

AEROBIC ENERGETICS OF SURFACE SWIMMING IN THE MUSKRAT *ONDATRA ZIBETHICUS*¹

FRANK E. FISH²

Department of Zoology, Michigan State University, East Lansing, Michigan 48824

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The surface swimming of muskrats (*Ondatra zibethicus*) was studied by forcing individual animals to swim against a constant velocity water current, ranging from 0.2 to 0.75 m/s, in a recirculating water channel. The swimming muskrat was enclosed in a metabolic chamber to monitor oxygen consumption as a measure of the aerobic power input. The metabolic rate ($\dot{V}O_2$) of swimming muskrats at a water temperature of 25 C was found to increase linearly over the range of test velocities. The computed cost of transport exhibited a curvilinear decrease with increasing velocity to a minimum of 0.75 m/s. Observations of free-swimming muskrats showed that they did not swim at the energetically most efficient velocity but at a lower mean velocity of 0.58 m/s. Departure from the expected swimming velocity was believed to be dependent on an addition of anaerobic metabolism to the aerobic metabolism and onset of fatigue at velocities above 0.6 m/s due to high drag.

INTRODUCTION

The mechanical work done by an aquatic animal swimming at a constant velocity is the product of the velocity and distance traveled. The energy necessary to perform this work is supplied from the metabolism of the animal. The metabolic expenditure represents the power input, while the power output is the realized portion that performs work opposing resistive forces.

The energetic costs of locomotion have been determined for numerous terrestrial animals (Schmidt-Nielsen 1972; Tucker 1975); data for swimming animals is

largely limited to fish (Webb 1977b). In the case of mammals, the theoretical energy utilization of swimming cetaceans has received much attention (Gray 1936; Ker-mack 1948; Parry 1949; Lang 1975). Empirically obtained measurements of metabolic expenditure by steady-state oxygen consumption for swimming mammals have only been accomplished on humans (Holmer 1972; DiPrampo et al. 1974) and sea lions (Costello and Whittow 1975; Kruse 1975).

The muskrat, *Ondatra zibethicus*, is of particular interest in that this semiaquatic rodent regularly swims at the air-water interface using a paddling mode of propulsion (Mizelle 1935). A comprehensive study of the energetics of this propulsive mode has not currently been undertaken. Because of its small size, the muskrat can serve as a manageable model for the examination of the development and utilization of power for swimming locomotion. Combining a biomechanical analysis of the paddling mode of the muskrat (Fish, in preparation) with metabolic data allows for an integrated approach to the study of energy utilization.

In addition, the muskrat affords the opportunity to examine the consequences of surface swimming for which the forces encountered are larger than submerged swimmers (Hertel 1966). Little attention

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² Present address: Department of Biology, West Chester State College, West Chester, Pennsylvania 19380.

has been paid to this aspect of aquatic locomotion despite the number of nonpiscine vertebrate swimmers which are restricted to the surface by their need of gaseous oxygen for respiration.

MATERIAL AND METHODS

EXPERIMENTAL ANIMALS

Ten muskrats (nine males and one female) were live-trapped in Ingham County, Michigan, during the spring and summer of 1978 and 1979. The mean body mass of the muskrats was 649 g (range 530–1,604 g) over the test period. To avoid mortality due to captivity throughout the period of testing, the animals were kept outdoors in large, concrete ponds at the Limnology Research Laboratory on the campus of Michigan State University. The ponds had a depth of approximately 2 m, allowing unrestricted swimming and diving. Abundant aquatic vegetation, which grew in the ponds, was readily consumed by the muskrats and used for bedding material. The diet was supplemented with apples. The ponds were equipped with platforms above the water. Nest boxes were provided on the platforms and

were modified for the capture of single animals when needed for testing.

