University of Montana
ScholarWorks at University of Montana

Graduate Student Theses, Dissertations, & Professional Papers

Graduate School

1976

# Aspects of the diving physiology of muskrats (Ondatra zibethica) : post-dive oxygen consumption and lactic acid levels

Eleanor Stetson
*The University of Montana*

Follow this and additional works at: https://scholarworks.umt.edu/etd
Let us know how access to this document benefits you.

Recommended Citation
Stetson, Eleanor, "Aspects of the diving physiology of muskrats (Ondatra zibethica) : post-dive oxygen consumption and lactic acid levels" (1976). *Graduate Student Theses, Dissertations, & Professional Papers*. 6525.
https://scholarworks.umt.edu/etd/6525

This Thesis is brought to you for free and open access by the Graduate School at ScholarWorks at University of Montana. It has been accepted for inclusion in Graduate Student Theses, Dissertations, & Professional Papers by an authorized administrator of ScholarWorks at University of Montana. For more information, please contact scholarworks@mso.umt.edu.

# ASPECTS OF THE DIVING PHYSIOLOGY OF MUSKRATS (ONDATRA ZIBETHICA): POST-DIVE OXYGEN CONSUMPTION AND LACTIC ACID LEVELS

BY

ELEANOR STETSON

B.A., MOUNT HOLYOKE COLLEGE, 1973

Presented in partial fulfillment of the requirements

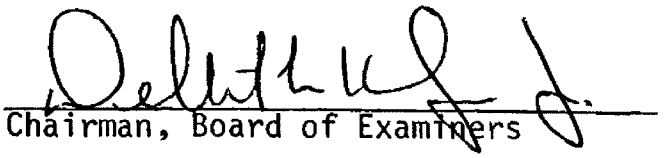
for the degree of

Master of Arts

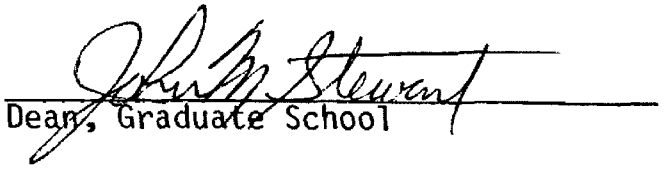
University of Montana

1976

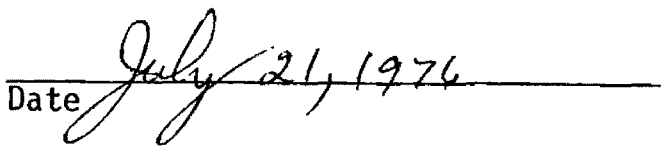
Approved by:



Chairman, Board of Examiners



Dean, Graduate School



Date

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

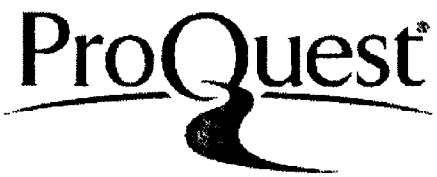
UMI Number: EP37326

All rights reserved

INFORMATION TO ALL USERS
The quality of this reproduction is dependent upon the quality of the copy submitted.

In the unlikely event that the author did not send a complete manuscript
and there are missing pages, these will be noted. Also, if material had to be removed,
a note will indicate the deletion.


UMI EP37326
Published by ProQuest LLC (2013). Copyright in the Dissertation held by the Author.
Microform Edition © ProQuest LLC.
All rights reserved. This work is protected against
unauthorized copying under Title 17, United States Code




ProQuest LLC.
789 East Eisenhower Parkway
P.O. Box 1346
Ann Arbor, MI 48106 - 1346

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Stetson, Eleanor, M.A., August 1976 Zoology

Aspects of the Diving Physiology of Muskrats (Ondatra zibethica): Post-dive Oxygen Consumption and Lactic Acid Levels (45 pp.)

Director: Dr. Delbert L. Kilgore DLK

The extensive literature on the physiological adaptations to diving does not include much information on semi-aquatic mammals or on unrestrained animals. Experiments with animals accustomed to dives of short duration are needed to determine the full range of variation in physiological adaptations among different diving animals. Comparison of restrained and unrestrained dives is necessary to assess the effect of restraint on an animal's diving responses.

Muskrats are medium sized semi-aquatic mammals accustomed to dives of short duration. Seven animals were used for a total of 31 restrained dives and nine animals were used for a total of 46 unrestrained dives. Dives were 0.5, 1, 2, 3, 4, or 5 minutes long. A paramagnetic oxygen analyzer continuously monitored the fractional oxygen concentrations before and after the dives. Oxygen consumption was calculated from the fractional oxygen concentration data. Body oxygen stores were estimated and blood levels of lactic acid were measured before, during and after 6 restrained dives to determine whether or not the non-lactic acid oxygen debt of seals, animals accustomed to prolonged dives, is apparent in muskrats also.

The ratio of the oxygen debt, assuming maintenance of the pre-dive oxygen consumption rate during the dive, to the actual post-dive excess oxygen consumption indicates either an increased oxygen consumption rate during the dive or an increase after the dive not caused by oxygen debt payment. The post-dive excess oxygen consumption increased with longer dives after both restrained and unrestrained dives. Regression of post-dive excess oxygen on dive time results in statistically equal regression equations for restrained and unrestrained dives indicating that restraint has no effect on the magnitude of the post-dive excess oxygen consumption. However, after unrestrained dives the mean rate at which the excess oxygen consumption occurred was always greater than after restrained dives.

A variable non-lactic acid debt appears to exist in muskrats but, because of the disagreement in the literature as to the fraction of the lactic acid which is oxidized in recovery, no definite conclusions can be made.



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

TABLE OF CONTENTS



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

## LIST OF ILLUSTRATIONS





Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

LIST OF TABLES





Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

ACKNOWLEDGEMENTS

Special thanks go to Dr. Delbert L. Kilgore who as my major advisor gave much of his time and assistance at all levels of this project. His constant encouragement and friendship were invaluable.

Thanks are also extended to Dr. Richard Fevold for his advice on the biochemical aspects of this study and for his critical review of the manuscript and to Dr. Phillip Wright for his advice on trapping muskrats and for his review of the manuscript.

Mr. Robert Twist, Director of the Ravalli Wildlife Refuge and Mr. David Maclay and Ms. Anne Maclay are extended thanks for allowing me to trap muskrats on land under their control.

All my fellow graduate students provided help and encouragement in various ways. Special thanks to all who helped me "handle" my muskrats.

I especially wish to thank the women at 707 Dickinson for empathy, laughter, encouragement, confidence, and friendship. Because of them the bad times were better and the good times, great.

A final thank you to Lee Fairbanks for his ceaseless support and encouragement and his belief that it was all worthwhile.



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

# CHAPTER I

## INTRODUCTION

The ability of some animals to dive for periods of time that exceed the length of dive possible, estimated from their oxygen stores, has been the subject of research since the late 1800's (Bert, 1870; Bohr, 1897; Richet, 1899). The physiological adaptations associated with the diving habit have been reasonably well studied in seals, but less is known about the adaptations of those animals that dive for only short periods of time. The literature on diving has been reviewed by Irving (1939), Scholander (1964), and more recently by Andersen (1966).

The physiological adaptations associated with diving include an intense submergence bradycardia accompanied by selective peripheral vasoconstriction, reduced sensitivity to carbon dioxide in the blood, and large oxygen stores resulting from increased blood volumes, high muscle myoglobin concentrations, and large blood oxygen capacities (Andersen, 1966). The large oxygen storage capacity and the selective peripheral vasoconstriction make it possible for the animal to maintain aerobic metabolism in the heart and brain while the major muscle masses function anaerobically. After a dive the animal must consume enough oxygen to replenish the oxygen stores and to restore the blood lactic



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

acid levels to pre-dive levels. Interestingly, Scholander (1940) reported the existence of a small non-lactic acid oxygen debt in seals in addition to the lactic acid oxygen debt and the oxygen stores debt. Whether this non-lactic acid debt exists in other diving animals is not known, as few measurements of post-dive oxygen consumption and blood levels of lactic acid have been made.

Variations in the physiological adaptations to diving of various mammals and birds are undoubtedly reflected in their diving habits. This is evidenced by the fact that seals, which are accustomed to prolonged diving, have a lower post-dive oxygen consumption than expected, indicating a metabolic rate during a dive lower than their pre-dive rate. Conversely, animals such as cats, not adapted for diving, have a higher post-dive oxygen consumption than expected, perhaps indicating a metabolic rate during dives which is higher than their pre-dive rate (Scholander, 1940). The full range of this response is not known as little work has been done on animals accustomed to dives of only short duration. Muskrats (Ondatra zibethica) are small mammalian divers accustomed to diving of this type and this study will examine the nature of their post-dive excess oxygen consumption after restrained dives and compare it to that in seals.

Muskrats are suitable subjects for this study not only because of their diving habits but also because of their size. They are small enough to allow experimental unrestrained dives to be performed in the laboratory. This is important because, despite the volume of literature on the physiology of diving mammals and birds, few experiments have involved measurements on unrestrained animals (Murdaugh, et al, 1961;

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Kooyman, et al, 1971; Harrison, et al, 1972; Kooyman & Campbell, 1972; Jones, et al, 1973; Kooyman, et al, 1973; Millard, et al, 1973). For purposes of comparisons between diving and non-diving animals and among different diving animals, the restrained dive is an excellent approach to the problem and, because of technical difficulties, it is often the only possible approach. However, diving animals are usually very active underwater and it would be of interest to know whether data collected during a restrained dive are good estimates of the same parameters during unrestrained dives. In this study comparison of the excess oxygen consumption after both restrained and unrestrained dives of muskrats will determine the effect of restraint on data obtained during diving experiments.

