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## Kinematics of Undulatory Swimming in the American Alligator

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Five juvenile alligators (*Alligator mississippiensis*) swam individually in a water channel at flow velocities from 13 to 95 cm/s by lateral undulations of the tail. Motion analysis of cine films revealed that the alligators swam by the generation of travelling waves initiating in the pelvic region. The wave pattern resembled undulatory modes utilized by fish. The posterior and lateral velocities of the travelling wave increased linearly with increased length-specific swimming velocity. The amplitude of the tail wave remained constant over the range of swimming velocities while frequency varied. The kinematics and propulsive morphology of the swimming juvenile alligators indicated a low performance mode of life. This is correlated with the prey-capture techniques of crocodilians.

THE American alligator, *Alligator mississippiensis*, is a semi-aquatic crocodilian which inhabits the waterways of the southeastern United States. Despite this organism's phylogenetic and commercial importance, our knowledge of the dynamics of swimming in the alli-

gator is poorly understood. Manter (1940) provided the only analysis to date of the swimming of an alligator. He reported, based on the movements of a single specimen, that the lateral undulations of the tail and body of the alligator were analogous to anguilliform propulsion. Lighthill (1969) stated that the alligator swam in an essentially carangiform mode and Seymour (1982) reported that sculling by the tail was used for propulsion.

My purpose was to detail the kinematics of the propulsive waves generated by swimming juvenile alligators. This study allows comparisons with analogous propulsive modes exhibited by previously studied aquatic vertebrates. Such comparisons might elucidate the habits of the alligator in relation to its aquatic locomotion.

#### MATERIALS AND METHODS

*Experimental animals.*—Five juvenile alligators were obtained from the Rockefeller Wildlife Refuge in Grand Chenier, Louisiana. The alligators were hatched at the refuge in Oct. and Nov. 1981 and raised in enclosures (Joanen and McNease, 1979). The alligators were 4 to 5 months old at the start of testing. During the experimental period, which lasted for three months, the alligators were maintained indoors on the campus of West Chester University. The five alligators were kept together in a 1.22 × 0.88 m enclosure. The enclosure included an artificial pond of dimensions 0.86 × 0.7 × 0.2 m, which allowed for swimming. A black slate platform for basking was provided, for which a lamp with a 100 W lightbulb was supplied. The ambient air temperature was maintained at approximately 22 C and the light regime was constant. Since maximal growth rates were not desired, the alligators were fed weekly on a diet of tuna and chicken (Star-Kist Foods). The average weight and length of the alligators over the experimental period were 259.1 g and 46.7 cm, respectively. The average growth rates for the five alligators were 0.1 cm/day and 1.4 gm/day.

*Water channel.*—Experiments on swimming were conducted in a recirculating water channel, based on a design by Vogel and LaBarbera (1978). A test section of the dimensions 87 × 29 × 19 cm was provided in which a single alligator was allowed to swim without interference. The upstream end of the working section was bounded by a plastic grid of 2.5 cm squares

which was 2.5 cm wide, and removed major turbulence from the water flow. The downstream end of the test section was bounded with hardware cloth. The top of the test section was formed by a Plexiglas box with air holes drilled in the sides for gaseous exchange.

Water velocity ( $U$ ) was controlled with a Mercury electric outboard motor (Model 10019) situated in the return channel located beneath the working section. 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 within the test section in an area where the alligators normally swam. Alligators swimming against the water current appeared to remain stationary relative to their position in the water channel. Thus, water velocity and swimming speed were assumed to be equivalent.

*Kinematic analysis.*—The alligators were tested at velocities ranging from 13 to 95 cm/s (0.27–1.82 body lengths/s). There was no sequence order of the test velocities for each alligator. The alligators either swam spontaneously in response to the water current or were induced to swim by prodding the tail. The animals swam for periods of 5 to 20 min. The length of the swimming period was determined by the willingness of the animal to swim steadily or the apparent onset of fatigue. The water temperature was maintained between 24 and 26 C.

Plexiglas windows were installed in the side and floor of the test section to allow observation and filming. To film simultaneous lateral and ventral views of the alligator, a mirror was positioned under the floor at a 45° angle to reflect the ventral image of the animal toward the camera.

Individual alligators swimming over the range of velocities were filmed at 65 frames/s with a Bolex H-16 reflex cinecamera equipped with a Kern Vario-Switar 100 POE zoom lens (1:1.9,  $f = 16$ –100 mm) using 16 mm film (Kodak Tri-X Reversal film 7278, ASA 160). Lighting was supplied by a bank of four 500 W photoflood lamps above the test section. For analysis of the films, frame-by-frame tracings were made of the sequential positions of the body midline using a stop-action projector (Lafayette Instrument Co., Model 00100). Data were collected on the kinematics of the propulsive tail movements and posture of the body.

