FUNCTION OF THE COMPRESSED TAIL OF SURFACE SWIMMING MUSKRATS (*ONDATRA ZIBETHICUS*)

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ABSTRACT.—The movement and function of the laterally flattened tail of surface swimming muskrats (Ondutra *zibethicus*) were studied by forcing individual animals to swim against a constant water flow of velocity ranging from 0.2 to 0.75m/s. Simultaneous lateral and ventral views of the swimming muskrats were filmed. During swimming the tail produces a series of traveling waves that moved posteriorly with increasing amplitude at a velocity faster than the muskrat was swimming. The characteristics of the traveling waves were analogous to the body and tail undulations observed in the swimming of anguilliform fish. Calculations showed that the tail provided a maximum of 1.4% of the total thrust power necessary to propel the muskrat at 0.75m/s. Amputation of a muskrat tail causes the animal to yaw while swimming. The compressed tail of the muskrat may allow for the effective generation of thrust in surface swimming by producing small amounts of thrust in conjunction with the prevention of yaw.

The laterally flattened or compressed **tail** of the semi-aquatic muskrat (*Ondatra zibethicus*) has been described in regard to function for thermoregulation (Johansen, 1962; Fish, 1979) and locomotion (Mizelle, 1935). The most controversial aspect of the function of the muskrat tail concerns its use during swimming. Dugmore (1914) and Johnson (1925) contended that swimming muskrats use their tail as a scull to produce thrust. Arthur (1931) stated that the tail is only used as a scull when a muskrat is swimming against a current, whereas Mizelle (1935) reported that sculling movements of the tail were only observed during submerged swimming. Other investigators, however, saw no apparent motion of the tail during swimming and considered the tail to have no function (Howell, 1930; Kirkwood, 1931; Svihla and Svihla, 1931).

In most of the above cases, swimming by muskrats and use of the tail were reported in little more than an anecdotal manner and they did not determine the exact nature of the tail movement or compute the thrust power generated by the tail, if acting as a scull. I studied the role of the compressed tail during surface swimming by using kinematic analysis and hydrodynamics. This allowed me to evaluate previous hypotheses concerning the function of the muskrat tail.

METHODS AND MATERIALS

Experimental animals.—Ten muskrats (nine male and one female) were livetrapped in Ingham Co., 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. The animals were maintained 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.*—Observations on swimming were conducted in a recirculating water channel, based on a design by Vogel and LaBarbera (1978). A working section was provided in the channel in which a single muskrat was allowed to swim without interference. 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, which removed turbulence from the water flow. The downstream end of the working section was bounded with a low voltage electrified grid that 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 was disconnected to the grid when the muskrat maintained steady swimming. During high speed trials, a removable wall was placed in the working section to constrict its cross-sectional area and thus increase the water velocity. Plexiglas windows were installed in the side and floor of the working section to allow for observation and filming. The windows were marked with a grid of 2 cm squares to act as reference points. To film simultaneous lateral and ventral views of the muskrat, a mirror was positioned under the floor at a 45" angle to reflect the ventral image of
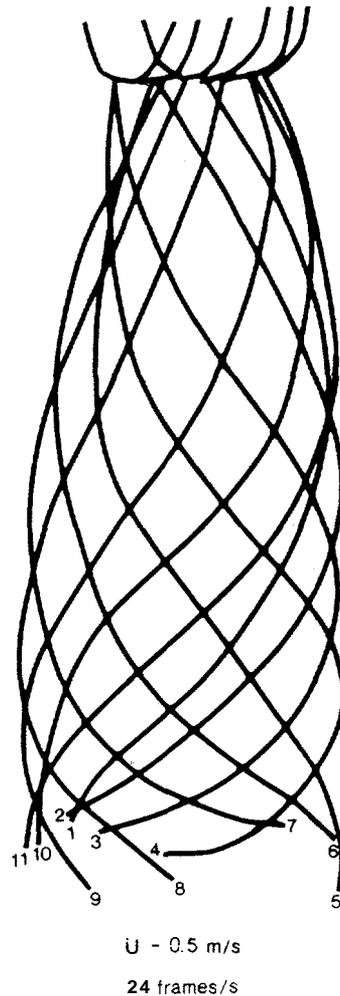
U - 0.5 m/s

24 frames/s

FIG. 1.— Sequential tracings of the tail for a complete propulsive cycle of a muskrat swimming at 0.5 m/ s. Frames of film are indicated for each tail position.

the animal toward the camera. The top of the working section was formed by a Plexiglas metabolic chamber, which was used for the measurement of oxygen consumption in another aspect of the study (Fish, 1980).

