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THE KINEMATICS OF SWIMMING IN ANURAN LARVAE

By RICHARD J. WASSERSUG

Department of Anatomy, Dalhousie University, Halifax, Nova Scotia, Canada, B3H 4J1

AND KARIN von SECKENDORF HOFF

Department of Biology, Dalhousie University, Halifax, Nova Scotia, Canada, B3H 4J1

SUMMARY

The kinematics of swimming in tadpoles from four species of anurans (*Rana catesbeiana* Shaw, *Rana septentrionalis* Baird, *Rana clamitans* Latreille and *Bufo americanus* Holbrook) was studied using computer-assisted analysis of high speed ($\geqslant 200$ frames s^{-1}) ciné records.

1. Tadpoles exhibit the same positive, linear relationship between tail beat frequency and specific swimming speed commonly reported for sub-carangiform fishes.

2. Tadpoles show an increase in the maximum amplitude of the tail beat with increasing swimming speed up to approximately 4 lengths s^{-1}. Above 4 lengths s^{-1}, amplitude approaches an asymptote at approximately 25 % of length.

3. Tadpoles with relatively longer tails have lower specific amplitudes.

4. Froude efficiencies for tadpoles are similar to those reported for most subcarangiform fishes.

5. *Bufo* larvae tend to have higher specific maximum amplitude, higher tail beat frequencies, lower propeller efficiencies (at least at intermediate speeds) and substantially less axial musculature than do comparable-sized *Rana* larvae. These differences may relate to the fact that *Bufo* larvae are noxious to many potential predators and consequently need not rely solely on locomotion for defence.

6. Tadpoles exhibit larger amounts of lateral movement at the snout than do most adult fishes.

7. The point of least lateral movement during swimming in tadpoles is at the level of the semi-circular canals, as assumed in models on the evolution of the vertebrate inner ear.

8. Passive oscillation of anaesthetized and curarized tadpoles at the base of their tail produces normal kinematics in the rest of the tail. This supports the idea that muscular activity in the posterior, tapered portion of the tadpole tail does not serve a major role in thrust production during normal, straightforward swimming at constant velocity.

9. The angle of incidence and lateral velocity of the tail tip as it crosses the path of motion are not consistent with theoretical predictions of how thrust should be generated. The same parameters evaluated at the high point of the tail fin (approximately midtail) suggest that that portion of the tail generates thrust most effectively.

10. Ablation of the end of the tail in passively oscillated tadpoles confirms that the terminal portion of the tadpole tail serves to reduce excessive amplitude in the more anterior portion of the tail, where most thrust is generated.

11. The posterior portion of the tail is important in reducing turbulence around a tadpole. It may also function to produce thrust during irregular, intricate movements, such as swimming backwards.

12. Tadpoles are comparable to subcarangiform fishes of similar size in their maximum swimming speed and mechanical efficiency, despite the fact that they have much less axial musculature and lack the elaborate skeletal elements that stiffen the fins in fishes. The simple shape of the tadpole tail appears to allow these animals efficient locomotion over short distances and high manoeuvrability, while maintaining the potential for rapid morphological change at metamorphosis.

INTRODUCTION

Tadpoles are readily distinguishable from virtually all other living aquatic vertebrates by their globose body and long flexible, tapered tail. While much has been written on how the shapes and sizes of fishes relate to their locomotor behaviour, tadpole locomotion has been poorly studied. What has been said about locomotion in anuran larvae is largely anecdotal and even occasionally contradictory. Gray in his classic work, *Animal Locomotion* (1968), does not deal with anuran larvae at all. Neither does Webb (1984) in a recent synthetic article on body form and locomotion in aquatic vertebrates. Lighthill (1975) makes the blanket assertion that the amphibian larva 'has inherited anguilliform motion . . . from fish ancestors'. In contrast, both Affleck (1950) and Romer (1966) suggest that the locomotion of the early, heavily-armoured, relatively inflexible ostracoderm fishes was similar to that of tadpoles. In the absence of any measurements of either swimming efficiency or the neuronal control of locomotion Romer wrote (p. 22) that '. . . the locomotion of the oldest vertebrates must have been of the relatively ineffective and uncontrolled type seen in a frog tadpole'. Since Romer made that statement there has been one preliminary study (Hoff & Wassersug, 1985) showing that swimming in tadpoles may, in fact, be no less efficient than in modern teleostean fishes. Other recent studies on tadpole locomotion have dealt with stamina (Wassersug & Sperry, 1977; Wassersug & Feder, 1983; Quinn & Burggren, 1983), locomotion in unusual habitats (e.g. terrestrial locomotion, Oldham, 1977; sub-aerial and fossorial locomotion, Wassersug & Heyer, 1983) and the development of neuronal control in amphibian larvae (e.g. Blight, 1976, 1977; Kahn, Roberts & Kashin, 1982; Kahn & Roberts, 1982a,b,c; Soffe & Roberts, 1982; Soffe, Clarke & Roberts, 1983; Stehouwer & Farel, 1980). Controversies in this latter area exist – the absence of much rigorous data on the kinematics of tadpole locomotion exacerbates the problem of understanding the locomotor control mechanisms of these organisms.

In this paper we try to remedy this situation by investigating the basic kinematics of anuran larval locomotion. We examine tadpoles of several species that differ in size and shape. Our goals are: (1) to understand how the size and shape of tadpoles relate to their kinematics and (2) to compare the kinematics of swimming in tadpoles with that of fishes.