WATER CHANNEL AND METABOLIC CHAMBER

Experiments on swimming were conducted in a recirculating water channel (fig. 1), based on a design by Vogel and LaBarbera (1978). A working section (fig. 1, *WS*) was provided in the channel in which a single muskrat was allowed to swim. The upstream end of the working section was bounded by a plastic grid (commercially termed "egg crate") in conjunction with a 5-cm-wide grid of plastic straws, both of which removed turbulence from the water flow and also prevented the experimental animal from escaping. The downstream end of the working section was bounded by a low-voltage electrified grid (fig. 1, *EG*) which prevented escape and stimulated swimming by the muskrat. Wires attached to the grid ran along the floor of the working section to prevent the animal from standing on the floor to rest. The voltage was controlled with a Powerstat (Superior Electric Co.). All electricity to the grid was disconnected when the muskrat maintained steady

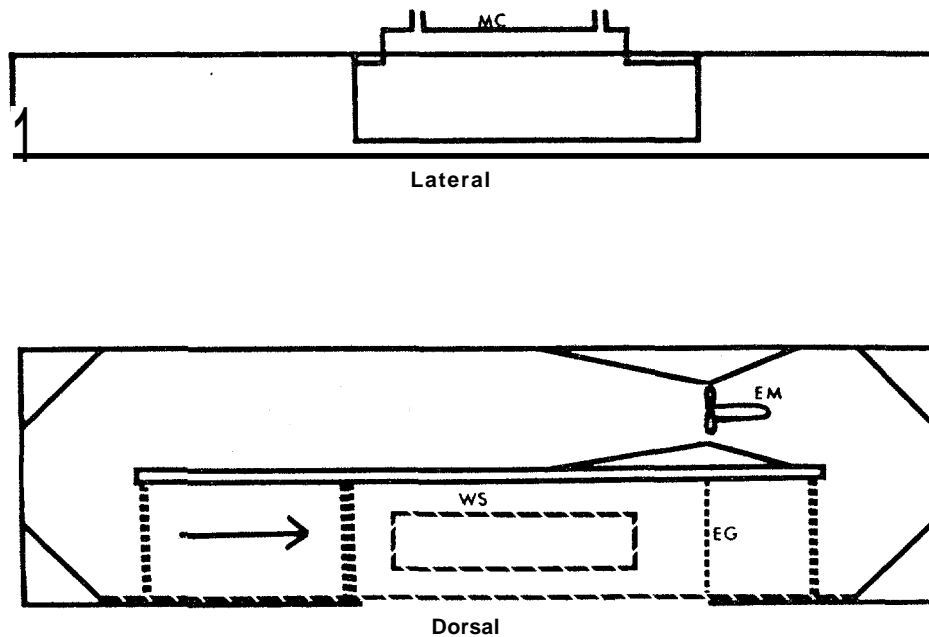


FIG. 1.—Water channel used in experiment. Arrows indicate the direction of water flow, driven by an electric motor, EM, in the return channel, RC. Broken lines illustrate the laminar flow grids or electric grid, EG (-----) and Plexiglas walls (—) in the working section, WS. MC represents the metabolic chamber.

swimming. During higher-speed runs, a removable wall was placed in the working section to constrict its cross-sectional area and thus increase the water velocity.

On top of the working section was a Plexiglas metabolic chamber (fig. 1, *MC*) of the dimensions of $75.5 \times 13.0 \times 26.0$ cm. Inlet and outlet air tubes entered through the walls of the chamber. The chamber was hinged to the inner wall of the water channel to allow for the introduction and removal of a muskrat. At its base, the metabolic chamber had a Plexiglas apron which extended over the working section. When the water channel was filled, the apron was slightly submerged below the water surface. This prevented any air leakage but had little effect on the water flow. The dimensions of the metabolic chamber were large enough for a single muskrat to swim against a constant current without interference.

Water velocity (U) was controlled by either a Sears 25 electric fishing motor (model no. 217.590091) or a Mercury electric outboard motor (model no. 10019) situated in the return channel (fig. 1, *RC*). Power to the motor was provided by a 12-V storage battery connected to a 6-A battery charger. Motor speed was related to water speed, determined by the time a drop of ink or neutrally buoyant particle traversed a given distance.

