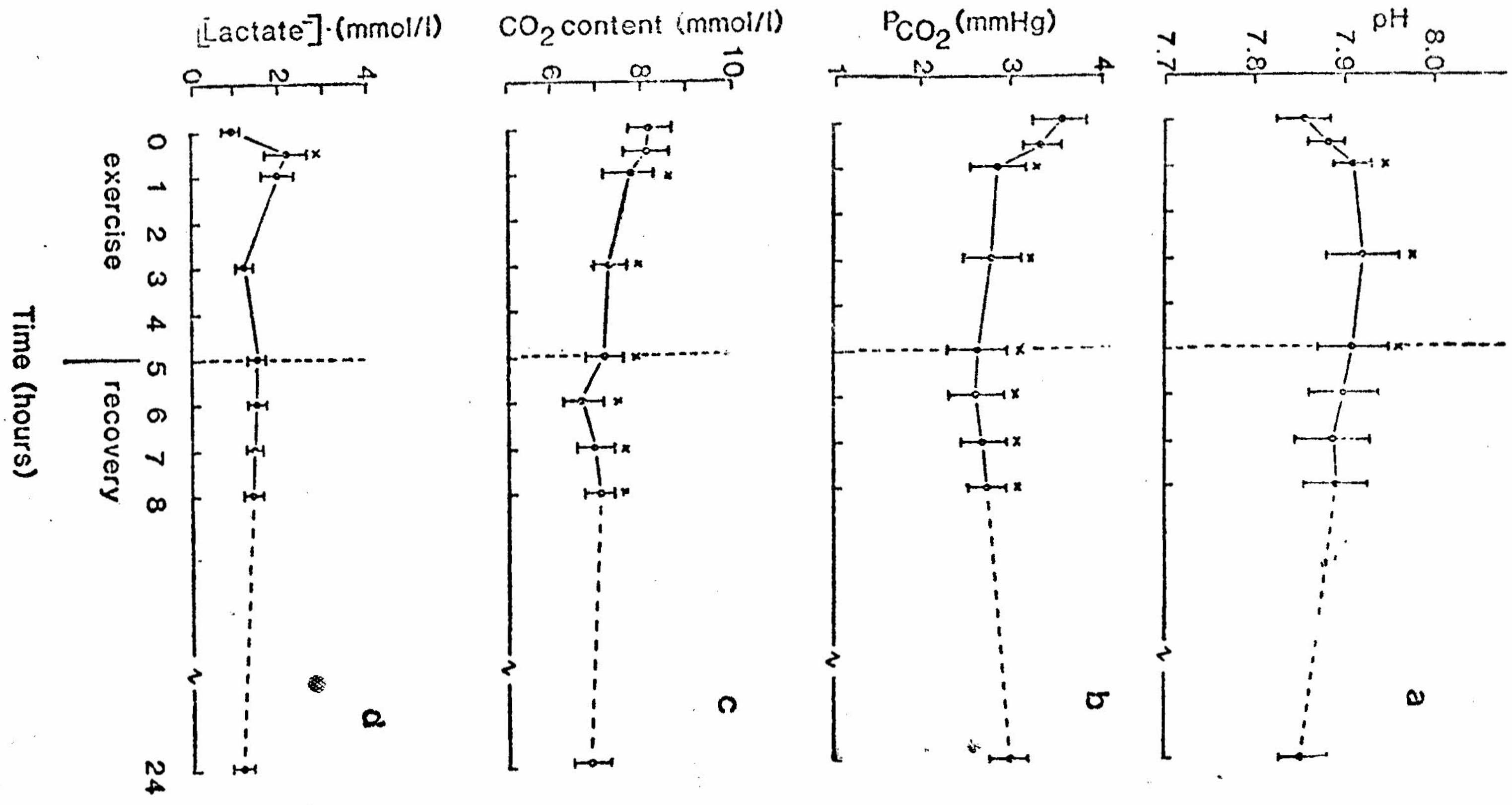

Fig. I. (a) pH, (b) P_{CO_2}, (c) total CO_2 content and (d) lactate concentration in simultaneously drawn arterial blood samples at rest, during exercise and recovery. (mean ± s.e., n = 6)
Time O—resting sample, x indicates experimental values significantly different ($p < 0.05$) from the resting values.