We do not explore either the kinetics or energetics of tadpole locomotion, in part because essential information on drag on tadpoles is lacking. We know of no studies on drag coefficients for tadpoles, although Wassersug & Heyer (1983) discuss whether or not certain tadpoles are streamlined based on their fineness ratios. Aleyev (1977, p. 28) states that tadpoles swim at Reynolds numbers (*Re*) greater than $5 \cdot 0 \times 10^3$. In the limited sample from the present study we document an *Re* range of $3 \cdot 5 \times 10^2$ to $3 \cdot 4 \times 10^4$. There is very little information on drag in this range, except for that on non-oscillating, inanimate objects.

Tadpoles of the four species we examined were chosen because they represent a large range in size and relative tail length for anuran larvae. *Rana catesbeiana* (bullfrog) larvae are quite large and have a relatively short tail (ranging from 58 to 62 % of total length). *Rana clamitans* (green frog) and *Rana septentrionalis* (mink frog) larvae are also large, but have proportionately longer tails (range 65–69 % of total length). Tadpoles of *Bufo americanus* (American toad) are smaller than the other three, but have body proportions similar to those of *Rana catesbeiana* (tail length equals 60 % of total body length).

The main kinematic parameters that we have selected for study are the classic ones – tail beat frequency and amplitude – analysed for fishes by Bainbridge over 25 years ago (1958). We also examined propeller efficiency and length of the propulsive wave. We have related these specifically to simple morphological features such as absolute body size, relative body proportions and the distribution of mass; and also, more generally, to the unique way of life of the anuran tadpole. For this first study we have concentrated on straightforward swimming at a constant velocity. Our analyses indicate that under these conditions not all of a tadpole's tail may be primarily involved in the generation of thrust. We thus report on a series of additional experimental manipulations designed to explore alternative roles that portions of a tadpole's tail may play in locomotion.

<center>MATERIALS AND METHODS</center>

Twenty-five tadpoles were filmed at 200 or 250 frames s^{-1} as they swam in either a flow tank, illustrated in Wassersug & Feder (1982) and following the design of Vogel & LaBarbera (1978), or a large open tank. The tanks contained O_2-saturated, aged, tap water at 22 ± 1 °C. Ciné recordings were made with a Locam (Redlake Corp., Campbell, California) high speed camera on 4X reversal film using a 50 mm macro lens approximately 1 m above the floor of the tanks. Illumination was provided by two 650 W incandescent lamps approximately 40 cm above the tank. Nine *R. catesbeiana* (total body length, L, ranges from $2 \cdot 9$–$9 \cdot 12$ cm), seven *R. septentrionalis* (L range $3 \cdot 5$–$6 \cdot 0$ cm), four *R. clamitans* (L range $3 \cdot 4$–$7 \cdot 1$ cm) and five *Bufo americanus* (L range $0 \cdot 96$–$3 \cdot 5$ cm) were used to film 40 sequences of normal swimming. All the tadpoles were between Gosner (1960) developmental stages 25 and 39; in this range

the forelimbs have not erupted and the hind limbs, which are small, are not used in propulsion (Wassersug & Sperry, 1977). The kinematics were examined using a Hewlett Packard film analysis system consisting of an HP9834A mini-computer and an HP9872A digitizer (Hewlett Packard Co., Palo Alto, California). The computer programmes used were modified versions of ones originally developed by J. Videler and his colleagues. The kinematic parameters were (calculated as in Videler & Wardle, 1978): forward velocity (U) in body lengths per second ($L s^{-1}$) measured at the snout; amplitude of the wave travelling down the tail (A) measured in body lengths (L); frequency of the tail beat (f) in beats per second (s^{-1}); wavelength (λ_b) of the wave travelling down the body, in body lengths (L); velocity of the travelling wave (V), in body lengths per second ($L s^{-1}$); lateral velocity of selected points along the body in $L s^{-1}$; and orientation of selected body segments to the path of forward motion (= angle of incidence), θ, in degrees. Froude efficiency (η), a derived measure of kinematic (propeller) efficiency, was also examined [$= 1 - 0.5(1 - U/V)$].

Precautions were taken to analyse only sequences of straightforward swimming at constant velocity. Straightness of the path of motion was assessed by linear regression on the path of the snout. For all sequences analysed the correlation coefficient, r, was greater than 0.95. Because tadpoles rarely swim steadily we were careful to select only those sequences that showed a total variation in velocity of less than ±0.25 times the mean velocity, and no net acceleration. All sequences were two or more tail beats and none were shorter than 0.25 s.

Amplitude of the tail beat was also examined in tadpoles with whole tails and tadpoles with portions of the tail ablated. These animals were anaesthetized with tricaine methylsulphonate (MS222; Sigma, St Louis, MO), curarized with intracardial injections of gallamine [1, 2, 3-tri (2-diethylaminoxy) benzene triethiodide; Flaxedil 100 Turbocurarine, Rhône-Poulenc, Montreal, Quebec). They were then mounted on a mechanical oscillator using a pin through the centre of the muscle mass and an additional stabilizing pin between the otic capsules attached to the bottom of the tank (Fig. 1). The rationale for this procedure is presented in the Results. Still photography and high-speed cinematography were both used to assess the amplitude of various points along the body for tadpoles in these oscillator preparations. In several oscillator preparations ink was injected into the water at the snout of the mounted animal. Photographs were then taken as the ink entrained around the animal and formed a wake.

Still photography was also used to examine the wake of normal tadpoles and tadpoles with partially ablated tails as they swam in a small aquarium containing a thin layer of milk along the bottom using the procedure of Rosen (1959). The animals used here normally swim along the bottom. Trails in the milk layer clearly showed the flow around and directly behind the tadpoles.