Musk rats were tested at velocities ranging from 0.2 to 0.75 m/s. The arrangement of test velocities for each muskrat was such that there was no apparent order. Each muskrat was forced to swim steadily at a given test velocity for a period of 10–30 min to obtain sufficient data. During the initial exposure to the apparatus, each muskrat learned to swim steadily and avoid the downstream electrified grid within 15 min. Data were collected only during subsequent trials when the muskrat was proficient in swimming against the current, so as to avoid biasing the results from excitation of the animals during the first trial runs.

OXYGEN CONSUMPTION

Mass-specific oxygen consumption ($\dot{V}O_2$), as a measure of metabolic rate, was monitored using an open-circuit system

conforming to condition **B** of Hill (1972). The oxygen content of dry, CO_2 -free air flowing out of the metabolic chamber was monitored with a Beckman C-2 paramagnetic oxygen analyzer. Ascarite (A. H. Thomas Co.) and Drierite (W. A. Hammond Co.) were contained in tubes downstream of the metabolic chamber to absorb CO_2 and water vapor, respectively, from the air flow. The rate of air flow into the metabolic chamber was measured with a calibrated Gilmont Model 1300 flowmeter. The flow rate into the chamber was approximately 3.0–3.8 liters/min for dry air at STP.

In order to obtain a realistic estimate of the energy expenditure of natural muskrat swimming, experimental animals were not made to fast prior to testing in order to control for specific dynamic action, and animals swam in water at 25 C. After the experimental animal was placed in the metabolic chamber, the muskrat was given 10–30 min to adjust to the apparatus and water temperature. During this period, the resting metabolic rate was recorded for the animal. During measurement of the resting $\dot{V}O_2$, the animals floated quietly with approximately one-third of the total body surface area above the water. Although some paddling movements were observed, these tended to be infrequent and did not appear to substantially influence $\dot{V}O_2$.

Diffusion of oxygen between the air flow and water could produce an error in the measured oxygen consumption. To test for this a gas of known composition (88% N_2 , 12% O_2) was passed through the metabolic chamber with the water current at a given velocity. Any change in the gas composition was monitored with the oxygen analyzer over a 30-min period. An error of approximately 1% of the actual value of oxygen in the gas was found at 0.7 and 0.75 m/s, probably due to the turbulence produced by the motor. Apparent metabolic rates at 0.7 and 0.75 m/s were adjusted to compensate for this factor.

ESTIMATION OF NATURAL SWIMMING SPEED

Observations were made on muskrats held in the concrete ponds to determine the routine swimming speeds. Individual

animals were timed as they traversed a measured distance using either a stopwatch or 16-mm films taken at 24 frames/s.

STATISTICAL PROCEDURE

Statistical analyses were made with reference to Simpson, Roe, and Lewontin (1960) and Steele and Torrie (1960). In order to perform the statistical analyses for the various data sets, trials on muskrats were assumed to be independent of one another. Variation about means was expressed as standard error (SE), and ± 1 standard deviation (SD) for the regression coefficients.