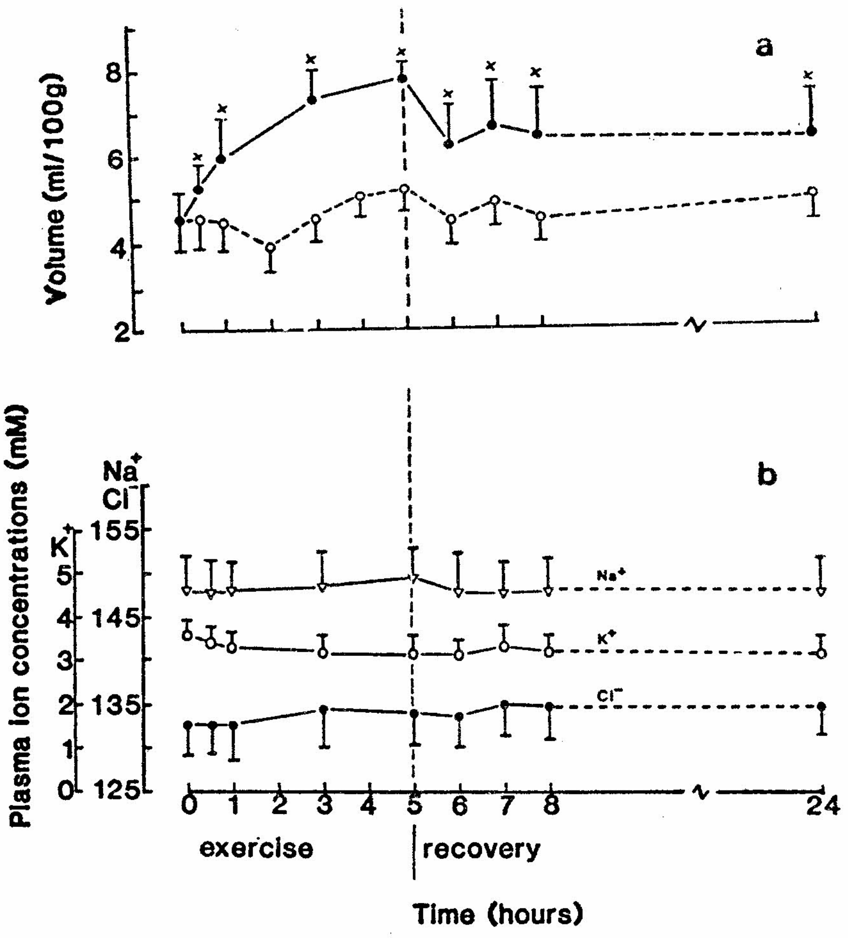

Fig. II. (a) Plasma volume at rest, during exercise and recovery for experimental (●) and control (o) fish.
(b) Plasma Na^+, K^+ and Cl^- concentrations at rest, during exercise and recovery (mean ± s. e., $n = 6$) x indicates experimental values significantly different ($p < 0.05$) from the resting values.

4. Discussion

During sustained exercise the significant increase ($p < 0.05$) in pH was due to the significant decreases ($p < 0.05$) in P_{CO_2} and total CO_2 content of blood (Fig 1). Stevens and Randall (1967) showed that during moderate swimming at approximately 1.8 l/sec, ventilation rate increased six fold in rainbow trout (*Salmo gairdneri*). It is possible that a similar increase in ventilation occurred in the fish in this study during sustained swimming. The decrease in P_{CO_2} during exercise may be due to more effective elimination of CO_2 from blood due to increased ventilation. But a number of workers have found that increased ventilation has little effect on the steady state difference in PCO_2

between arterial blood and water (Lenfant and Johansen, 1972; Randall and Cameron 1974; Cameron, 1973). An increase in ventilation would only be effective in reducing an elevated P_{CO_2}, resulting from an increase in CO_2 production, to its initial steady state value. In water breathing species in order to have sufficient O_2 uptake a large ventilatory rate is needed because of the low solubility of O_2 in water. But since solubility of CO_2 in water is much higher than that of O_2 and if the respiratory quotient is around unity, this means that the gill is hyperventilated with respect to CO_2, and P_{CO_2} will be rather insensitive to variations in ventilation rate.