Muscle distribution was determined by dissection of preserved specimens.

<div align="center">RESULTS</div>

<div align="center">*Basic kinematics*</div>

Tail beat frequencies for all four species are plotted against swimming speed in Fig. 2. The highest absolute swimming speed that we recorded was 55 cm s^{-1}, while the
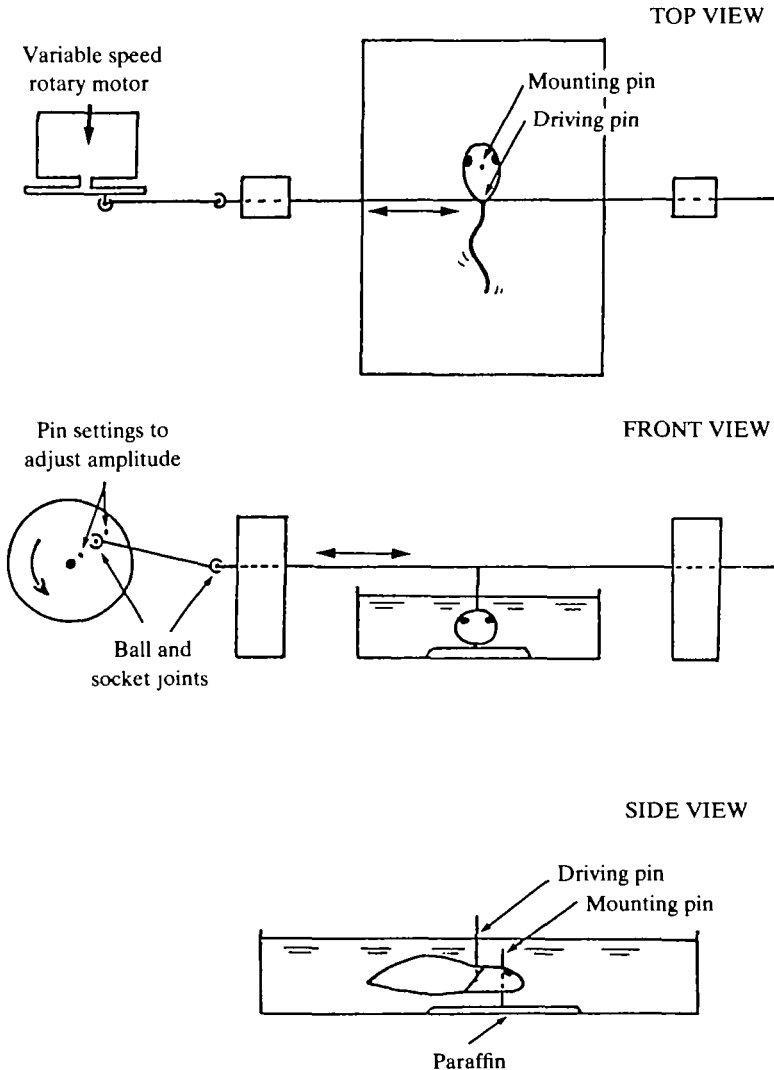
TOP VIEW

Fig. 1. Schematic drawings of apparatus used for passively oscillating anaesthetized and curarized tadpoles; three views.

highest specific swimming speed that we recorded was $11 \cdot 25 \, \text{L s}^{-1}$. The highest tail beat frequency was $16 \cdot 7 \, \text{s}^{-1}$. These values were recorded for a *Rana catesbeiana* larva of $4 \cdot 7$ cm total length.

The relationship of tail beat frequency to specific swimming speed is positive, linear and highly significant ($r = 0 \cdot 955$, $P < 0 \cdot 001$). A single regression line fits all species and is plotted on Fig.2. *Bufo* larvae show a slight tendency to have a higher tail beat frequency for any swimming speed than do the *Rana* larvae, but not significantly so (analysis of covariance, $F = 2 \cdot 1$, $P > 0 \cdot 1$).

Specific maximum amplitude, which occurs at the tail tip, is plotted against specific swimming speed for all species in Fig. 3. The highest amplitude recorded was 27 % of body length. This was for our smallest tadpole, a *Bufo* larva of $0 \cdot 96$ cm total length,
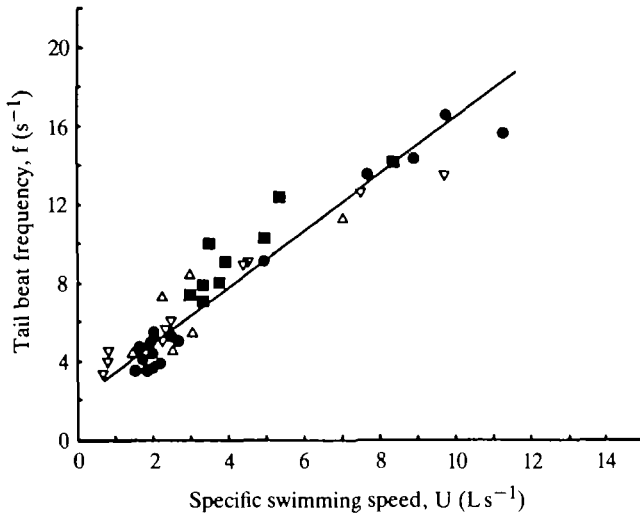
Fig. 2. Plot of tail beat frequency against specific swimming speed for larvae of all four species. In this and subsequent figures ● = *Rana catesbeiana*, △ = *Rana septentrionalis*, ▽ = *Rana clamitans*, and ■ = *Bufo americanus*. Total $N = 40$. The equation for the regression line is $f = 1·31U + 2·75$; $r = 0·955$, $P < 0·001$. L = body length.