Since muskrats' diving habits are quite different from the diving habits of seals the non-lactic acid oxygen debt mentioned earlier may or may not be evident in muskrats. The simultaneous measurement of post-dive oxygen consumption and blood lactic acid levels in this study will elucidate the relationship between these two parameters in muskrats.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

# CHAPTER II

# METHODS AND MATERIALS

## Trapping and Maintenance

Muskrats (Ondatra zibethica) were trapped from sloughs along the Bitterroot River, south of Missoula, Montana during the fall of 1974 and 1975. A total of 12 individuals (5 males, 7 females) were used in these experiments. Their mean body mass was 1.011 kg (range 0.638 to 1.539 kg). The animals were individually housed in cages and maintained on lettuce, carrots, and Purina dog chow. Drinking water was provided ad libitum. All experiments were conducted between July 1975 and February 1976.

## Restrained Dives

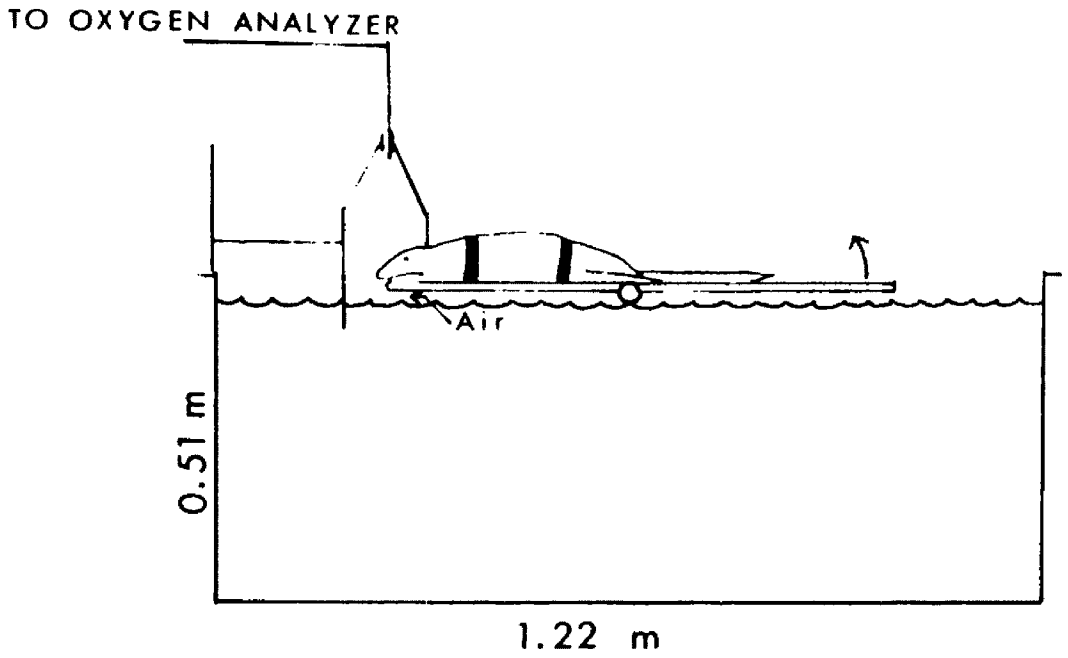
A diving board mounted on a large aquarium (1.22 x 0.40 x 0.51 m) was used for the restrained dives (Fig. 1). The board was attached to a metal rod supported on two ball bearings and could be held level or tilted into the water with ease. The animal was secured on the board with cloth straps around each foot; these were tied to small cleats. Velcro straps were used to restrain the animal's body and tail and a padded U-bolt held the animal's neck. Secured in this manner the

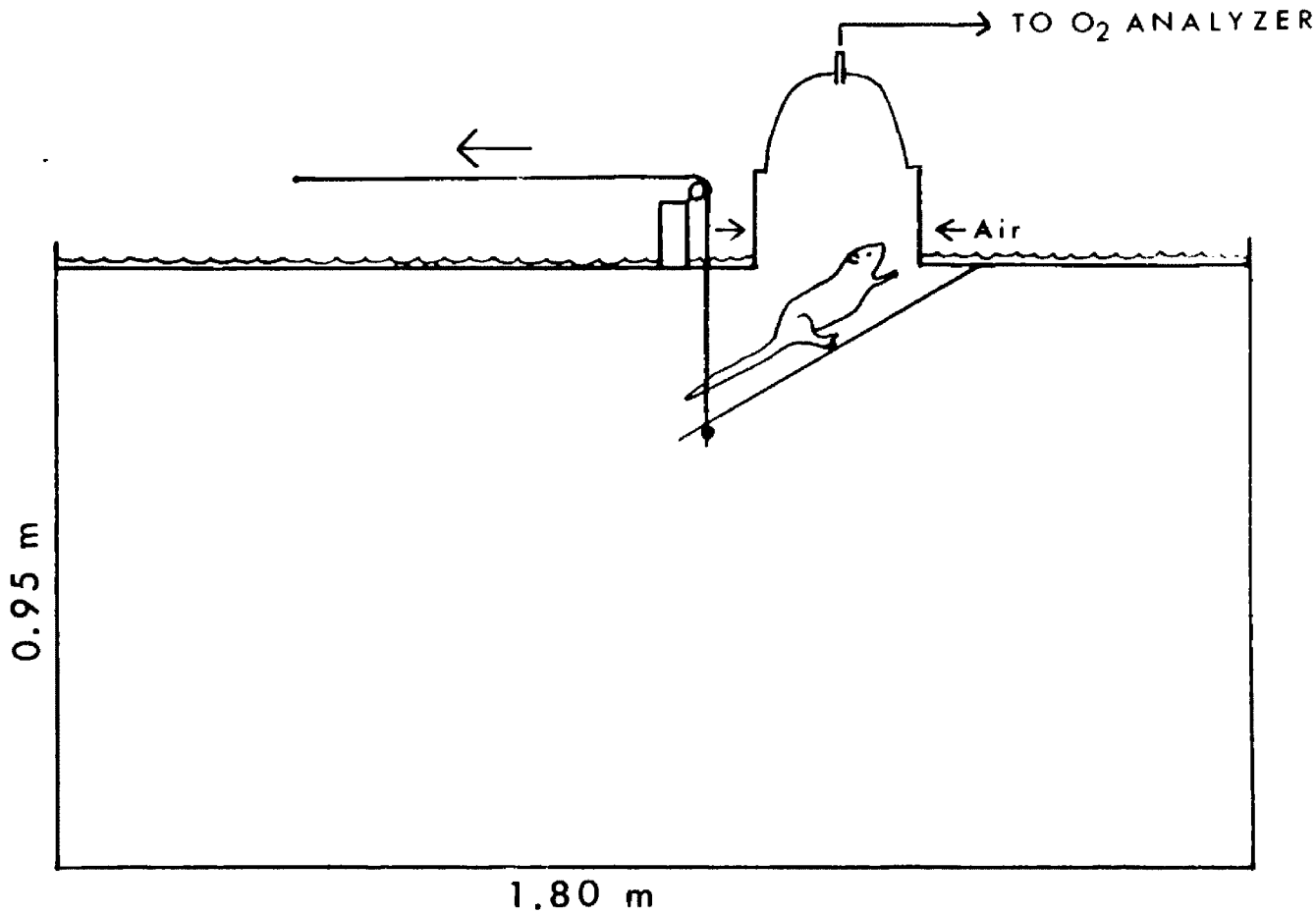


Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Figure 1: Restrained dive apparatus (top) and unrestrained dive apparatus (bottom) drawn to scale.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.




Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

animal's respiratory movements were unimpeded.

A half gallon plastic bottle was modified into a hood which fit snugly over the animal's head when the animal was above water. Room air was drawn through the hood at a rate of 3.58 to 6.88 l/min and was sufficient to prevent any loss of expired air. The flow of air through the hood was held constant during each experiment. The fractional concentration of oxygen in the excurrent hood air ($FE_{O_2}$) was continuously monitored during an experiment and only after an animal reached a resting level of metabolism were animals dived. An animal was assumed to be at rest when oxygen consumption remained relatively steady (± 3% to ±6% of resting) for a 7 to 15 minute period. After a dive, the animal was allowed to return to at least within 12 to 24% above the pre-dive oxygen consumption rate before being removed from the board.

Seven different animals were used. Six 0.5 minute dives, six 1 minute dives, eight 2 minute dives, five 3 minute dives, and six 4 minute dives were done for a total of 31 restrained dives. No animal was dived more than two times in one day and often only once.

Unrestrained Dives

Experiments on unrestrained diving muskrats were conducted in a glass-fronted tank (0.77 x 1.84 x 0.96 m) covered with a piece of masonite mounted approximately 2 cm below the water surface (Fig. 1). A trapdoor in the masonite, when open, was the animal's only breathing hole and was the only exit and entrance to the tank. The door was weighted and hinged and could be raised and lowered by a rope attached to a pulley above the tank. The full body hood consisted of a wooden

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

box (0.21 x 0.21 x 0.14 m) with a clear plastic dome 20 cm in height on top. The volume of the hood without the animal was 13.6 l. Air was drawn into and through the box through a series of holes 2 cm from the bottom on each side. The closed trapdoor formed the floor of the box so when the door was opened the animal was free to dive. During the experiments air flow was maintained at 7.44 l/min.

Fractional concentration of oxygen in the excurrent air was continuously monitored as in the restrained dive experiments and resting metabolic rate was ascertained in the same manner. When a resting rate was established, the animal was permitted to dive, after which the door was closed. The animal had no access to the surface and ordinarily swam continuously during the dive. The door was opened approximately 5 seconds before the end of the dive. Therefore, actual dive times varied from desired dive time by a few seconds ($-1.85 \pm 0.34$ to $4.48 \pm 0.72$ sec). After the dive the animal was allowed to return to its pre-dive resting metabolic rate before the experiment was terminated.