RESULTS

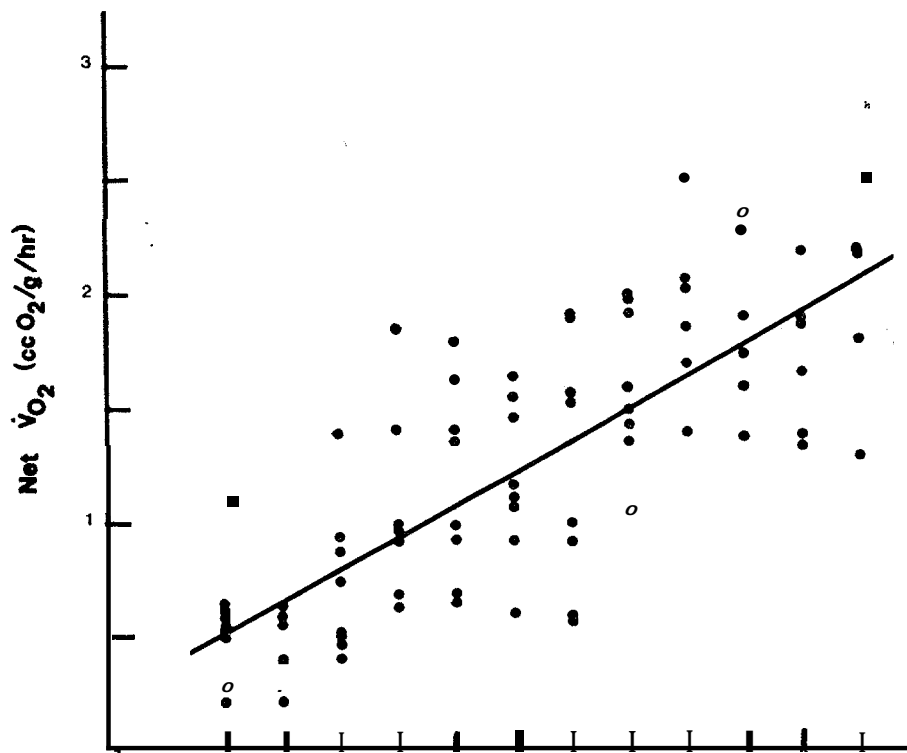
METABOLIC RESPONSES

The mean oxygen consumption, $\dot{V}O_2$, for muskrats resting in water at 25 C was 0.88 ± 0.33 cc O_2 /g/h (no. = 87), which was 62% lower than the values reported for restrained muskrats in water at the same temperature (Fish 1979) and 17%

higher than the predicted metabolic rate of 0.75 cc O_2 /g/h for muskrats in thermoneutrality (Schmidt-Nielsen 1979).

In the water channel, muskrats swam similar to the description by Mizelle (1935). They normally swam at the water surface maintaining a concavely arched back. The forelegs were held under the chin, while the hindfeet moved in a paddling mode by alternating strokes. The laterally compressed tail was thrown into a series of waves that traveled posteriorly in the horizontal plane faster than the speed of the animal. The movements of the tail, although similar to anguilliform locomotion of fish, generated negligible thrust compared with that of the hindfeet (Fish 1980).

Values of the net $\dot{V}O_2$ (total - resting) for muskrats swimming in water at 25 C increased linearly as the swimming velocity, U , increased from 0.2 to 0.75 m/s (fig. 2). Although superficial observation of the data suggest the presence of a plateau



above 0.6 m/s, this could not be proved statistically. The best-fit relationships between the net and total $\dot{V}O_2$ and U were calculated as straight lines using least-squares linear-regression technique and were both highly significant at $P < .001$ (table 1).

The difference between the calculated maximum $\dot{V}O_2$ based on the regression equation of total $\dot{V}O_2$ and U , and the resting $\dot{V}O_2$ (aerobic scope of activity) for the muskrat was found to be 2.00 cc $O_2/g/h$, so that maximum aerobic metabolic expansibility was only 3.3 times resting $\dot{V}O_2$. This value increases only slightly to 3.8 when the calculated maximum $\dot{V}O_2$ and predicted metabolic rate for muskrats in thermoneutrality are compared. This is slightly less than the metabolic expansibility for small mammals (Wunder 1970) and is far below the values for humans and dogs (Pasquis, Lacaille, and Dejours 1970). However, the value of 3.3 is similar to the maximum values of 3.3 (Hart 1962) and 2.7 (McEwan, Aitchison, and Whitehead 1974) for muskrats exposed to a range of air temperatures from -60 to 34 C.

Several animals were observed to be fatigued after 20 min of sustained swimming at velocities of 0.7 and 0.75 m/s, as shown by the inability of the muskrats to swim against the water current. As a result, the animals could no longer prevent contact with the downstream electric grid.

ROUTINE VELOCITY

Routine velocities were determined continuously by paddling animals that appeared to maintain a constant forward motion. During the collection of these

data, muskrats were believed to be fully accustomed to the observer. Routine velocities were measured for muskrats swimming both toward and away from the observer.

Muskrats were found to swim about a mean velocity of 0.58 ± 0.02 m/s over a range of 0.43–0.72 m/s (fig. 3).

The stippled area indicated in figure 3 represents the single observation of a muskrat swimming at 0.3 m/s while carrying food in its mouth. Although the muskrat traveled at a slow velocity, the frequency of propulsive movements by the legs increased to 1.4 times the mean frequency of animals swimming without food. The food consisted of long filamentous pondweeds, which probably greatly increased drag, which was compensated for by increased propulsive movements.