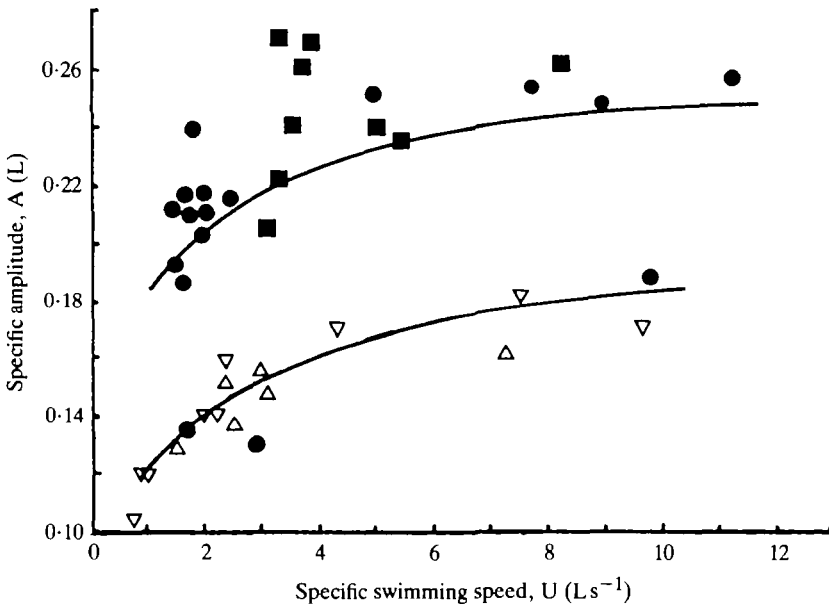Fig. 3. Plot of the maximum specific amplitude, recorded at the tail tip, against swimming speed. Symbols and sample size are the same as in Fig. 2. Two log curves are fitted to the data. The top curve is for the tadpoles with relatively shorter tails; i.e. *Rana catesbeiana* and *Bufo americanus*. The bottom curve is for species with proportionately longer tails, *R. septentrionalis* and *R. clamitans*. The equation for the top line is $\ln A = 0·135 \ln U - 1·68$; $r = 0·46$, $P < 0·05$. The equation for the lower one is $\ln A = 0·165 \ln U - 2·06$; $r = 0·77$, $P < 0·001$. L = body length.
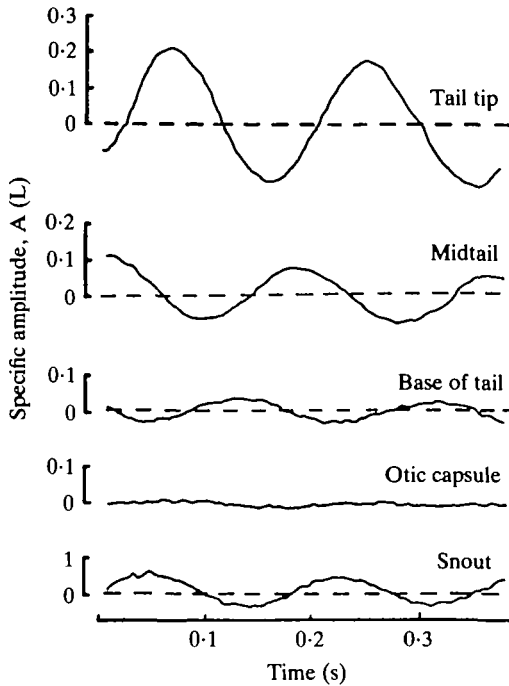
Fig. 4. Plots of the path of motion for selected midline points along the body of a *Rana catesbeiana* larva swimming at 2·4 L s⁻¹ from left to right. Two tail beat cycles are illustrated. Amplitudes are given on the vertical axis. The actual path of forward motion for the animal as a whole is most closely represented by the path of the point between the otic capsules (second trace from bottom). All other points on the body oscillate about this path and would overlie the trace for the otic capsules. For clarity, however, we have separated the traces by an amount proportional to the position of each point along the body from tip of snout to tip of tail. Note the high amplitude for the tip of the snout in this figure. L = body length.

swimming at approximately $3·5\,L\,s^{-1}$. The next three highest amplitudes are also from *Bufo* tadpoles. Two curves are presented for the data in Fig. 3. Both are logarithmic, and provide superior fits than either linear or hyperbolic curves. The higher line is for the larvae with relatively shorter tails, *B. americanus* and *R. catesbeiana*. The lower line is a fit for the longer-tailed forms, *R. clamitans* and *R. septentrionalis*. For both groups specific amplitude increases with swimming speed up to about $4\,L\,s^{-1}$ then remains constant. Both regression lines shown here are significant (top line: $r = 0·46$, $P < 0·05$; lower line: $r = 0·77$, $P < 0·001$) and are superior to a single line fit for these data. An analysis of covariance shows that the lines do not differ in slope, but they do differ in elevation. The mean specific amplitude for all longer-tailed larvae swimming above $4\,L\,s^{-1}$ is 0·17. The mean for the shorter-tailed forms in the same specific velocity range is 0·25. For swimming speeds of $1–12\,L\,s^{-1}$ the shorter-tailed forms have a specific amplitude approximately 30 % higher than the longer-tailed forms.