Nine different animals were used for a total of 46 dives including six 1 minute dives, eight 2 minute dives, eleven 3 minute dives, fourteen 4 minute dives, and seven 5 minute dives. No animal was dived more than three times in one day and usually only once.

## Measurement of Oxygen Consumption

The fractional concentration of oxygen in the excurrent hood air and room air ($F_{IO_2}$) were measured with a Beckman (Model G2) paramagnetic oxygen analyzer (see Appendix 1). The oxygen analyzer was calibrated by varying the pressure in its cell and the calibration was

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

checked with a certified primary gas standard before each run. The equation used to calculate oxygen consumption rate from data obtained from the oxygen analyzer was that of Tucker (1968; Equation 3).

Flow of air through the hoods was measured with a flowmeter which had previously been calibrated with a NBS certified Vol-U-Meter (Brooks, Model #1058-7A) and was held constant by a sub-atmospheric pressure regulator (Moore Products, Model 44-20).

The post-dive excess oxygen consumption ($V_{O_2}$) is the oxygen consumed above that which would have been consumed if the animals had maintained a resting oxygen consumption rate after the dive. The post-dive excess $V_{O_2}$ was determined by measuring the area bounded by the post-dive excess $V_{O_2}$ curve above and the hypothetical resting oxygen consumption rate below with a planimeter and comparing it to an area with a known oxygen consumption.

All volumes are reported at standard temperature and pressure (STP).

## Lactic Acid Determinations

Blood samples were taken before, during, and after six restrained dives. Of these, five dives were 2.5 minutes in duration and one was 2.0 minutes. Because of the small sample size, each dive was evaluated individually.

Blood samples for the lactic acid assay were collected from a cannula (PE 90) positioned in the femoral artery under a general anesthetic. The muskrats were anesthetized with sodium pentabarbital (35 mg/kg body mass) and were allowed to recuperate for 20 to 30 hours be-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

fore being used in the diving experiments. Clotted cannulae were a chronic problem, hence sodium heparin was injected intramuscularly (5 mg/kg body mass) approximately 5 minutes before the cannula was inserted into the artery.

Sixteen to twenty blood samples were collected during a single diving experiment. In most cases, three samples were taken before the dive, three during the dive and the remaining samples were collected at varying intervals after the dive. The last sample was taken about 90 minutes after the dive. A 0.25 ml sample was collected each time and the blood was replaced with heparinized isotonic saline. Blood samples were immediately combined with 0.5 ml cold 8% perchloric acid in a small polyurethane centrifuge tube. This combination was mixed vigorously (Beckman/Spinco 154 micromixer) and centrifuged. The clear supernatant was assayed for lactic acid using procedures outlined in Sigma Technical Bulletin - 726UV/826UV and employing a Beckman DU spectrophotometer.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

# CHAPTER III

# RESULTS

## Magnitude of Post-dive Excess Oxygen Consumption

A typical pattern of oxygen consumption before, during and after a two minute restrained dive is shown in Figure 2. The restrained dives were characterized by an immediate increase in oxygen consumption followed by a steep decline and then a rather extended plateau during which the oxygen consumption rate approached the pre-dive level. Oxygen consumption records following unrestrained dives lacked this plateau and were characterized by a more gradual increase and decrease in oxygen consumption.

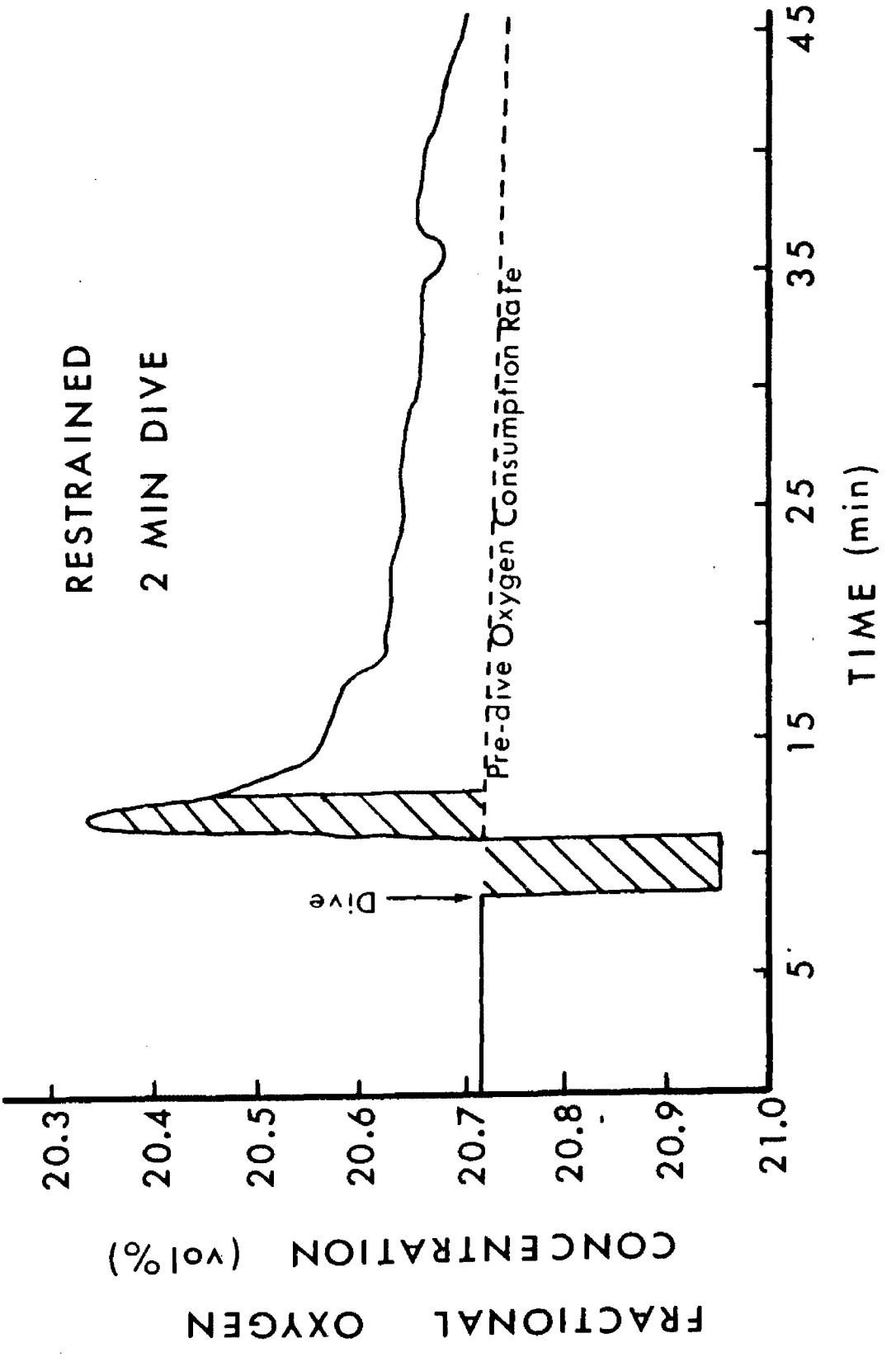
During a dive an animal should theoretically incur an oxygen debt which minimally should equal the oxygen consumed for the duration of the dive assuming the animal was at rest. The post-dive excess oxygen consumption should compensate for this oxygen debt. The post-dive excess oxygen consumption and oxygen debt for each dive are shown in Appendix 2. The post-dive excess oxygen consumption was found to be quite variable, but increased as did oxygen debt with longer dive times (Table 1). The oxygen debts incurred during 3 minute and 4 minute unrestrained dives are nearly the same. The resting oxygen consumption



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Figure 2: Typical 2 minute restrained dive curve. Shaded sections indicate equivalent oxygen consumptions and show the portion of the post-dive excess oxygen consumption necessary to pay off the oxygen debt.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.




Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 1: Post-dive excess oxygen consumption ($V_{O_2}$), oxygen debt (OD), and mean percentage of $V_{O_2}$ accounted for by OD for restrained and unrestrained dives at each dive time. $V_{O_2}$ and OD values are means ± one standard error.

| | Restrained Dives | | | Unrestrained Dives | | |
|---|---|---|---|---|---|---|
| Dive Time (min) | $V_{O_2}$ (ml/kg) | $O_2$ Debt (ml/kg) | $\frac{OD}{V_{O_2}}$ X 100 | $V_{O_2}$ (ml/kg) | $O_2$ Debt (ml/kg) | $\frac{OD}{V_{O_2}}$ X 100 |
| 0.5 | 62 ±11 | 6 ±0.6 | 11 | | | |
| 1.0 | 93 ±23 | 11 ±0.3 | 16 | 92 ±18 | 15 ±0.5 | 18 |
| 2.0 | 189 ±52 | 25 ±0.7 | 23 | 175 ±16 | 23 ±2.0 | 15 |
| 3.0 | 302 ±66 | 35 ±3.0 | 15 | 398 ±70 | 51 ±4.0 | 18 |
| 4.0 | 321 ±44 | 48 ±2.0 | 17 | 374 ±47 | 50 ±4.0 | 17 |
| 5.0 | | | | 475 ±59 | 74 ±8.0 | 17 |

rate of the animals used in these 3 minute dives was uniformly higher than the average resting rate of all the animals, thus increasing the calculated oxygen debt.