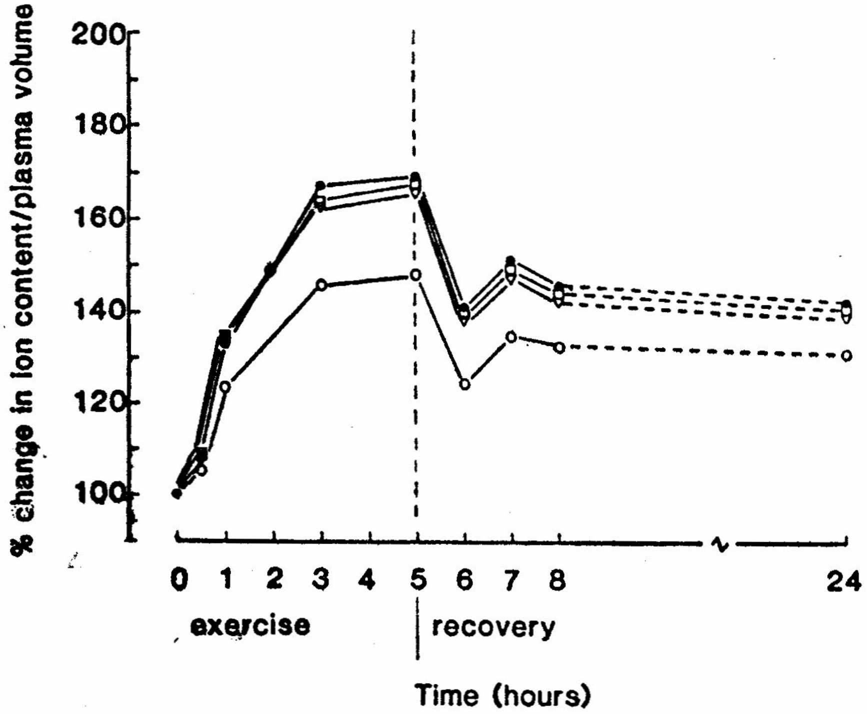

Fig. III. Percentage changes in plasma volume and total plasma ion contents at rest, during exercise and recovery for fish shown in Fig 2.
Plasma volume ☐, Na$^+$ △, K$^+$o, Cl$^-$ ●.
Resting plasma volume, 10.08 ml
Resting ion contents: Na$^+$, 1.49 mmoles; K$^+$, 0.037 mmoles and Cl$^-$, 1.33 mmoles

Sustained exercise produced no significant changes in ion concentrations. This indicates that compensations for ion regulation were effected in these fish. The significant increase in plasma volume during exercise indicates passive diffusion of water across the gills into blood. At the same time an uptake of Na$^+$, K$^+$ and Cl$^-$ must have occurred as seen from the marked increases in plasma ion contents (Fig. 2b). These results differ from those of Wood and Randall (1973). They exercised rainbow trout at a moderate speed of approximately 1.2 l/sec for 8 hours. They found that a Na$^+$ deficit occurred during the first and second hours of swimming, and that by the third and subsequent hours of activity the fish returned to a state of positive Na^+ balance. The fact that the plasma ion concentrations were maintained close to resting values throughout swimming may be due to compensatory reductions in the permeability of the gill epithelium and activation of Na^+ uptake pump due to changes brought about by the onset of exercise.

Immediately after termination of exercise it is expected that blood flow through the gills return to a resting pattern. As a consequence a decrease in plasma volume occurred, which was paralleled closely by decreases in ion contents, so that the plasma ion concentrations were maintained. Even at the end of 24 hours plasma volume was not fully corrected. The changes in Na^+ and Cl^- contents closely paralleled the changes in plasma volume, to maintain iso-osmolarity, these two ions being the predominantly osmotically active solutes in the extracellular fluid. It is most likely that the marked increase in Na^+ and Cl^- contents by over 60% of their respective resting values was due to the uptake of these ions from the environmental water rather than from muscle tissue. Evidence for Na^+/H^+ and HCO_3^-/Cl^- exchanges at the gill epithelium as part of the mechanisms of Na^+ and Cl^- accumulation has been found in trout by Kerstetter *et al* (1970) and Kerstetter and Kirschner (1972). If such exchange mechanisms were involved in these fish the increase in Na^+ and Cl^- contents of plasma during exercise would mean that equivalent amounts of H^+ and HCO_3^- are transferred to the environmental water. Therefore since the uptake of Na^+ and Cl^- by plasma was significantly high the reduction in P_{CO_2} during exercise could be linked to these ion exchanges across the gill epithelium.

The respiratory alkolosis in dorsal aortic blood could have been due to the combined effects of hyperventilation and the result of uptake of Na^+ and Cl^- into plasma. But since a number of workers have shown that ventilation has little effect in reducing P_{CO_2} this alkolosis could be attributed to the elimination of H^+ and HCO_3^- resulting from the uptake of Na^+ and Cl^-.

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