Three *R. catesbeiana* points are nearer the lower line than the higher line and account for the relatively low '*r*' value for the higher line. The two of these points with the lowest specific amplitudes are from our largest individual tadpoles. When specific amplitude is regressed on total length for all tadpoles that swam at specific velocities
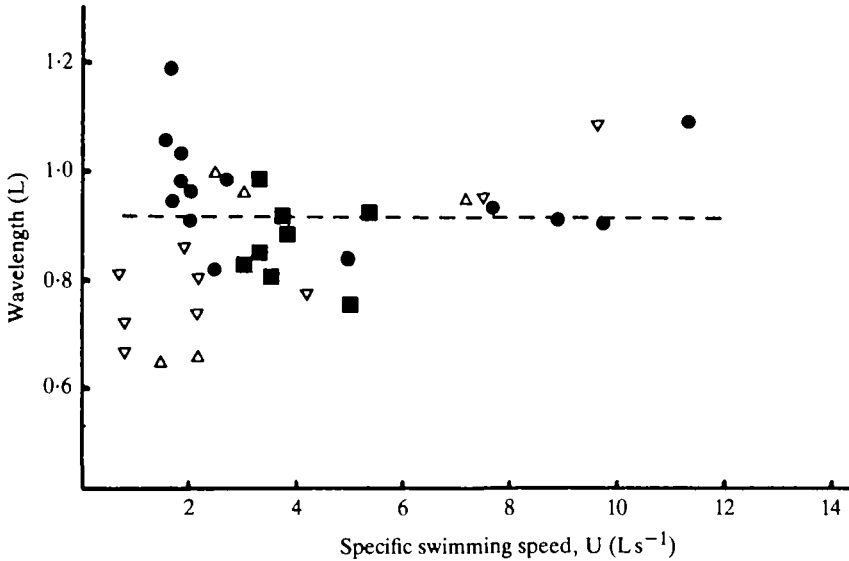
Fig. 5. Plot of the wavelength, λ_b, for the propulsive wave against specific swimming speed. Symbols and sample size as in Fig. 2. The overall mean wavelength is 87% ± 10 % L($\bar{X}$ ± s.e.), represented by the dotted line. The correlation of these variables is not significant for the pooled sample ($r = 0.22$; $P > 0.1$); however, there is a positive correlation of λ_b with U for the long-tailed tadpoles, *Rana septentrionalis* and *R. clamitans*. The equation for that relationship is $\lambda_b = 0.04U + 0.69$; $r = 0.65$; $P < 0.01$). L = body length.

greater than $3 \, L \, s^{-1}$, there is a significant, negative, linear correlation ($N = 13$ with no individual used more than once; $r = -0.62$, $P < 0.02$).

The two points on Fig. 3 for *R. catesbeiana* at the highest velocities are from the same individual but they differ greatly in maximum specific amplitude. There is some indication that they represent two different swimming modes.

Fig. 4 is a plot of the position of selected points along the body traced through two wave cycles for a *Rana catesbeiana* tadpole. These plots indicate that there is a substantial lateral movement of the snout of tadpoles as they swim in a straight line. This anterior oscillation, or yaw, was approximately 25 % of maximum amplitude observed in all the species and was found over most of the speed range. The point along the body that shows the least lateral displacement at any specific speed was 20 ± 2 % of the distance from the tip of the snout to the tip of the tail in the short-tailed forms and 16 ± 2 % in the long-tailed forms. This corresponds to a point between the middle and posterior edge of the otic capsules in all tadpoles examined. The deviation seen in Fig. 4 from a straight line for the otic capsule trace is easily within the range of our digitizing error.

Fig. 5 shows the relationship of the length of the propulsive wave to specific swimming speed. Wavelengths range from 55 to 119 % of the body length for swimming speed between $0.73 \, L \, s^{-1}$ and $11.25 \, L \, s^{-1}$. The mean wavelength ($\bar{X}$ ± s.e.) was 92 ± 26 % for the short-tailed forms and slightly less, i.e. 82 ± 15 %, for the longer-tailed forms. The overall mean was 87 ± 10 %. These values establish that our tadpoles swim in a subcarangiform mode (i.e. wavelength greater than 0.5 body lengths and amplitude increasing rapidly over the posterior one-third of the body), if one follows definitions in the literature for swimming modes based on the length of the propulsive
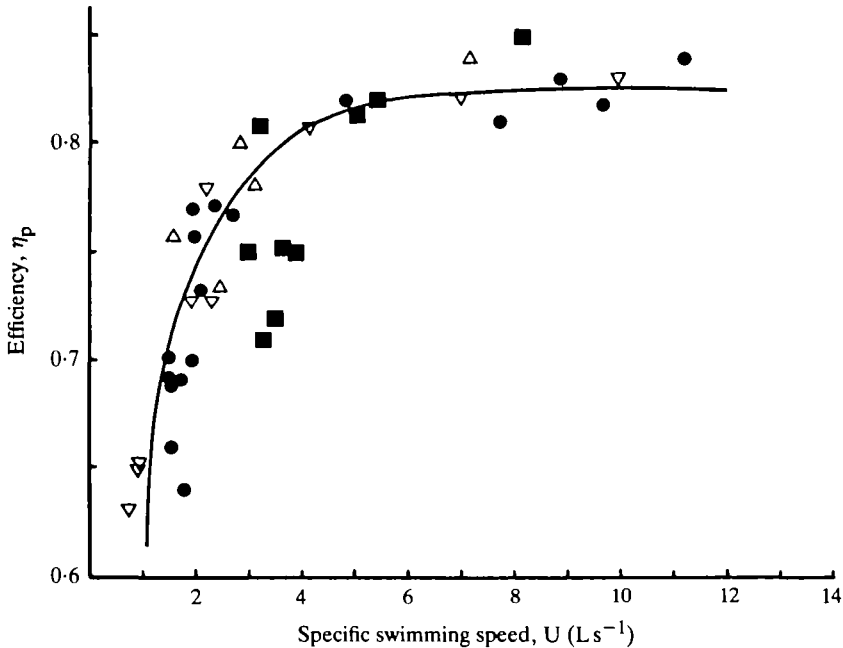
Fig. 6. Plot of Froude (propeller) efficiency against specific swimming speed. Symbols and sample size as in Fig. 2. The data have been fitted to the hyperbolic curve shown in the figure. The equation for this line is $\eta = 0.787 - 0.116/U^2$; $r = 0.74$, $P < 0.001$.