The ratio between oxygen debt and post-dive excess oxygen consumption indicates that proportion of the post-dive excess oxygen consumption used to pay off the resting oxygen debt during the dive and corresponds to the shaded sections in Figure 2. This percentage varies considerably (see Appendix 2). However, the mean percentages for various dive times range from only 11% to 23% (Table 1). These mean percentages for different dive times for both restrained and unrestrained dives are not statistically different ($p > 0.05$) (Table 2). Also the mean percentage of all the restrained dives (16.8%) is not statistically different from that (16.9%) of all the unrestrained dives ($F_S = 0.02$, $df = 1/51$, $p > 0.05$). It is evident that post-dive excess oxygen consumption is considerably greater than the oxygen debt incurred during the dive assuming resting conditions and that the ratio of oxygen debt to post-dive excess oxygen consumption is independent of dive time or type of dive.

## Post-dive Excess Oxygen Consumption versus Dive Time

As previously stated, the post-dive excess oxygen consumption increased with longer dives (Table 1). This relationship is also shown in Figure 3. A weighted regression line fitted to the data and passing through the origin is described by the equation $Y = 92X$ where Y is the post-dive excess oxygen consumption in milliliters per kilogram body mass and X is the dive time in minutes. This regression explains 82%

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

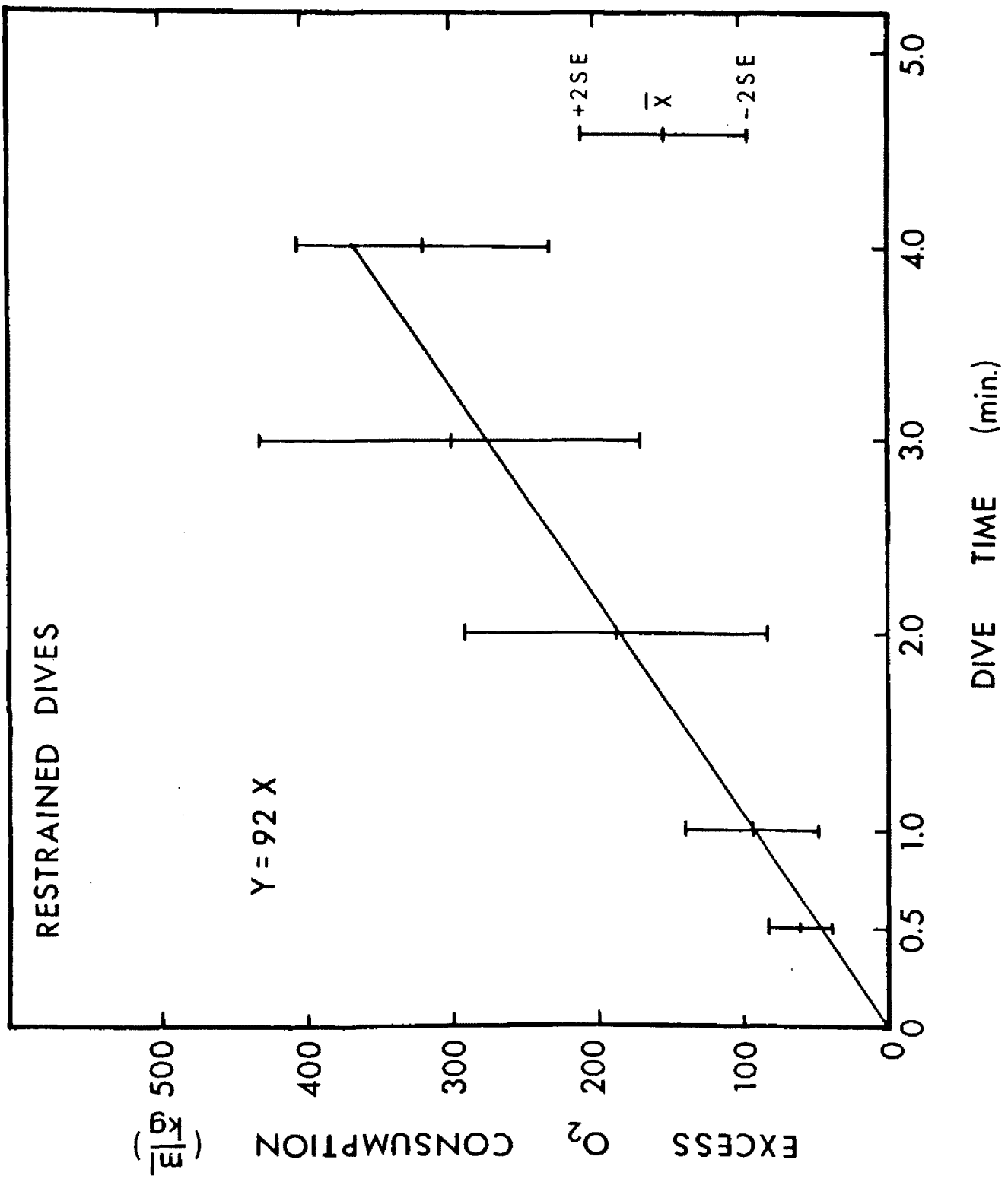
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 2: Analysis of variance of the mean percentage of $V_{O_2}$ accounted for by OD at different dive times and for both restrained and unrestrained dives. Abbreviations as defined in Table 1. Percentages were transformed before completing the statistical analyses. Method of Sokal & Rohlf, 1969.

| | Restrained | | | Unrestrained | | |
|---|---|---|---|---|---|---|
| Source of Variation | df | MS | $F_S$ | df | MS | $F_S$ |
| Dive Time | 4 | 58.07 | 0.79 | 4 | 5.99 | 0.14 |
| Error | 26 | 73.90 | | 41 | 42.97 | |

Figure 3: Relationship between post-dive excess oxygen consumption and dive time for restrained dives. The regression is described by Y = 92X. Method for weighted regression through the origin from Steel & Torrie, p. 179 (1960).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.




Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

of the variation in Y and is highly significant ($F_S$ = 136.92, df = 1/30, $p < 0.001$). A test of the hypothesis that the line passes through zero yielded a $F_S$ value of 3.07 (df = 1/29, $p > 0.05$) indicating that the line does pass through zero.

Figure 4 shows the same relationship between mean excess oxygen consumption and dive time but for unrestrained dives. The weighted regression line through the origin is explained by the equation, Y = 93X. The regression explains 87% of the variation in Y and is highly significant ($F_S$ = 304.64, df = 1/45, $p < 0.001$). Again, the assumption that the regression line passes through zero is valid ($F_S$ = 0.08, df = 1/44, $p > 0.1$).

The slopes of these two regression lines are not significantly different (T = 0.10, df = 75, $p > 0.5$), indicating that for equal length dives the excess oxygen consumption is statistically the same for both unrestrained and restrained diving muskrats.

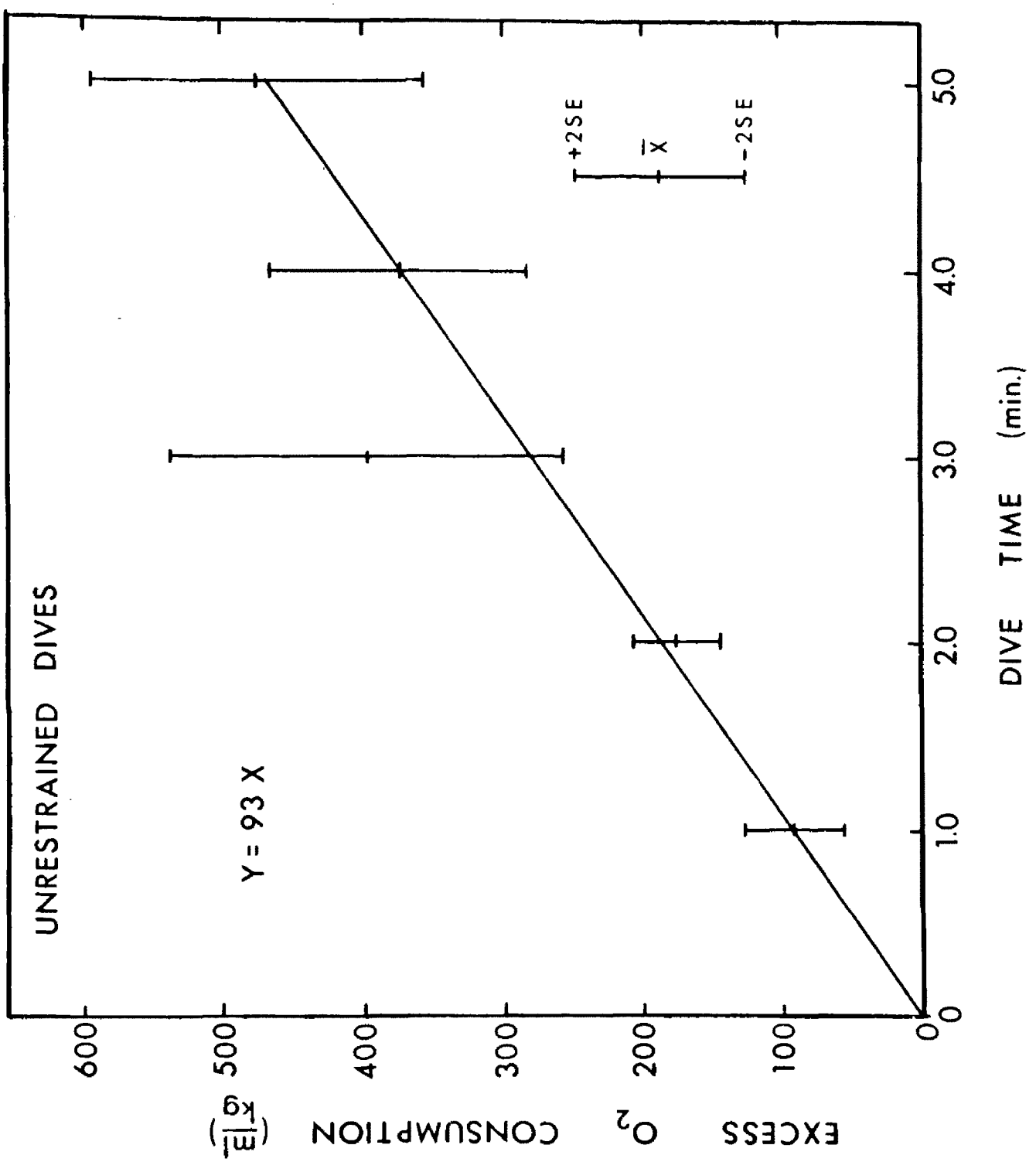
Recovery Time

The total number of minutes required for recovery from each dive are shown in Appendix 3. Recovery was assumed to be complete when the oxygen consumption had reached the pre-dive level or at least to within 24% above that level. The recovery time was variable and generally increased with increasing dive time (Table 3). For equal length dives the number of minutes to recovery is significantly greater for restrained dives than for the unrestrained dives. T-tests were performed on the four dive times for which both restrained and unrestrained data were available. For 1 minute, 2 minute, 3 minute, and 4 minute dives

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Figure 4: Relationship between post-dive excess oxygen consumption and dive time for unrestrained dives. The regression is described by Y = 93X. Method for weighted regression through the origin from Steel & Torrie, p. 179 (1960).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.




Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 3: Mean total recovery time in minutes for each dive time, both restrained and unrestrained dives. Values are means ± one standard error of the mean.

| Dive Time (min) | Restrained Dives (min) | Unrestrained Dives (min) |
|---|---|---|
| 0.5 | 18.25 ±3.14 | |
| 1.0 | 23.00 ±2.57 | 14.30 ±2.25 |
| 2.0 | 33.80 ±5.83 | 19.75 ±1.16 |
| 3.0 | 52.20 ±8.47 | 31.30 ±4.74 |
| 4.0 | 44.90 ±5.71 | 30.60 ±3.36 |
| 5.0 | | 34.80 ±5.20 |

the probability that the recovery time for restrained dives was greater than that for unrestrained merely by chance was less than 0.05; 1 minute dives ($t = 2.55$, $df = 10$), 2 minute dives ($t = 2.37$, $df = 14$), 3 minute dives ($t = 2.32$, $df = 14$), 4 minute dives ($t = 2.26$, $df = 18$).

## Estimated Oxygen Stores

The estimated oxygen stores for each animal used in the lactic acid experiments are summarized in Table 4. Oxygen stores include oxygen in the lung, blood oxygen, and oxygen bound to myoglobin in the muscle. The oxygen available in the lungs was estimated using Stahl's (1967) equation for total lung capacity ($TLC = 53.5M^{1.06}$) where M is the mass in kilograms. The fractional concentration of oxygen in the lung was assumed to be 14%. Oxygen stores in the blood were estimated from blood volume and the oxygen capacity of the blood. The blood volume of muskrats was determined by Irving (1934) to be 10% of their body mass and the oxygen capacity of their blood is 25 ml/100 ml blood (Irving, 1939). Of this total blood volume, one third was assumed to be arterial and 95% saturated, the remaining two thirds to be venous with an oxygen saturation 5 vol% less than the arterial blood (Lenfant, et al, 1970).

Robinson (1939) estimated that 35% of the body weight in seals was muscle, but 40% was chosen in this case as muskrats have less blubber than do seals. Muscle myoglobin content was estimated at 2% of the wet weight of the muscle, a figure close to actual measurements obtained from penguins (Weber, et al, 1973) and from sea otters, but lower than those obtained from seals (Lenfant, et al, 1970). The oxygen-combining ability of myoglobin is 1.34 ml $O_2$/g myoglobin (Robinson, 1939).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 4: Estimated oxygen stores for each muskrat used in the lactic acid experiments. See text for specific information on how stores were estimated.

| Experiment | Animal Mass (kg) | Oxygen Stores | | | Total Oxygen Stores (ml) |
|---|---|---|---|---|---|
| | | Lung (ml) | Blood (ml) | Muscle (ml) | |
| 1a | 0.847 | 6.3 | 17.3 | 9.1 | 32.7 |
| 2a | 0.830 | 6.1 | 17.0 | 8.9 | 32.0 |
| 3a | 0.920 | 6.9 | 18.8 | 9.9 | 35.6 |
| 4a | 1.197 | 9.1 | 24.5 | 12.8 | 46.4 |
| 5a | 0.790 | 5.8 | 16.2 | 8.5 | 30.5 |
| 3 | 1.075 | 8.1 | 21.9 | 11.5 | 41.5 |

Lactic Acid

The lactic acid concentration in the blood remained low throughout the dive (Figure 5) in all instances except one. After a dive there was an immediate increase in blood levels of lactic acid. Only 4 to 13% of the total increase in lactic acid following a dive occurred during the dive (Table 5). During the dive in which lactic acid concentration increased substantially, 70% of the total increase in lactic acid occurred during the dive.

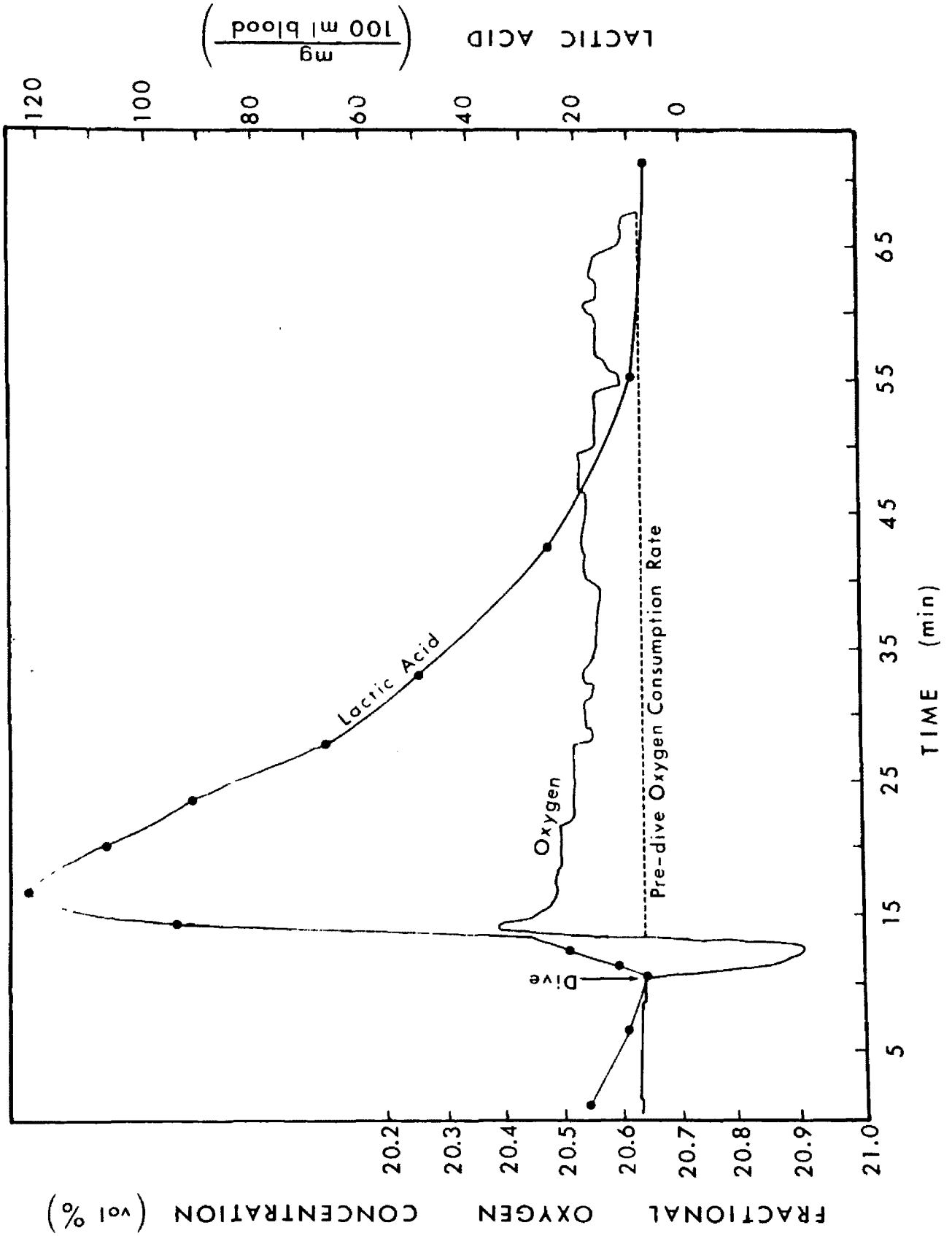
Table 5 also shows the estimated amount of oxygen that would be required to oxidize the accumulated lactic acid after each dive. The total amount of lactic acid (LA) per kilogram animal mass following a dive was computed with the formula; 0.75 $LA_b$ = LA/kg given by Margaria, et al (1963) where LAb is the amount of lactic acid in grams per liter of blood. One-fifth of this total lactic acid is then oxidized to convert the remaining 4/5 into glycogen (Scholander, 1940). The amount of oxygen required to effect this oxidation can be calculated, since 3 moles of oxygen are required to oxidize 1 mole of lactic acid (Margaria, et al, 1933).

The relationship between the sum of the oxygen stores plus the estimated amount of oxygen used in the oxidation of lactic acid and the total post-dive excess oxygen consumption is shown in Table 6. In all cases the oxygen stores plus oxygen used in the lactic acid oxidation was less than (39 to 90%) the total excess in oxygen consumption.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Figure 5: Oxygen consumption and blood levels of lactic acid before, during and after a 2.5 minute dive. (Exp. 1a) The increase in lactic acid during the dive was assumed to be linear.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.




Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 5: Maximal lactic acid (LA) concentration, percentage of total LA increase occurring during the dive, grams LA removed in recovery, and oxygen required for removal of LA for lactic acid experiments.

| Experiment | Animal Mass (kg) | Maximal LA Concentration (mg/100ml blood) | % LA Increase During Dive | Grams LA Removed During Recovery | Oxygen Required For Oxidation of LA (ml) |
|---|---|---|---|---|---|
| 1a | 0.847 | 114.67 | 12 | 0.73 | 108 |
| 2a | 0.830 | 100.67 | 70 | 0.55 | 83 |
| 3a | 0.920 | 142.43 | 13 | 0.91 | 136 |
| 4a | 1.197 | 79.06 | 13 | 0.74 | 110 |
| 5a | 0.790 | 142.03 | 13 | 0.66 | 97 |
| 3 | 1.075 | 125.32 | 4 | 0.79 | 119 |

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 6: Comparison of post-dive excess oxygen consumption and the oxygen necessary for replenishing oxygen stores and removing lactic acid.

| Experiment | (1) Post-dive Excess Oxygen Consumption (ml) | (2) Oxygen Stores plus Oxygen for lactic acid Oxidation (ml) | $\frac{(2)}{(1)} \times 100$ (%) |
|---|---|---|---|
| 1a | 192 | 141 | 73 |
| 2a | 203 | 115 | 57 |
| 3a | 251 | 172 | 68 |
| 4a | 404 | 156 | 39 |
| 5a | 141 | 128 | 90 |
| 3 | 194 | 161 | 83 |

# CHAPTER IV

## DISCUSSION

Previous work by Scholander (1940) on seals and by Andersen (1961) on alligators indicates that the post-dive excess oxygen consumption is usually insufficient to account for the oxygen debt incurred during a dive if it is assumed that the pre-dive resting rate is maintained throughout the dive. This is true even after dives in which the seals struggled. Both authors suggested as a possible explanation that metabolism (as indicated by oxygen consumption) is reduced during a dive. A reduction in metabolism (as measured by reduced body temperatures) during diving has actually been observed by Scholander, et al (1942) in seals, by Jackson (1968) in the turtle, Pseudemys scripta, and by Andersen (1959) in ducks.

However, not all diving animals respond to forced dives by reducing their metabolic rate. Scholander (1940) found that in penguins the post-dive excess oxygen consumption was much greater than the oxygen debt incurred during the dive if a resting oxygen consumption rate was assumed for the period of the dive, and the same result was obtained when manatees were forcibly dived (Scholander & Irving, 1941). In both instances, the animals struggled during the dives. Muskrats' metabolic



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

response to diving is similar to that of penguins and manatees in that the post-dive excess oxygen consumption is 4 to 9 times greater than the oxygen debt incurred, assuming a resting oxygen consumption rate during the dive. Struggling was never continuous but did occur periodically during some of the dives.

There are two possible explanations for a post-dive oxygen consumption which is greater than expected. The animals are either, not maintaining a resting oxygen consumption rate during the dive or the post-dive excess oxygen consumption is superimposed on an oxygen consumption rate which is greater than the pre-dive oxygen consumption rate. The factors that might increase oxygen consumption rate during a dive include activity, thermal stress, and/or hormonal changes. Hart (1971) reports that the maximal possible oxygen consumption that can be maintained for at least 20 minutes by a muskrat is 3.5 times their basal oxygen consumption rate, but for shorter periods of time, e.g. the length of these dives, it is likely that they could maintain their oxygen consumption rate at even higher levels as is possible in humans (20 times normal for several minutes).

Yet, activity during the dive, in itself, cannot fully explain the larger than expected post-dive oxygen consumption observed in muskrats. In a number of dives in which the animal remained essentially motionless throughout the dive the post-dive oxygen consumption still exceeded the oxygen debt, assuming a resting oxygen consumption rate during the dive, by a factor of 2 to 8. In addition to increases due to the occasional activity, muskrats have been observed to have an oxygen consumption rate in water 1.18 to 1.3 times their oxygen con-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

sumption rate in air at the same temperature (Shcheglova, 1964) which may account for a portion of the increase in oxygen consumption that is apparent in muskrats even when there is minimal activity. The only hormonal changes likely to be of any importance are those involved with the release of epinephrine. This causes only a relatively small increase in metabolic rate but it also might contribute to the increase in oxygen consumption during dives with minimal activity. It is likely that the increases seen even with only minimal activity during the dive result from a combination of these factors.

These same factors might also affect oxygen consumption after a dive, but activity is minimal after restrained dives, and would probably not contribute greatly to an increase in oxygen consumption. After unrestrained dives the animals did commonly groom, so this activity could result in some of the increase in oxygen consumption after unrestrained dives. Again, release of epinephrine could cause a small portion of any increase in oxygen consumption rate.

Physical activity causes the greatest increases in oxygen consumption rate and while it may not be able to account for all the excess oxygen consumption after a dive it probably accounts for the major part of it. In the restrained dive experiments, this physical activity occurred during the dive whereas in the unrestrained dive experiments it was most likely a combination of the swimming and post-dive grooming.

The major procedural difference between these restrained and unrestrained dives was in the freedom of movement allowed the animal. The length of the dive was regulated in both instances. Because of this, any differences observed between the restrained and unrestrained dives should be due to the activity of swimming, yet the excess oxygen con-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

sumptions after restrained and unrestrained dives of equal duration are quantitatively similar. The increased activity of the unrestrained dives appears not to have affected the magnitude of the excess oxygen consumption after the dive. Apparently the energetic cost of swimming is not great in muskrats. Kooyman, et al (1973) found this to be true also in seals. Therefore, when measuring the magnitude of the post-dive oxygen consumption in muskrats, a restrained dive is a good approximation of the unrestrained situation.

Although the excess oxygen consumptions after restrained and unrestrained dives are quantitatively similar, there do appear to be qualitative differences. The rate at which this excess oxygen is consumed after restrained dives is slower than the rate at which it is consumed after unrestrained dives. The recovery after a restrained dive of a muskrat shows the same characteristic curve as that obtained from other diving mammals -- an initial rapid oxygen consumption rate followed by a lower slowly decreasing rate until recovery is complete. The recovery curve of an unrestrained dive drops more quickly from the initial increase.

Recovery may possibly have been faster after unrestrained dives because of the grooming activity that commonly took place after the dive. Newman, et al, (1936) found that the rate of removal of lactic acid is faster after exercise if some moderate level of exercise is maintained, thus the grooming may have aided in the recovery process.

The small amount of lactic acid that appears in the blood during the dive in comparison to the amount which appears after the dive indicates that muskrats, like other diving animals, exhibit circulatory

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

adjustments which isolate the muscle masses during a dive, reserving oxygen for less tolerant tissues such as brain and heart.

There is disagreement in the literature as to what fraction of the accumulated lactic acid formed anaerobically is actually oxidized to provide the energy for the resynthesis of the remaining lactic acid into glycogen. Meyerhof (1927) determined this fraction to be 1/3 to 1/6. Scholander (1940) used 1/5 and that fraction was used in this study also. Other authors have proposed using 1/10 (Margaria, et al, 1933) or 1/13 (Margaria, et al, 1963). When using one of these fractions of the total lactic acid to estimate the amount of oxygen necessary to effect the removal of the lactic acid, the assumption is made that all the lactic acid removed is converted to glycogen. There is evidence that this is not true. Stainsby & Welch (1966) and Freyschuss & Strandell (1967) have observed the uptake of lactic acid by muscle in situ. Lactic acid is also removed from the coronary arterial blood in quantities that suggest that it is utilized as an energy source by the heart (McGinty & Miller, 1932).

The sum of the oxygen stores and the oxygen necessary for lactic acid oxidation was always less than the actual post-dive excess oxygen consumption (Table 6). A variable non-lactic acid debt appears to exist in muskrats but if a greater percentage of the lactic acid was assumed to be oxidized, the entire post-dive excess oxygen consumption can be accounted for by oxygen stores plus oxygen necessary for lactic acid oxidation. The percentage of the lactic acid that had to be oxidized to account for the entire excess oxygen consumption varied for the six dives performed (1a, 29%; 2a, 42%; 3a, 32%; 4a, 65%; 5a, 22%; 3, 26%).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Because of the above difficulties in assessing that portion of the lactic acid accumulated during a dive that is actually oxidized, it is difficult to make definite conclusions as to the presence or absence of a non-lactic acid debt in muskrats.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

# CHAPTER V

## SUMMARY

The extensive literature on the physiological adaptations to diving does not include much information on semi-aquatic mammals or on unrestrained animals. Most of the research on diving mammals has been done using seals, animals accustomed to prolonged diving. The extent of the adaptations to diving varies among different diving animals and probably reflects the diving habits of the animal. Muskrats are medium-sized semi-aquatic mammals accustomed to dives of short duration.

This study examined the post-dive excess oxygen consumption in muskrats and determined whether the non-lactic acid oxygen debt observed in seals is also present in muskrats. Comparisons are also made of restrained and unrestrained dives to determine the effect of restraint on an animal's physiological responses to diving.

Seven animals were used for a total of thirty-one restrained dives. Dives were performed with the animal secured on a board which could be tilted into the water. Dives were 0.5, 1, 2, 3, or 4 minutes in duration. Nine animals were used for a total of forty-six unrestrained dives. Unrestrained dives were performed in a large tank



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

with only one opening used for both an entrance and exit and lasted 1, 2, 3, 4, or 5 minutes. Dive time was regulated by opening and closing the trapdoor over the opening to the tank.