Water velocity (U) was controlled by either a Sears 25 electric fishing motor (Model No. 217.590091) or a Mercury electric outboard moter (Model No. 10019) situated in the return channel. 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. Because muskrats swimming against the water current appeared to remain stationary relative to their position in the water channel, the water velocity and swimming speed were assumed to be equivalent.

Kinematic *analysis.*—Muskrats were tested at velocities ranging from 0.2 to 0.75 m/s. There was no order to the sequence of test velocities for each muskrat. Each muskrat was forced to swim steadily at a given test velocity for a period of 10 to 30 min.

Individual muskrats swimming over the range of test velocities were filmed **at** 24 and 50 frames/s with a Bolex H-16 SB motion picture camera equipped with a Kern Vario-Switar 100 POE zoom lens (1:1.9, f = 16—100 mm) using 16-mm motion picture film (Kodak 4-X Reversal film 7277, **ASA** 320). The camera was driven with an ESM 13 V DC motor. Lighting was supplied by three 250 W flood lamps surrounding
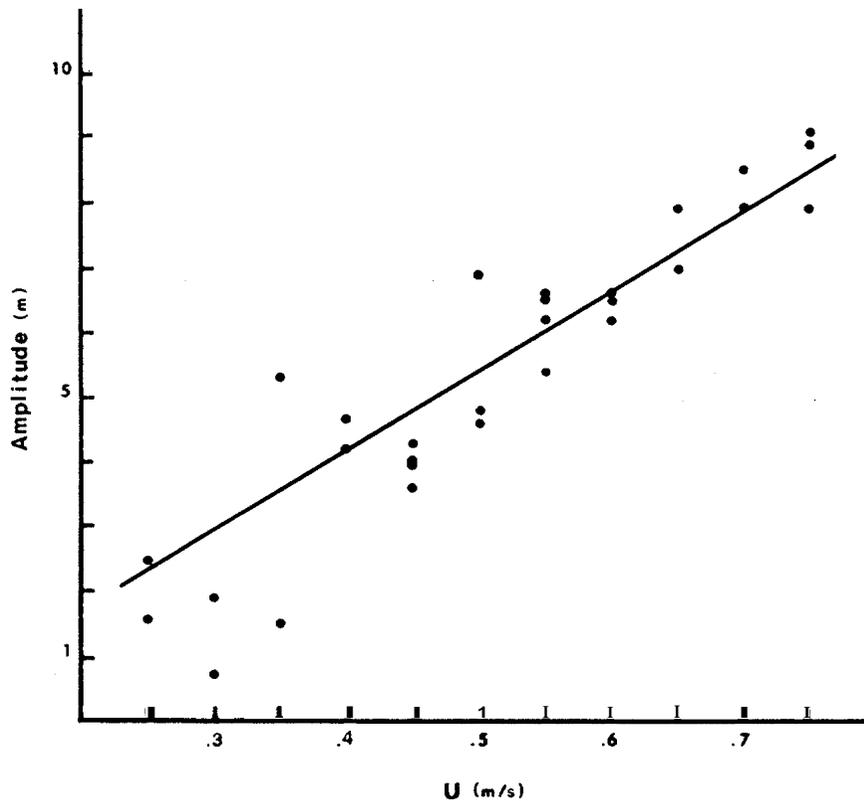
FIG. 2.—Plot of the amplitude at the tip of the muskrat tail as a function of the swimming velocity, U. The least-squares regression equation was computed as: Amplitude $= 12.19U - 0.66$.

the working section. For analysis, sequential tracings of the propulsive appendages were made from the films using a stop-action projector (Lafayette Instrument *Co.*, Model 00100).