DISCUSSION

The relationship between metabolic rate and U in surface swimming animals varies depending on the species and its propulsive mode. The muskrat exhibited a linear increase in $\dot{V}O_2$ with increasing U . Humans (Nadel et al. 1974), which swim by a modified paddling mode, and marine iguanas (Gleeson 1979), which swim by lateral undulations of the body and tail, also showed a linear increase of metabolic rate with increasing velocity. Ducks, swimming by a paddling stroke similar to that of the muskrat, have a relatively constant oxygen consumption below 0.5 m/s and a curvilinear increase from 0.5 to 0.7 m/s (Prange and Schmidt-Nielsen 1970). Sea turtles and sea lions exhibited exponential increases in oxygen consumption with increasing velocity (Kruse 1975;

TABLE 1
REGRESSION EQUATIONS FOR METABOLIC RATES, $\dot{V}O_2$, OF MUSKRATS
SWIMMING AT VARIOUS VELOCITIES, U

METABOLIC RATE	VELOCITY RANGE (m/s)	$\dot{V}O_2 \pm SE = aU + b$		No.	CORRELATION COEFFICIENT
		<i>a</i>	<i>b</i>		
Total2–.75	2.60 $\pm .10$.93	87	.71*
Net2–.75	2.81 $\pm .08$	-.05	87	.78*

* Highly significant at $P < .001$.

Prange 1976), both of which have a low profile in the water and use a lift-based propulsion mechanism (Walker 1971; English 1976).

The variety of metabolic relationships with swimming velocities observed for different surface swimmers contrasts with the homogeneous pattern observed for fish. Results of studies on the various modes of swimming have shown that fish have a consistent exponential relationship between their metabolic rates and swimming velocities regardless of the propulsive mode (Webb 1975a, 1975b; Gordon et al. 1979).

These very different relationships between metabolic rate and swimming velocity for surface and submerged swimmers can be compared in terms of a common measure of efficiency—the cost of transport, defined as the metabolic energy used to transport a unit mass a given dis-

tance in a given time (i.e., $\dot{V}O_2/U$). It takes into account differences in the resistance of the environment, the internal resistance of the body, and the efficiency of locomotion (Tucker 1970). Costs of transport for the muskrat were calculated from the data for total $\dot{V}O_2$ measured at various speeds and the computed values from the regression of total $\dot{V}O_2$ from table 1, which were converted to caloric values assuming 1 liter $O_2 = 4.8$ kcal (fig. 4). The cost of transport decreased with increasing U , and the lowest value was approximately 5.1 kcal/kg/km occurring at a U of 0.75 m/s. Most aquatic animals show U-shaped relationships with a clearly defined minimum. The lowest value in the present study was assumed to be equivalent to this minimum cost of transport.

In comparison with primary swimming vertebrates (fig. 5), the minimum cost of transport for muskrats was high. For