During restrained diving experiments the animal's head was covered by a plastic hood and during the unrestrained diving experiments the animal sat in a whole body hood. Room air was drawn through these hoods and the fractional concentration of oxygen in the excurrent hood air was continuously monitored with a paramagnetic oxygen analyzer before and after each dive. Oxygen consumption was calculated from the fractional oxygen concentration data. Lactic acid levels were determined in blood samples which were taken from the muskrat's femoral artery before, during, and after six different restrained dives. Body oxygen stores were estimated from the literature.

The post-dive excess oxygen consumption after all dives was greater than the oxygen debt incurred assuming maintenance of the pre-dive oxygen consumption rate. This indicates either an increased oxygen consumption rate during the dive or after the dive. The increase in the oxygen consumption rate in restrained experiments probably occurs during the dive and is due partially to intermittent struggling. The increase in unrestrained experiments probably occurs both during the dive (swimming activity) and after the dive (grooming).

The post-dive excess oxygen consumption increased with longer dives after both restrained and unrestrained dives. Regression of post-dive excess oxygen consumption on dive time results in statistically equal regression equations for restrained and unrestrained dives. This indicates that the activity of swimming is not energetically

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

costly for muskrats and that restraint has no quantitative effect on the post-dive excess oxygen consumption. However, there appears to be a qualitative difference between restrained and unrestrained dives in that the total time to recovery is always shorter after unrestrained dives than after restrained dives of the same duration.

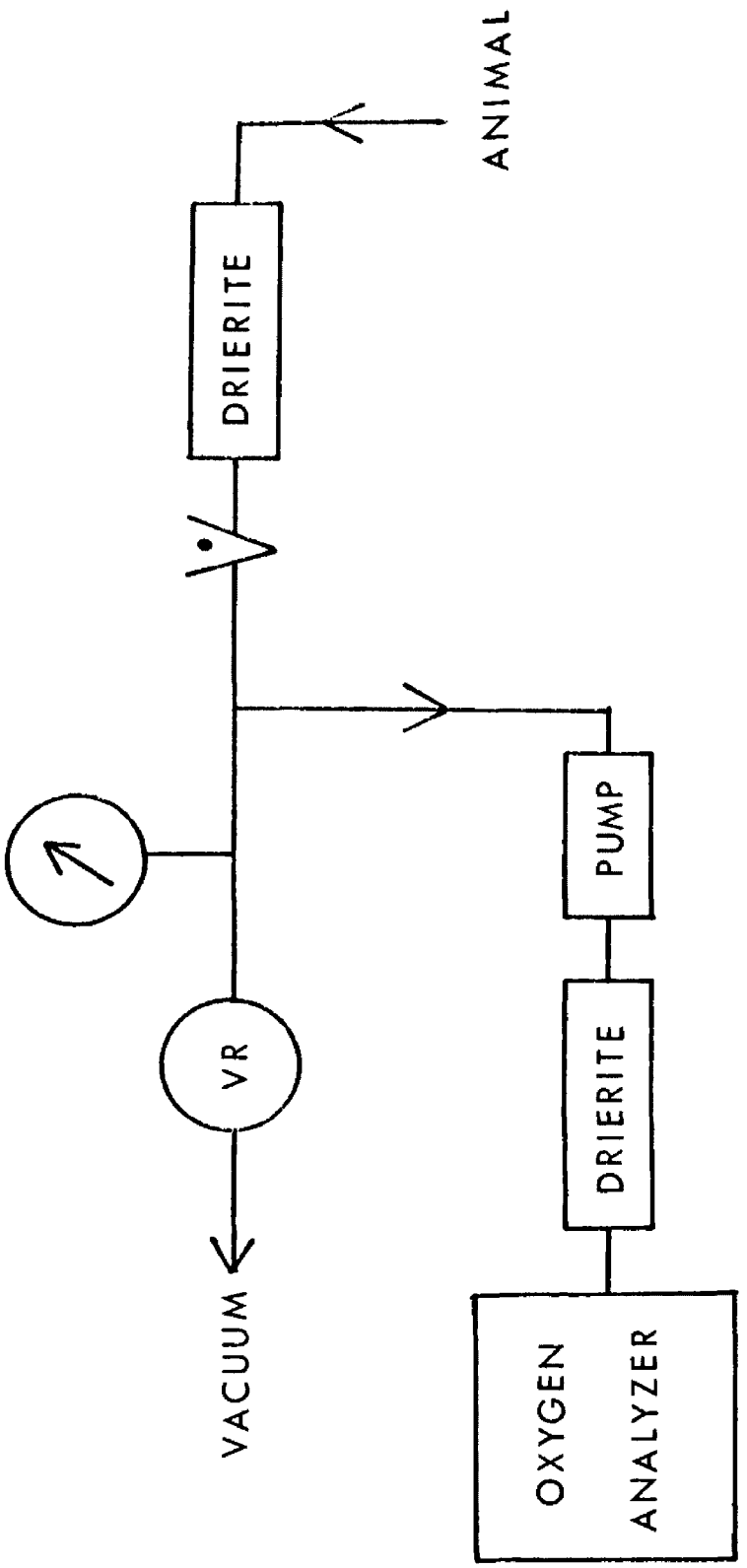
Comparison of the volume of oxygen necessary to replenish the oxygen stores plus the lactic acid oxidation oxygen and the actual post-dive excess oxygen consumption suggests a non-lactic acid debt in muskrats but, because of the disagreement in the literature as to the fraction of the lactic acid which is oxidized in recovery, no definite conclusions can be made as to the existence of a non-lactic acid oxygen debt in muskrats.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

# APPENDIX 1

Flow system utilized for oxygen consumption measurements. VR is a vacuum regulator and $\dot{V}$ is a flowmeter.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.




Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

## APPENDIX 2

Post-dive excess oxygen consumption ($V_{O_2}$), oxygen debt (OD), and percentage of $V_{O_2}$ accounted for by OD for each dive, both restrained and unrestrained.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

## Restrained Dives

| Dive Time (min) | $VO_2$ (ml/kg) | $O_2$ Debt (ml/kg) | $\frac{O_2 \text{ Debt}}{VO_2} \times 100$ |
|---|---|---|---|
| 0.5 | 51 | 5 | 10 |
| 0.5 | 38 | 6 | 16 |
| 0.5 | 59 | 6 | 10 |
| 0.5 | 114 | 9 | 8 |
| 0.5 | 63 | 5 | 8 |
| 0.5 | 48 | 7 | 15 |
| 1.0 | 31 | 10 | 32 |
| 1.0 | 70 | 10 | 14 |
| 1.0 | 62 | 11 | 18 |
| 1.0 | 171 | 10 | 6 |
| 1.0 | 157 | 11 | 7 |
| 1.0 | 66 | 12 | 18 |
| 2.0 | 31 | 22 | 71 |
| 2.0 | 315 | 27 | 9 |
| 2.0 | 110 | 25 | 23 |
| 2.0 | 161 | 25 | 16 |
| 2.0 | 488 | 27 | 6 |
| 2.0 | 82 | 23 | 28 |
| 2.0 | 176 | 26 | 15 |
| 2.0 | 151 | 23 | 15 |
| 3.0 | 483 | 30 | 6 |
| 3.0 | 241 | 44 | 18 |
| 3.0 | 389 | 33 | 9 |
| 3.0 | 299 | 41 | 14 |
| 3.0 | 97 | 29 | 30 |
| 4.0 | 286 | 44 | 15 |
| 4.0 | 421 | 43 | 10 |
| 4.0 | 245 | 54 | 22 |
| 4.0 | 482 | 43 | 9 |
| 4.0 | 286 | 56 | 20 |
| 4.0 | 205 | 50 | 24 |

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

## Unrestrained Dives

| Dive Time (min) | $V_{O_2}$ (ml/kg) | $O_2$ Debt (ml/kg) | $\frac{O_2 \text{ Debt}}{V_{O_2}} \times 100$ |
|---|---|---|---|
| 1.0 | 79 | 16 | 20 |
| 1.0 | 72 | 13 | 18 |
| 1.0 | 63 | 16 | 25 |
| 1.0 | 180 | 15 | 8 |
| 1.0 | 66 | 14 | 21 |
| 1.0 | 93 | 14 | 15 |
| 2.0 | 174 | 20 | 12 |
| 2.0 | 137 | 27 | 20 |
| 2.0 | 191 | 22 | 12 |
| 2.0 | 178 | 22 | 12 |
| 2.0 | 154 | 17 | 11 |
| 2.0 | 220 | 22 | 10 |
| 2.0 | 244 | 26 | 11 |
| 2.0 | 100 | 31 | 31 |
| 3.0 | 577 | 57 | 10 |
| 3.0 | 343 | 74 | 22 |
| 3.0 | 699 | 34 | 5 |
| 3.0 | 853 | 35 | 4 |
| 3.0 | 249 | 60 | 24 |
| 3.0 | 134 | 44 | 33 |
| 3.0 | 326 | 49 | 15 |
| 3.0 | 202 | 37 | 18 |
| 3.0 | 317 | 67 | 21 |
| 3.0 | 173 | 62 | 36 |
| 3.0 | 509 | 39 | 8 |
| 4.0 | 291 | 57 | 20 |
| 4.0 | 360 | 57 | 16 |
| 4.0 | 243 | 41 | 17 |
| 4.0 | 225 | 50 | 22 |
| 4.0 | 162 | 54 | 33 |
| 4.0 | 224 | 52 | 23 |
| 4.0 | 564 | 44 | 8 |
| 4.0 | 496 | 49 | 10 |
| 4.0 | 169 | 51 | 30 |
| 4.0 | 310 | 50 | 16 |
| 4.0 | 339 | 48 | 14 |
| 4.0 | 687 | 44 | 6 |
| 4.0 | 578 | 51 | 9 |
| 4.0 | 583 | 53 | 9 |