RESULTS

Observations on muskrats swimming at **0.2** m/s were omitted from the analysis, because constant propulsive motions by the animals were not required to maintain position against the water **flow.** From **0.25** to 0.75, the muskrats swam at the water surface using their legs as described by Mizelle (**1935**). The forelegs were held under the chin, while the hind feet moved in a paddling mode by alternating strokes. The paddling mode was divided into power and recover phases (Fish, **1980**). 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 (Fig. **1**). At least one-half to one full wavelength was observed in the tail. Amplitude increased along the tail and reached a maximum at the tip. These traveling waves were analogous to the tail and body movements seen **in** the swimming of anguilliform fish (Breder, **1926**).

The frequency of the generation of traveling waves remained constant over the range of test velocities at a mean of **2.35 ± 0.03 (SE)** Hz. The amplitude of the tail increased linearly with increasing **U** (Fig. **2**). The regression was found to be highly significant ($P < 0.001$; d.f. = **28**; r = 0.85). This relationship differs from that in fish, where the amplitude is constant as swimming velocity increases (Bainbridge, **1958**; Hunter and Zweifel, **1971**).

The motion of the tail appeared to be synchronized with the hindfoot stroke. As one hindfoot

TABLE 1.—Mean($\pm$ *SE*) tail wave parameters of swimming muskrats.

U (m/s)	Frequency (cycles/s)	Amplitude (m)	W (m/s)	V (m/s)	w (m/s)	P_T ($\times 10^{-4}$ W)
0.25	2.48 (0.30)	0021 (0.005)	0.11 (0.01)	0.43 (0.06)	0.05 (0.01)	2.15 (0.75)
0.3	2.20 (0.58)	0.075 (0.005)	0.18 (0.07)	0.47 (0.03)	0.07 (0.03)	7.55 (5.25)
0.35	2.40 (0.23)	0.034 (0.019)	0.17 (0.08)	0.51 (0.02)	0.05 (0.02)	6.75 (5.05)
0.4	2.34 (0.16)	0.045 (0.001)	0.23 (0.02)	0.55 (0.01)	0.06 (0.01)	10.85 (2.85)
0.45	2.46 (0.12)	0.040 (0.001)	0.22 (0.02)	0.59 (0.01)	0.05 (0.01)	9.58 (1.67)
0.5	2.34 (0.18)	0.054 (0.007)	0.28 (0.02)	0.62 (0.03)	0.05 (0.01)	14.03 (4.28)
0.55	2.26 (0.05)	0.062 (0.003)	0.31 (0.01)	0.69 (0.02)	0.06 (0.01)	20.50 (2.86)
0.6	2.43 (0.11)	0.064 (0.001)	0.35 (0.01)	0.76 (0.01)	0.07 (0.00)	28.13 (1.07)
0.65	2.09 (0.09)	0.075 (0.005)	0.35 (0.04)	0.79 (0.01)	0.06 (0.01)	27.70 (6.40)
0.7	2.53 (0.25)	0.081 (0.004)	0.45 (0.02)	0.89 (0.02)	0.10 (0.00)	58.00 (2.30)
0.75	2.34 (0.04)	0.086 (0.004)	0.45 (0.02)	1.01 (0.03)	0.12 (0.01)	71.80 (7.13)

was accelerated posteriorly, initiating the power phase of the stroke cycle, the base of the tail was swept to the opposite side of the body, thus generating the traveling wave. The paddling frequency was found to remain constant at **2.5** $\pm$ **0.06** (SE) **Hz** over the range of swimming velocities. However, the frequencies of the tail and hindfeet were significantly different (a paired t-test, d.f. $= 28; P < 0.001$). This difference was probably due **to** the independent estimation of both frequencies from film analysis for each trial.

DISCUSSION

Howell (**1930**) reviewed the morphology and function of the tail in various aquatic mammals. A number of semi-aquatic representatives of the orders Insectivora and Rodentia possess a laterally compressed tail. The depth of the tail is often increased by either a fleshy keel (e.g., *Ondatra, Potomogale, Desmana*) or a keel of stiff hairs (e.g., *Neomys, Nectogale*). The function of such tails in aquatic locmotion has been debated, especially in the case of the muskrat. My results showed that the compressed tail moves in a wavelike manner. This motion was characterized by the generation of traveling waves with more than one-half wavelength within the tail (Breder, **1926**). In fish, the wave is produced through serial contraction of myomeres (Grillner, **1974**). For the muskrat, long tendons inset along the length of the tail and assist in lateral flexion. **To** produce the traveling wave pattern observed in swimming, the tail probably acts **as** a hybrid oscillator as proposed by Blight (**1977**), where the tail is stiff at the base and flexible toward the tip. Thus the wave sequence is produced by the resistance of the water against the sides of the tail as it is muscularly flexed.