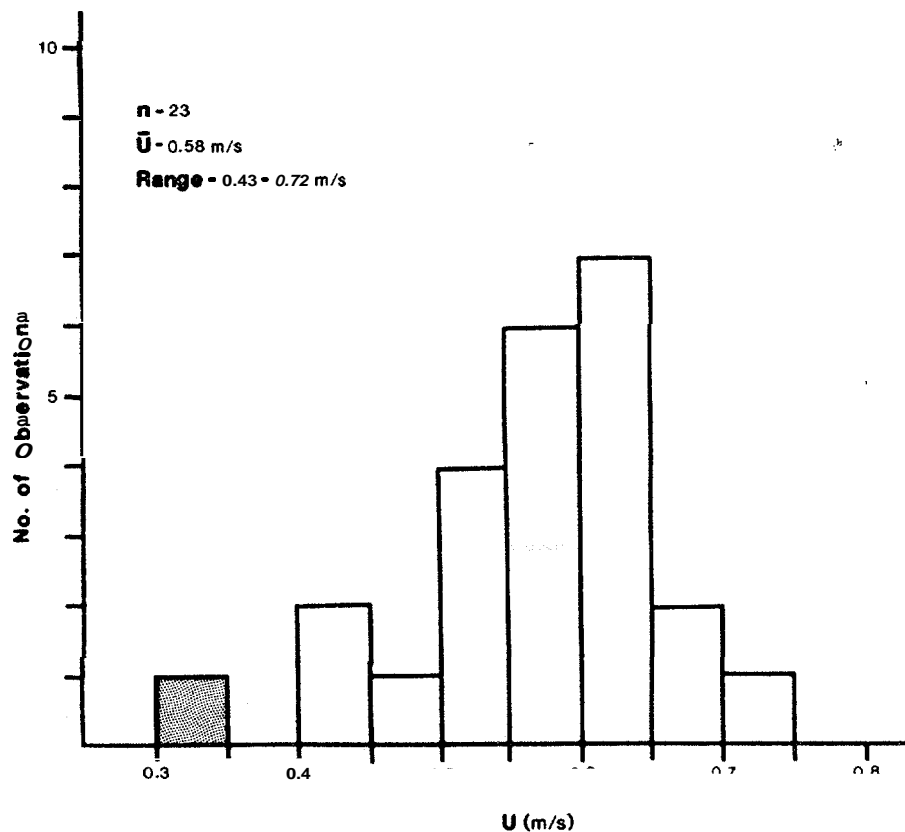


FIG. 3.—Numbers of observations of swimming speeds, U , of muskrats freely moving in a large pond. The stippled area shows a single result for an animal swimming while carrying food.

example, the minimum cost of transport for the muskrat was 13.5 times greater than similarly sized fish as represented by the salmon (Brett 1964), which is the lowest cost found for any mode of locomotion (Schmidt-Nielsen 1972; Tucker 1975). However, costs for secondary swimmers are high, similar to the muskrat. Humans were relatively more inefficient than muskrats in that their minimum costs of transport were 30 times that of fish (DiPrampero, personal communication). Minks, which paddle using only the forefeet, have a minimum cost of transport at 20 C higher than that of the muskrat at 25 C (Williams, personal communication). The duck is similar (Prange and Schmidt-Nielsen 1970). These surface swimmers all use a drag-based mechanism for locomotion. Values for the green sea turtle (Prange 1976), sea lions (Costello and Whittow 1975; Kruse 1975), and the marine iguana (Gleeson 1979) are lower

than those for the muskrat. Since the sea turtle and sea lion use a lift-based propulsor and the marine iguana lateral undulatory swimming, it seems that these locomotory modes are more effective than a drag-based mechanism. In addition, the high costs of transport for the muskrat, duck, mink, and humans are possibly attributable to high drag due to surface swimming, and maintenance of exercise metabolism and thermoregulation in a highly thermally conductive medium. The importance of thermoregulation is illustrated by a reduction of the aerobic energetic expenditure and consequently the cost of transport from 5.1 to 4.1 kcal/kg/km for muskrats in thermoneutrality at a water temperature of 30 C (Fish 1980), a 20% reduction.

Because of the energetic savings experienced by an animal swimming at the velocity of its minimum cost of transport, it would be predicted that the muskrat