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Unrestrained Dives (cont.)

| Dive Time (min) | $V_{O_2}$ (ml/kg) | $O_2$ Debt (ml/kg) | $\frac{O_2 \text{ Debt}}{V_{O_2}} \times 100$ |
|---|---|---|---|
| 5.0 | 784 | 59 | 8 |
| 5.0 | 338 | 56 | 17 |
| 5.0 | 552 | 52 | 9 |
| 5.0 | 452 | 59 | 13 |
| 5.0 | 333 | 97 | 29 |
| 5.0 | 452 | 94 | 21 |
| 5.0 | 414 | 99 | 24 |

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

# APPENDIX 3

Recovery time in minutes for each restrained and unrestrained dive.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

| Restrained | | Unrestrained | |
|---|---|---|---|
| Dive Time (min) | Recovery Time | Dive Time (min) | Recovery Time |
| 0.5 | 32 | 1.0 | 11 |
| 0.5 | 11 | 1.0 | 13 |
| 0.5 | 13 | 1.0 | 9 |
| 0.5 | 19 | 1.0 | 23 |
| 0.5 | 21 | 1.0 | 12 |
| 0.5 | 15 | 1.0 | 19 |
| 1.0 | 18 | 2.0 | 18 |
| 1.0 | 29 | 2.0 | 17 |
| 1.0 | 20 | 2.0 | 27 |
| 1.0 | 30 | 2.0 | 22 |
| 1.0 | 27 | 2.0 | 22 |
| 1.0 | 15 | 2.0 | 17 |
| | | 2.0 | 18 |
| 2.0 | 26 | 2.0 | 19 |
| 2.0 | 55 | | |
| 2.0 | 27 | 3.0 | 45 |
| 2.0 | 22 | 3.0 | 24 |
| 2.0 | 62 | 3.0 | 42 |
| 2.0 | 14 | 3.0 | 66 |
| 2.0 | 35 | 3.0 | 20 |
| 2.0 | 31 | 3.0 | 14 |
| | | 3.0 | 28 |
| 3.0 | 58 | 3.0 | 21 |
| 3.0 | 47 | 3.0 | 29 |
| 3.0 | 74 | 3.0 | 14 |
| 3.0 | 59 | 3.0 | 42 |
| 3.0 | 23 | | |
| | | 4.0 | 25 |
| 4.0 | 40 | 4.0 | 25 |
| 4.0 | 45 | 4.0 | 24 |
| 4.0 | 32 | 4.0 | 18 |
| 4.0 | 67 | 4.0 | 18 |
| 4.0 | 56 | 4.0 | 17 |
| 4.0 | 31 | 4.0 | 51 |
| | | 4.0 | 42 |
| | | 4.0 | 18 |
| | | 4.0 | 28 |
| | | 4.0 | 33 |
| | | 4.0 | 54 |
| | | 4.0 | 42 |
| | | 4.0 | 37 |

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Unrestrained

| Dive Time (min) | Recovery Time |
|---|---|
| 5.0 | 64 |
| 5.0 | 27 |
| 5.0 | 38 |
| 5.0 | 34 |
| 5.0 | 23 |
| 5.0 | 25 |
| 5.0 | 33 |

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

# LITERATURE CITED

Andersen, H.T. (1959) Depression of metabolism in the duck during diving. Acta Physiol. Scand. 46, 234-239.

Andersen, H.T. (1961) Physiological adjustments to prolonged diving in the American alligator. Acta. Physiol. Scand. 53, 23-45.

Andersen, H.T. (1966) Physiological adaptations in diving vertebrates. Physiol. Rev. 46, 212-243.

Bert, P.(1870) Lecons sur la physiologie comparee de la respiration. Paris: Bailliere 526-553. As cited in Andersen, H.T. (1966) Physiological adaptations in diving vertebrates. Physiol. Rev. 46,212-243.

Bohr, C. (1897) Bidrag til Svommerfuglernes Fysiologi. K. Danske Vidensk. Selsk. No. 2. As cited in Andersen, H.T. (1966) Physiological adaptations in diving vertebrates. Physiol. Rev. 46, 212-243.

Freyschuss, U. and T. Strandell. (1967). Limb circulation during arm and leg exercise in supine position. J. Appl. Physiol. 23, 163-170.

Harrison, R.J., S.H. Ridgway, and P.L. Joyce.(1972) Telemetry of heart rate in diving seals. Nature 238, 280.

Hart, J.S. (1971) In: "Comparative Physiology of Thermoregulation" (G.C. Whittow, ed.), pp. 2-149. Academic Press, New York.

Irving, L. (1934) On the ability of warm blooded animals to survive without breathing. Sci. Month. 38, 422-428.

Irving, L. (1939) Respiration in diving mammals. Physiol. Rev. 19, 112-134.

Jackson, D.C. (1968) Metabolic depression and oxygen depletion in the diving turtle. J. Appl. Physiol. 24(4), 503-509.

Jones, D.R., H.D. Fisher, S. McTaggart, and N.H. West. (1973) Heart rate during breath-holding and diving in the unrestrained harbor seal (Phoca vitulina richardi). Can. J. Zool. 51(7), 671-680.

Kooyman, G.L. and W.B. Campbell. (1972) Heart rates in freely diving Weddell seals, Leptonychotes weddelli. Comp. Biochem. Physiol. 43A, 31-36.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Kooyman, G.L., D.H. Kerem, W.B. Campbell and J.J. Wright. (1971) Pulmonary function in freely diving Weddell seals, Leptonychotes weddelli. Respir. Physiol. 12, 271-282.

Kooyman, G.L., D.H. Kerem, W.B. Campbell, and J.J. Wright. (1973) Pulmonary gas exchange in freely diving Weddell seals, Leptonychotes weddelli. Respir. Physiol. 17, 283-290.

Lenfant, C., K. Johansen and J.D. Torrance. (1970) Gas transport and oxygen storage capacity in some pinnipeds and the sea otter. Respir. Physiol. 9, 277-286.

Margaria, R., P. Cerretelli, P.E. diPrampero, C. Massari, and G. Torelli. (1963) Kinetics and mechanism of oxygen debt contraction in man. J. Appl. Physiol. 18(2), 371-377.

Margaria, R., H.T. Edwards and D.B. Dill. (1933) The possible mechanisms of contracting and paying the oxygen debt and the role of lactic acid in muscular contraction Am. J. Physiol. 106, 689-715.

McGinty, D.A. and A.T. Miller, Jr. (1932) Studies on the coronary circulation. II. The absorption of lactic acid and glucose and the gaseous exchange of heart muscle. Am. J. Physiol. 103, 712-720.

Meyerhof, O. (1927) Recent investigations on the aerobic and anaerobic metabolism of carbohydrate. J. Gen. Physiol. 8(6), 531-542.

Millard, R.W., K. Johansen and W.K. Milsom. (1973) Radiotelemetry of cardiovascular responses to exercise and diving in penguins. Comp. Biochem. Physiol. 46A, 227-240.

Murdaugh, H.V., J.C. Seabury and W.L. Mitchell. (1961) Electrocardiogram of the diving seal. Circulation Res. 9, 358-361.

Newman, E.V., D.B. Dill, H.T. Edwards and F.A. Webster. (1936) The rate of lactic acid removal in exercise. Am. J. Physiol. 118, 457-462.

Richet, C. (1899) De la resistance des canards a l'asphyxie. J. Physiol. Pathol. Gen. 1, 641-650. As cited in Andersen, H.T. (1966) Physiological adaptations in diving vertebrates. Physiol. Rev. 46, 212-243.

Robinson, D. (1939) The muscle hemoglobin of seals as an oxygen store in diving. Science 90, 276-277.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Scholander, P.F. (1940) Experimental investigations on the respiratory function in diving mammals and birds. Hvalradets Skrifter Norske Videnskaps-Akad. Oslo 22, 1-131.

Scholander, P.F. (1964) Animals in aquatic environments: diving mammals and birds. In: Handbook of Physiology. Section 4. Adaptation to the Environment, edited by D.B. Dill, E.F. Adolph and C.G. Weber. Washington, D.C., American Physiological Society, pp. 729-739.

Scholander, P.F., and L. Irving. (1941) Experimental investigations on the respiration and diving of the Florida manatee. J. Cell. Comp. Physiol. 17, 169-191.

Scholander, P.F., L. Irving and S.W. Grinnell. (1942) On the temperature and metabolism of the seal during diving. J. Cell. Comp. Physiol. 19, 67-78.

Shcheglova, A.I. (1964) Specific features of heat exchange in the muskrat. In: Experience in the study of regulating physiological functions under the natural conditions of existence of the organisms. Akad. Nauk. SSSR: Moscow-Leningrad. 6, 183-190

Sokal, R.R. and F.J. Rohlf. (1969) In: Biometry, p. 372. W.H. Freeman Co., San Francisco.

Stahl, W.R. (1967) Scaling of respiratory variables in mammals. J. Appl. Physiol. 22(3), 453-460.

Stainsby, W.N. and H.G. Welch. (1966) Lactate-metabolism of contracting dog skeletal muscle *in situ*. Am. J. Physiol. 211, 177-183.

Steel, R.G.D. and J.H. Torrie. (1960) In: Principles and Procedures of Statistics, p. 179. McGraw-Hill Book Co., Inc. New York.

Tucker, V.A. (1968) Respiratory exchange and evaporative water loss in the flying budgerigar. J. Exp. Biol. 48, 67-87.

Weber, R.E., E.A. Hemmingsen and K. Johansen. (1974) Functional and biochemical studies of penguin myoglobin. Comp. Biochem. Physiol. 49B, 197-214.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.