Since muskrat tail movements are similar in character to the propulsive undulations of fish, pre-existing hydrodynamics models for the calculation of thrust and power for fish can be used to determine whether the muskrat tail acts as a scull. A simplified bulk momentum version of Lighthill's slender body model (Lighthill, **1969**; Webb, **1978**) was employed to determine the thrust power produced by the muskrat tail. The mean thrust power of the tail in watts, P_T, is the power output generated by the tail to propel the animal forward. P_T is calculated as:

$$P_T = mw\,UW - \tfrac{1}{2}mw^2U, \tag{1}$$

where m is the virtual mass per unit length, *w* is the relative velocity of the tail, and **W** is the tail trailing edge lateral velocity. The virtual mass per unit represents the relatively large mass of fluid accelerated by the tail (Webb, **1975**) and is given as:

$$m = k_T\rho(d_T{}^2/4), \tag{2}$$

where k_T **is** a constant equal to **1.0** (Lighthill, 1970), ρ is the density of water equal to 1,000 kg/m^3, and d_T is the maximum depth of the tail given as a mean value of **1.64** $\pm$ 0.13 (SE) cm from specimens used in this study. An average value of m was therefore computed on **0.21** kg/
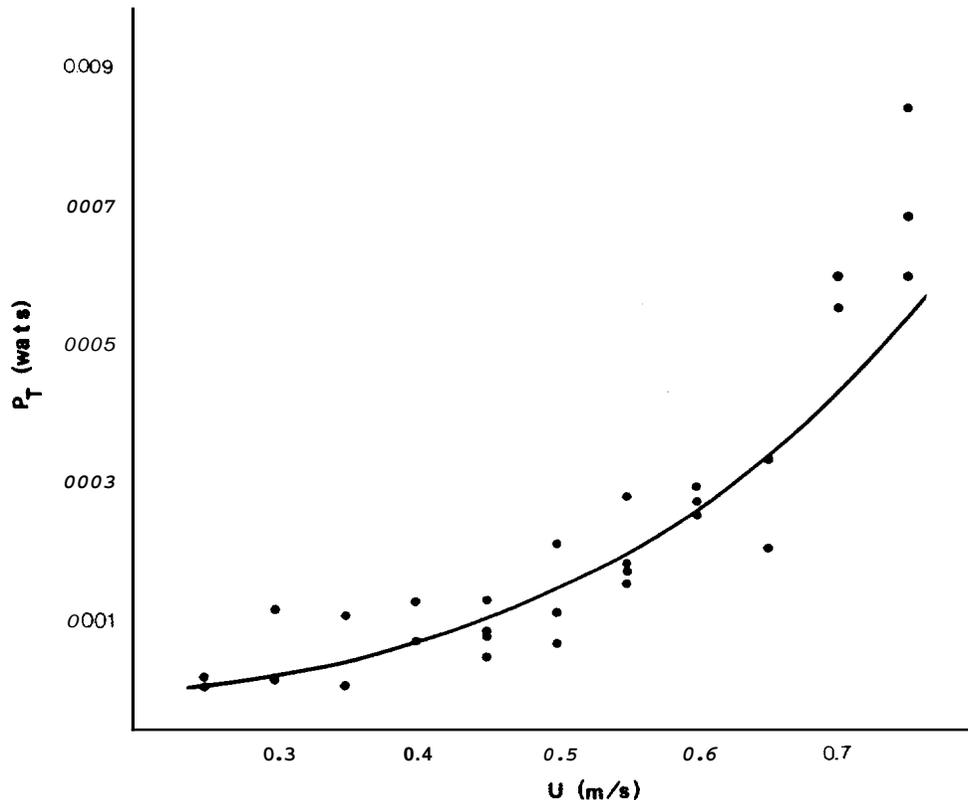
FIG. 3.—The thrust power generated by the muskrat tail, P_T, as a function of the swimming velocity, U. The least-squares regression equation was computed as: $P_T = 0.01U^{3.01}$.