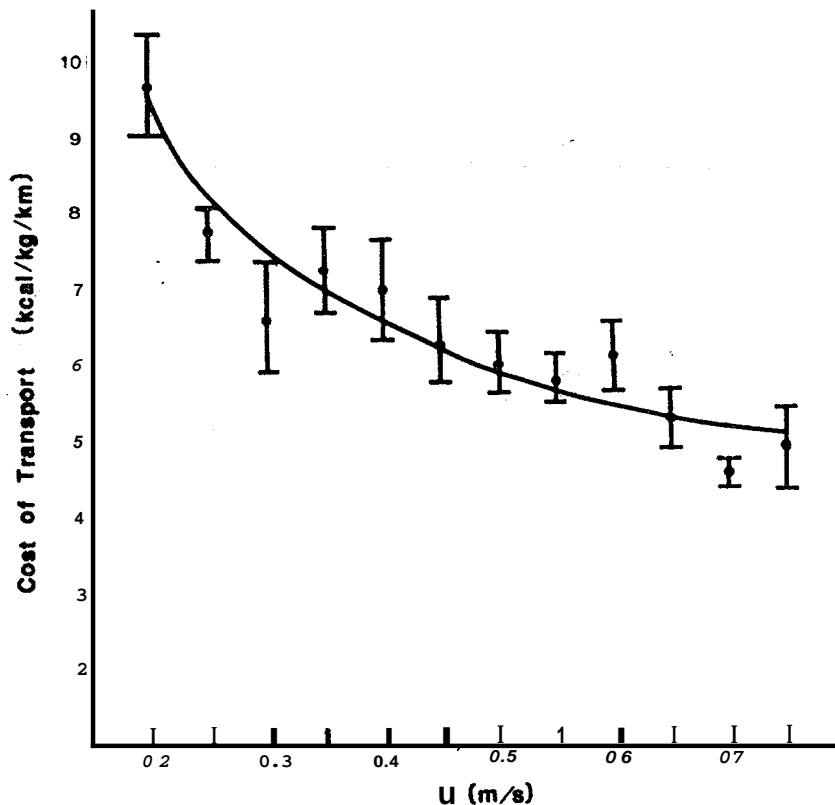


FIG. 4.— The cost of transport shown as a function of swimming velocity, U . The solid line represents the cost of transport calculated from the regression equation of total $\dot{V}O_2$ from table 1. The solid dots represent the mean values for muskrats swimming at each U , while the vertical lines represent \pm one standard error (SE).

would normally cruise at 0.75 m/s. This velocity would be considered to represent the optimal cruising speed (Weihs 1973; Ware 1978), to maximize the distance traveled for a given amount of energy expended. Prange and Schmidt-Nielsen (1970) found that the duck normally swam at the appropriate speed, in this case of 0.48 m/s. Sea turtles (Prange 1976) and flying birds (Tucker 1971) move at speeds close to the optimum in long migrations. In this manner, the animals were able to migrate long distances by minimizing the energetic expenditure and thus optimize the utilization of stored fat, which ultimately limits the migration.

The muskrat, however, does not swim most frequently at the speed of its least cost of transport of 0.75 m/s. In this study, muskrats were observed to swim normally

at a mean velocity of 0.58 m/s. The discrepancy is probably due to fatigue-related anaerobiosis as suggested by the behaviors of animals swimming at high velocities. In addition, some individuals tended to show a limit in their $\dot{V}O_2$ between 0.6 and 0.75 m/s at a level approximately three times the resting $\dot{V}O_2$. These observations suggest that the muskrat reached an aerobic capacity limit at the higher velocities when increased power input to generate thrust may be supplied by anaerobic metabolism. This is common in vertebrates. Brett (1964) showed that salmon swimming above four body lengths per second peak in their aerobic metabolism and go into oxygen debt. Webb (1971) believed that moderate activity, such as cruising in trout, was not associated with any significant level of anaerobic