wave (Webb, 1975; p. 33). For all species pooled there is no significant relationship between wavelength and specific swimming speed ($r = 0.03, P > 0.5$); however, there is a positive correlation for these variables when the long-tailed forms are examined separately ($r = 0.658, P < 0.01$). A much better predictor of wavelength than swimming speed was, simply, tadpole size. We found that 86% of the variance in wavelength could be explained by size alone.

In Fig. 6 we present one of the several available measures of propeller efficiency (cf. Webb, 1975), Froude efficiency (η), plotted against specific swimming speed. The lowest η value recorded was 0·63. There are no major differences between the species except that *Bufo* may be a bit less efficient than the other species at intermediate speeds (3–4 L s^{-1}). This follows directly from the slightly higher tail beat frequencies for *Bufo* shown in Fig. 2. The overall pattern in Fig. 6 is one of propeller efficiency increasing steadily as swimming speed increases from 1 to 4 L s^{-1} then asymptotically approaching a value of 0·84. This general pattern is the same one reported for several fish species (Webb, 1975, 1984) and the asymptote is consistent with the maximum efficiency predicted by slender body theory (Lighthill, 1960, 1970). The line in Fig. 6 is a hyperbolic fit to all of the data and the correlation is very good ($r = 0.74$, $P < 0.001$). A better fit ($r = 0.83$) can, however, be achieved for all points below 3 L s^{-1} with a straight line intersecting the y-axis at 0·6. This is consistent with the prediction from slender body theory that 0·5 is a lower limit for Froude efficiency during normal undulatory locomotion (Webb, 1984).

Some of the kinematic features that distinguish tadpoles from fishes can be related to differences in muscle mass and muscle distribution along the body. The
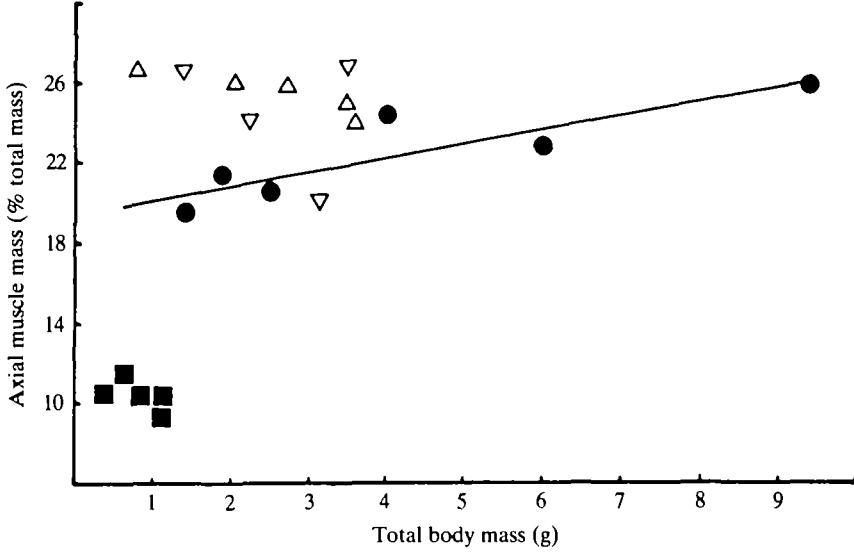
Fig. 7. Plot of axial muscle mass (as a percentage of total body mass) against total body mass. All measurements are for wet weight. The symbols are the same as in Fig. 2. There is no significant correlation ($P > 0.1$) between these variables for either the short-tailed or long-tailed tadpoles collectively. However, *Rana catesbeiana* alone exhibits a positive correlation; i.e., axial muscle mass = 0.069 total mass + 19.6; $r = 0.88$, $P < 0.001$). The line for this relationship is shown in the figure. Note the small amount of muscle in *Bufo* larvae.
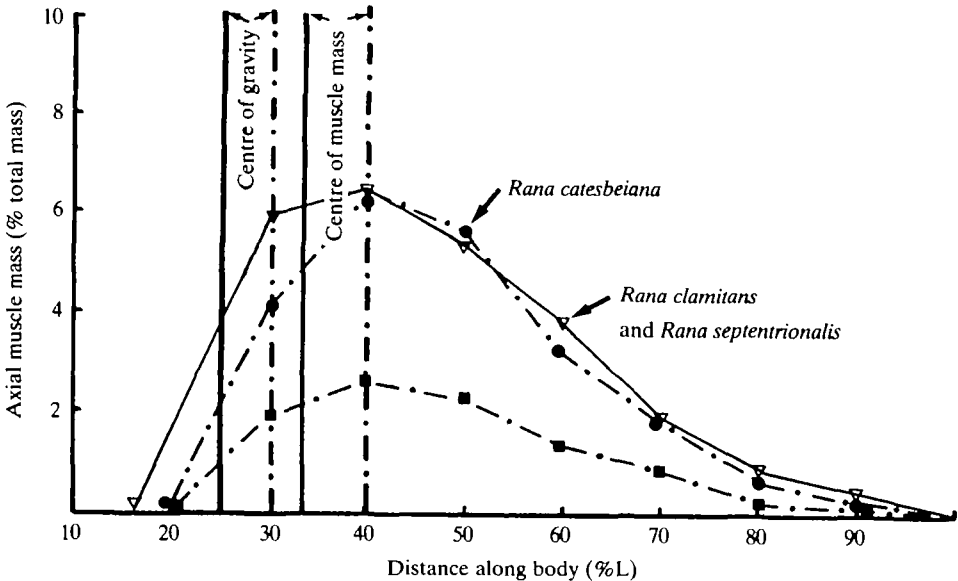