m. This value is probably a slight over-estimate due to the tapering effect of the tail. The relative velocity of the tail was calculated from:

$$w = W(V - U/V), \tag{3}$$

where V **is** the backward velocity of the propulsive wave. The values for w are only approximations, since the water velocity, U, passing the tail was probably modified by the turbulence in the wake **of** the body and hindfeet. The mean values for each wave parameter at each U are presented in Table **1.**

The thrust power, P_T, was found to increase curvilinearly with increasing **U** and was significant at $P < 0.001$ (d.f. $= 27$; $r = 0.89$; Fig. **3).** The thrust power computed from the slender body model represented **67–89%**of the total power generated by the tail. The remainder of the total power is the kinetic energy lost to the wake in the production of turbulence. For the muskrat, the kinetic energy lost **is** probably an underestimate, since the tail undulations of the surface swimming muskrat lose energy in the production of both turbulence and waves. Energy loss by the generation of surface waves is the major cost of propulsion for ships (Schmidt-Nielsen. **1972). Because** the Lighthill model was designed for submerged undulatory locomotion, a greater percentage of the total power than calculated is probably lost in generating a wake.

The thrust power generated by lateral undulations of the tail was maximum at only **1.4%**of the total power required to propel the muskrat at **0.75** m/s (Fish, **1980).** The proportion of thrust generated by the tail appears far too small in comparison to the total energy requirements

to be significant. What then is the function of the compressed tail in the muskrat? For a well insulated endothermic homeotherm such as the muskrat, a compressed tail could give a high surface-to-volume ratio. The tail could act as an effective thermoregulatory device for the control of whole-body insulation (Fish, **1979).** However, terrestrial mammals do not possess unfurred, compressed tails for thermoregulation: it therefore seems unlikely that compressed tails in semi-aquatic mammals have evolved solely in response to thermoregulatory needs, and that a hydro-dynamic explanation may be more appropriate.

Webb **(1973)** suggested that the deep caudal fin found in most fish has evolved for high acceleration and high speed maneuverability. Because muskrats in the present investigation were only allowed to swim in a straight path, it was impossible to judge whether they used their tails for maneuverability. Acceleration was evaluated by examining fast-start performance. An electric shock stimulus was applied to a single resting muskrat over ten trials. The response of the muskrat was filmed at **50** frames/s. When shocked, the muskrat vertically flexed the posterior part of its body and tail at approximately 90° to the horizontal. Upon extension of the body, the hindfeet were accelerated posteriorly in unison with only a slight lag by one of the feet. This action rapidly accelerated the muskrat forward. At this time the tail, although showing a large lateral displacement, was ventrally flexed until the body was totally extended and the paddling cycle had resumed.

In these trials, the tail did not appear to function in generating increased thrust during rapid starts. However, a dorso-ventrally flattened or depressed tail could effectively generate thrust for acceleration through rapid flexion and extension of the body. For mammals such as otters, sirenians, and cetaceans, which possess a depressed tail and swim by flexion and extension of the body (Parry, **1949;** Tarasoff et al., **1972;** Hartmann, 1979), the tail may function in this manner.

One muskrat that had its taii surgically removed appeared to accelerate more slowly than animals with tails. At the higher test velocities slight yawing motions were visible. Increased yaw impedes propulsion by increasing the resistance to forward movement. These yawing motions were hypothesized to be the direct result of the alternating strokes by the hindfeet in the paddling mode. Due to the imbalance of forces from the recovery and power phases of the stroke cycle, a torque should develop about the center of the pelvic region resulting in rotation of the head toward the power phase side. In animals with tails which are moved synchronously with the hindfoot stroke, the base of the tail moves to the side opposite the hindfoot which is initiating the power phase. Lateral forces generated by the tail would then counterbalance the yawing *so* that the muskrat would present a more streamlined frontal view to the water flow.

Yawing would also be kept to a minimum due to the morphology of the muskrat. The vertical orientation of the hindfeet for paddling provides a small moment arm in the horizontal plane from the center of the pelvis, so that the torque would be reduced. In addition, the paddle propulsor *is* situated at the posterior end of the body providing a large inertial mass to oppose the lateral forces creating yaw, similar to deep bodied fish (Lighthill, **1969).** My results suggest that the compressed tail in muskrats functions to assist in the effective generation of thrust. This is accomplished through lateral undulations which generate a small thrust in conjunction with reduced drag by preventing yaw.

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