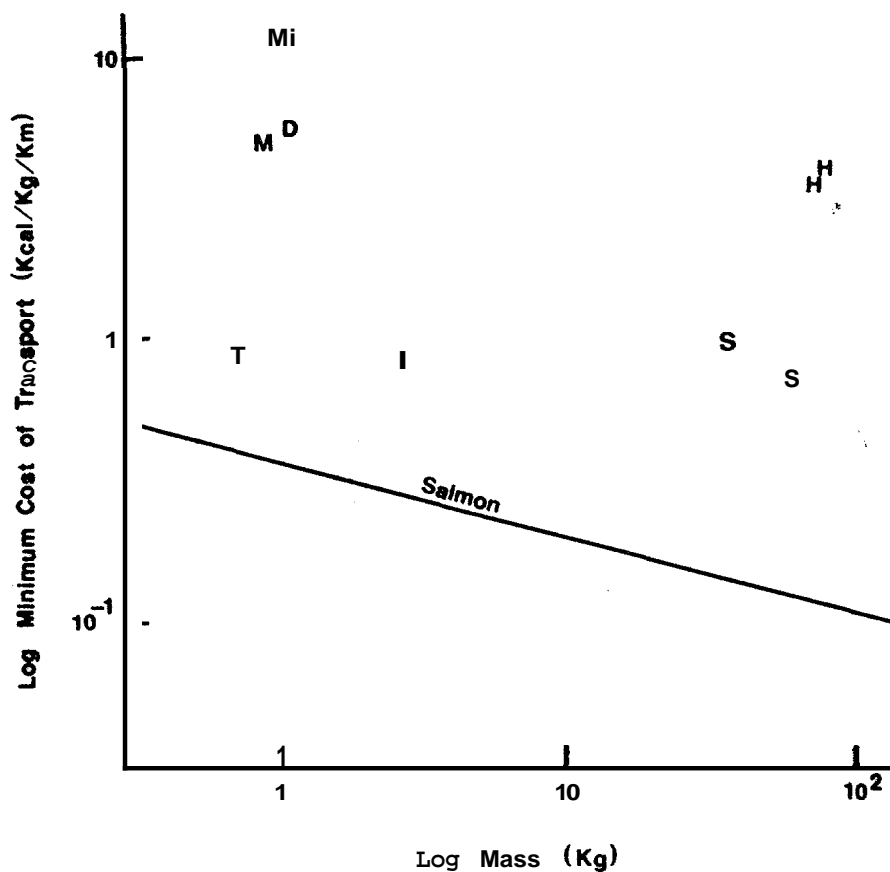


FIG. 5.— Comparison of the minimum cost of transport over the range of body masses. The symbols represented are the duck, *D*; humans, *H*; marine iguana, *I*; muskrat, *M*; mink, *Mi*; sea lions, *S*; and sea turtle, *T*. The solid line is the minimum cost of transport for the salmon over the entire range of body masses.

metabolism. However, when velocities of the trout reached 80% of the critical speed, he felt that the anaerobic energy comprised a significant amount of the total energy expenditure. Swimming horses showing a linear increase of oxygen consumption with increasing work effort demonstrated no plateau in $\dot{V}O_2$, even though they utilized a large anaerobic component (Thomas et al. 1980). Terrestrial locomotion by young lions has demonstrated that blood lactate increases with increasing speed at submaximal levels (Chassin et al. 1976).

In the muskrat, small amounts of lactic acid probably accumulated at submaximal levels, most likely due to the lag of the circulatory system in supplying the active tissues at the initiation of activity (DiPrampo, Cerretelli, and Piiper 1970; Margaria 1972).

Hydrodynamic arguments suggest there would be a sudden increase in drag at the speeds at which anaerobic metabolism is believed to occur. Such an increase in the drag on the muskrat would be due to the interference between the diverging surface waves formed at the bow and stern of the animal. Constructive interference of the diverging waves as the muskrat approaches its "hull speed" (Prange and Schmidt-Nielsen 1970) would situate the animal in a wave trough equal to the body length. At velocities greater than the hull

speed, the drag would increase asymptotically, thus requiring a greater energetic expenditure. The major cost of propulsion for ships is the energy lost in the production of surface waves (Schmidt-Nielsen 1972).

For the muskrat with a mean waterline length of 0.25 m, the hull speed would be 0.63 m/s (Prange and Schmidt-Nielsen 1970), which was the velocity above which swimming muskrats showed fatigue and probably anaerobiosis. In addition, the hull speed of the muskrat was close to the mean routine swimming velocity for unrestricted animals. Prange and Schmidt-Nielsen (1970) found that the predicted hull speed of ducks occurred at the maximum sustained swimming velocity.

For the muskrat which maintains a semiaquatic existence, the energetic demands of paddling locomotion are large in comparison with swimming modes which maintain a nearly continuous thrust force over the entire propulsive cycle. In addition, the large energy requirement for paddling at the air-water interface would be mandated by the increased drag due to the formation of surface waves. However, the muskrat may reduce its energetic expenditure by swimming at speeds which would efficiently utilize the power input without incurring increased wave drag and subsequent increased metabolism by anaerobiosis.

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