Fig. 8. The relative distribution of axial musculature along the length of tadpoles from the tip of the snout to the tip of the tail. Axial muscle mass was weighed in sections $0.1L$ long. The symbols are the same as in Fig. 2 except that *Rana clamitans* and *R. septentrionalis* do not differ and are pooled. The vertical lines indicate the centre of gravity and the centre of muscle mass for the long-tailed (—) and short-tailed (···) tadpoles respectively. Note that the centre of muscle mass is posterior to the centre of gravity and approximately at the base of the tail in all tadpoles. Note the small amount of muscle overall in *Bufo* (lowest curve), and in the terminal portion of the tail in all species.
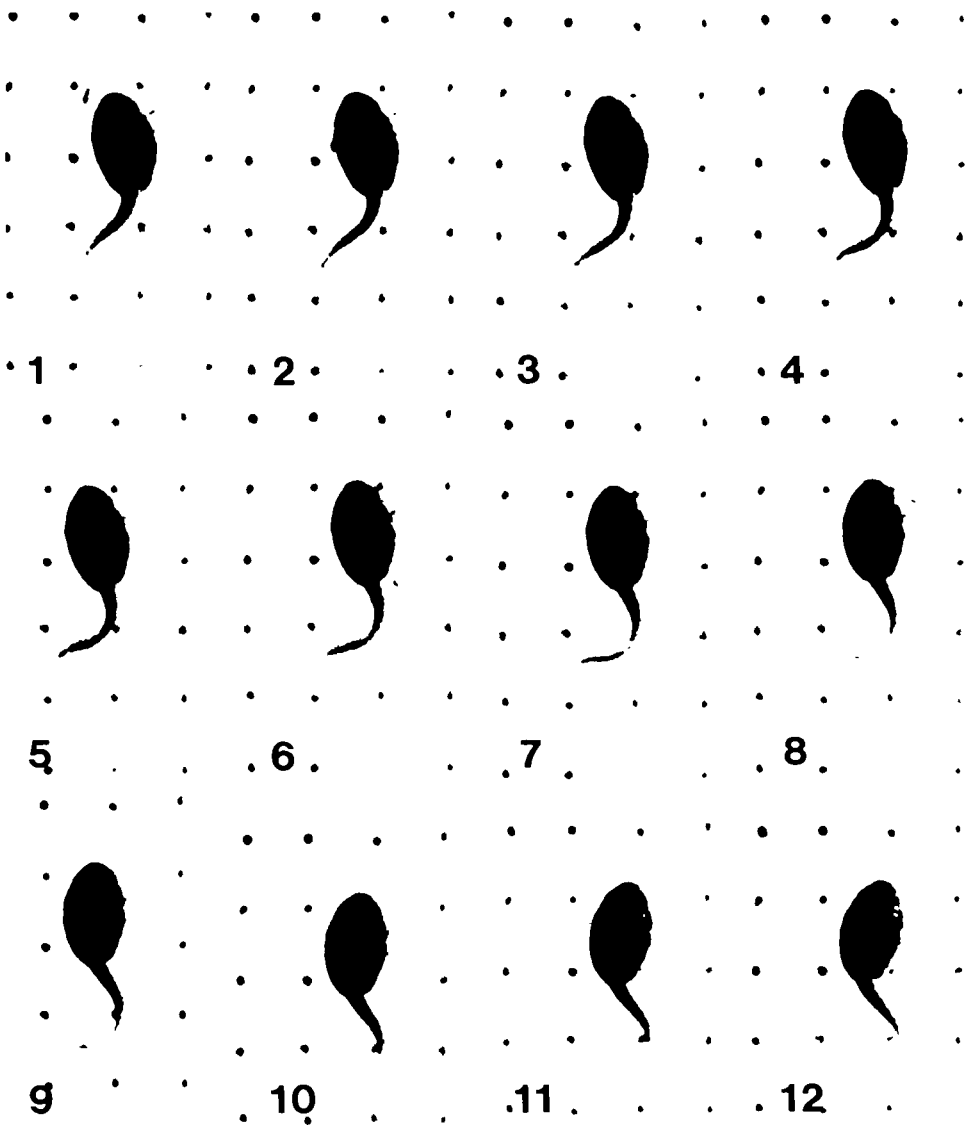
Fig. 9. A series of twelve frames of a swimming *Rana catesbeiana* tadpole filmed from above at 200 frames s^{-1}. The reference dots on the background grid are at 1·0-cm intervals. Note that the tail tip in frames 9 and 10 moves forward in the same direction as the tadpole.