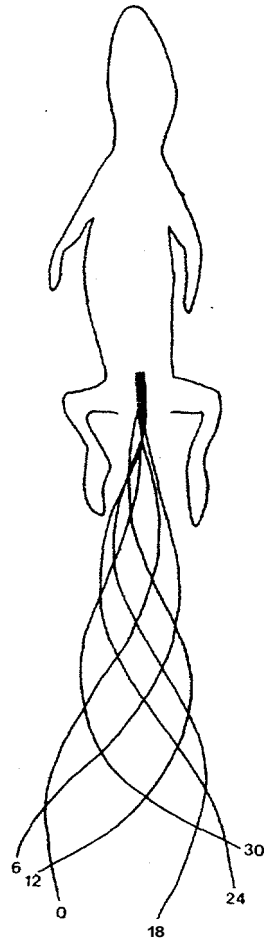


Fig. 1. Sequential tracings of the tail for a complete propulsive cycle of an alligator swimming at 27 cm/s. Frames of film are indicated for each tail position. Only a single tracing was made of the body.

*Statistical procedures.*—A total of 20 trials were made for the alligators. In order to perform the statistical analyses for the various data sets, trials on the alligators were assumed to be independent of one another, since tests at each velocity were performed separately. Variation about means was expressed as  $\pm$  one standard error (SE). Regression lines were computed with the least squares regression method. Since the size of the alligators varied both between and within individuals over the test period, swimming velocities were standardized as the length-specific velocity expressed as  $U/L$  in units of body lengths/s.

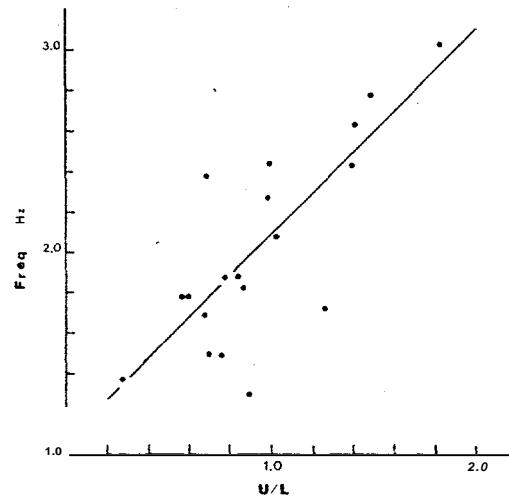


Fig. 2. Plot of frequency in Hz against the length-specific swimming velocity,  $U/L$ , in body lengths/s. The regression is: frequency =  $1.03 U/L + 1.07$ .

#### RESULTS AND DISCUSSION

During surface swimming, the juvenile alligators swam with just the dorsal surface of the head, including the nose, above the water surface. The submerged body was inclined at a mean angle of  $8.6^\circ \pm 0.9$ , so that the midpoint of the body and tail was submerged to a mean depth of  $1.6 \pm 0.1$  times the body depth. During steady swimming, the legs were adducted against the body and tail with the plantar surfaces of the feet directed medially. The legs were moved only for maneuvering and stability.

The main propulsive effector of the surface-swimming alligator was the laterally compressed tail. Travelling waves in the tail appeared to be initiated in the pelvic region at the base of the tail (Fig. 1). The waves moved posteriorly down the length of the tail faster than the animal was swimming. The amplitude ( $A$ ) of the wave increased steadily along the tail, spreading from the pelvic region at an angle of  $13^\circ$ , and reaching a maximum at the tail tip. At least one-half to one full wavelength ( $\lambda$ ) occurred in the tail at any instant. Over the tail length, the wave did not resemble a truly sinusoidal oscillation. The  $\lambda$  decreased toward the tip of the tail. This is due to the posteriorly increasing amplitude for the travelling wave over an inextensible body (Webb, 1975). Lateral bending of the trunk and yawing movements of

the head also occurred during swimming. Lateral bending of the head and trunk were minimal in the cervical and pelvic regions of the body.

Such a wave pattern is analogous to the anguilliform mode of swimming exhibited in certain fish (Breder, 1926; Webb, 1975). However, in the alligator the propulsive waves are confined to the tail. The specific wavelength expressed as the ratio,  $\lambda/L$ , and the specific amplitude expressed as  $A/L$  were 0.57 and 0.24, respectively, indicating the use of the anguilliform swimming mode by the alligator (Webb, 1975). Previously, Manter (1940) had similarly identified the swimming mode from the swimming sequence of one immature alligator moving at a single velocity. Manter (1940) found the swimming of the alligator to differ from the eel (Gray, 1933) by the narrow range of flexion of the trunk.

Over the range of swimming velocities, the amplitude at the tip of the alligator tail was nearly constant at  $11.0 \pm 0.3$  cm. Likewise, the wavelength of the travelling wave was constant at  $26.4 \pm 0.5$  cm for all swimming velocities. However, the frequency of the propulsive cycle was linear with swimming velocity (Fig. 2); the regression was highly significant ( $P < 0.001$ ;  $df = 18$ ;  $r = 0.76$ ).

The relationships of amplitude and frequency to  $U$  found for alligators were similar to corresponding results exhibited by piscine undulators which employ frequency modulation (Bainbridge, 1958; Hunter and Zweifel, 1971; Videler, 1981). The average lateral ( $W$ ) and longitudinal ( $V$ ) velocities of the travelling wave both increased linearly with increasing size-specific velocity,  $U/L$ ; the regressions ( $W = 0.32 U/L + 0.18$ ;  $V = 0.44 U/L + 0.17$ ) were highly significant ( $P < 0.001$ ;  $df = 18$ ;  $r = 0.83$  and  $0.86$ , respectively).

The relationship between  $V$  and  $U$  is important in the efficient generation of thrust and use of energy. For uniform swimming velocity,  $V$  must be greater than  $U$  for the alligator to generate thrust. When  $V$  is large relative to  $U$ , greater energy loss occurs due to increased work done by the lateral water motion into the wake (Lighthill, 1970; Webb, 1978). As  $V$  declines toward  $U$ , less energy is shed in accelerating water laterally by the tail and propulsive efficiency increases (Webb, 1978).

The ratio  $U/V$  indicates the efficiency of undulatory propulsive systems. For the alligators in this study,  $U/V$  increased curvilinearly to-

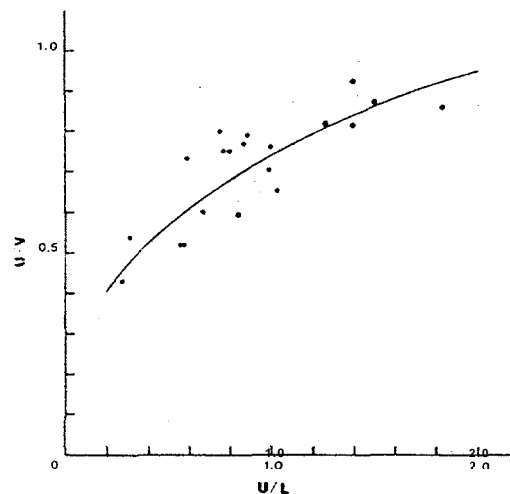


Fig. 3. Relationship between  $U/V$  and  $U/L$  exhibiting a curvilinear rise according to the equation  $U/V = 0.75 U/L^{0.35}$ . The regression, determined by logarithmic transformation, was significant ( $P < 0.001$ ;  $df = 18$ ;  $r = 0.84$ ).

ward an asymptote over the range of the size-specific velocity (Fig. 3). As in fish (Webb, 1978), propulsive efficiency of the alligator apparently increases with swimming velocity. However, the shape of the curve suggests that the alligators were approaching a limit to their swimming capacity, where the travelling waves could no longer be generated at a high enough rate for  $V$  to remain greater than  $U$ .

Decreased swimming capacity may be compounded further by the morphology of the alligator. The head and trunk have a depressed profile, which encourages yawing, and, with the numerous scaly protuberances over the entire body, may increase energy loss through increased drag. The mass of water (virtual mass) affected by tapering tails, such as that in the alligator, progressively decreases toward the tip (Lighthill, 1970; Webb, 1975). The caudal segments of tapering tails can contribute little thrust compared to the anterior segments and may add to frictional drag and kinetic energy loss to the wake (Webb, 1978).

Energy losses to the wake may be reduced partially by the presence of high dorsal crests of epidermal scales on the tail. Additionally, the increasing amplitude along the tail length in this study and by Manter (1940) could possibly increase  $W$  toward the tail tip, thereby compensating for the reduced virtual mass. However,

such compensatory movements, while increasing thrust, would simultaneously increase energy loss to the wake (Lighthill, 1971).

The propulsive morphology of the alligator and utilizations of the anguilliform mode of swimming are characteristic of organisms adapted for low swimming speed and low efficiency (Lindsey, 1978), and low acceleration performance (Webb, 1973, 1977). Such a mode of life should be expressed in the behaviors employed in food capture by the alligator and other crocodilians of similar propulsive morphology. Observations on caimans (*Caiman crocodilus*) by Schaller and Crawshaw (1982) and crocodiles (*Crocodylus niloticus*) by Pooley and Gans (1976) support this contention. Caimans were reported to wait for fish to come into "snapping distance" or use their body and tail to herd fish toward their mouths (Schaller and Crawshaw, 1982). Pooley and Gans (1976) also observed similar low effort prey capture techniques in African crocodiles. For both species, ambush in conjunction with rapid lateral movements of the head were used over active pursuit. When lunging for prey, crocodiles and caimans combine the actions of the lateral undulations of the tail with the backward movement of the webbed feet (Pooley and Gans, 1976; Schaller and Crawshaw, 1982).

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