longer-tailed species tend to have slightly more axial muscle (24–27 % of total mass) than do the shorter-tailed *R. catesbeiana* (20–26 % of total mass), and much more than *B. americanus* (9–11 % of total mass) (Fig. 7). This may relate to both the higher amplitudes and the lower efficiencies of *Bufo* tadpoles at medium speeds. Our small sample did not show any significant correlation between total mass and axial muscle mass in the long-tailed ranids and *Bufo*, but *Rana catesbeiana* (which has by far the largest size range) did show an increase in the relative amount of muscle with size ($r = 0.88$, $P < 0.01$).
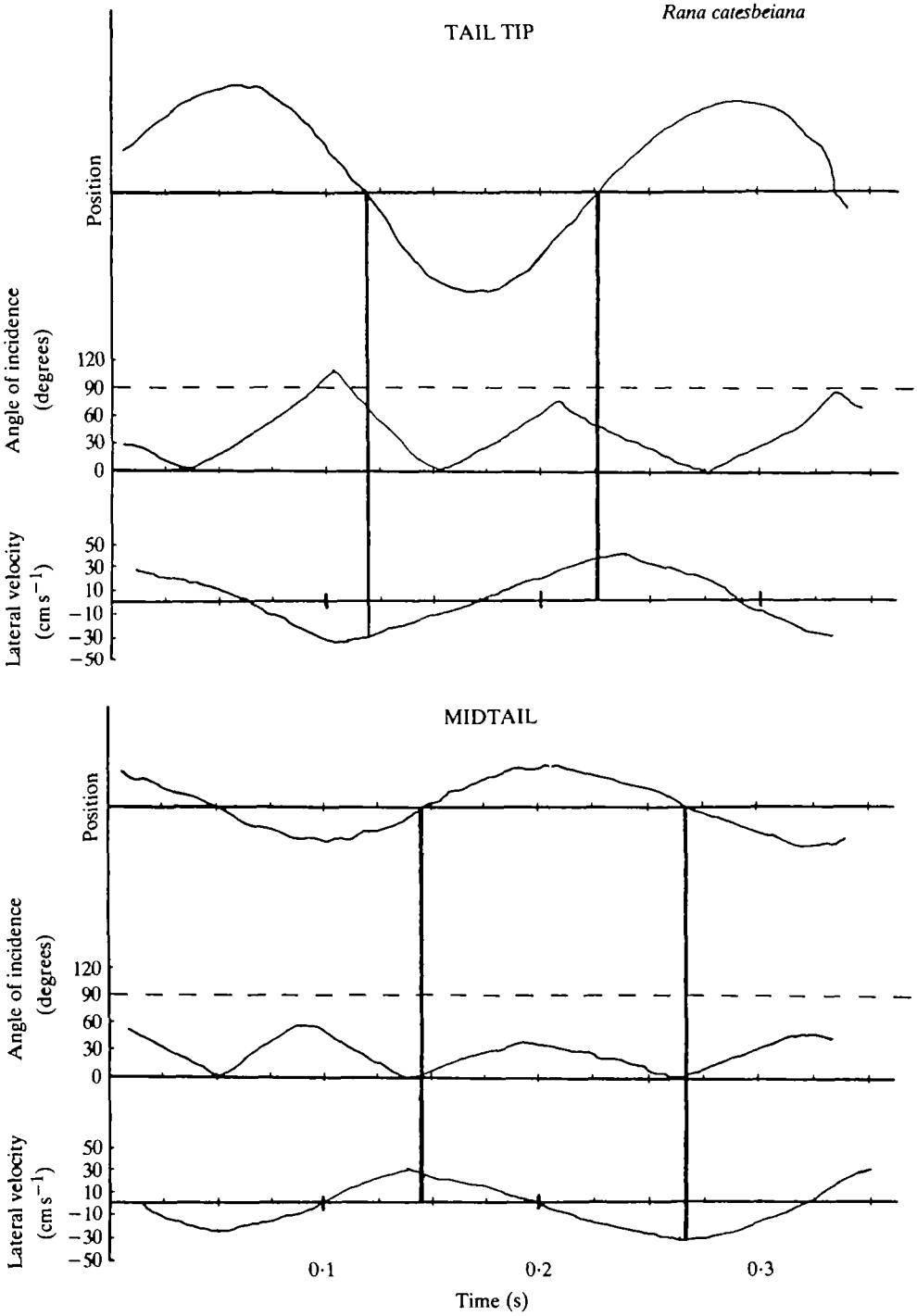
Fig. 10

Muscle is similarly distributed in tadpoles of all four species, with most of the muscle around the base of the tail and very little (< 5 % total mass) posterior to the high point of the tail fin – approximately midtail in these species (Fig. 8). The centre of mass in all the species lies anterior to the centre of muscle mass but posterior to the centre of oscillation during normal swimming (i.e. the point between the otic capsules, cf. Figs 4, 8).

The kinematics of the terminal portion of the tadpole tail

During the analysis of the filmed sequences described above, we noted that the caudal portion of the tadpole tail often curved more than 90 ° from the path of forward motion and thus moved forward in the same direction as the tadpole (e.g. frames 9 and 10 in Fig. 9). This motion would necessarily have retarded the tadpole, if it were the result of active muscle contraction in the posterior portion of the tail and if it had exceeded the forward velocity of the animal. However, it was observed in many film sequences where the tadpoles were swimming at a constant velocity. In Fig. 10 we present a set of graphs that compare the position, the angle between the surface of the body and the path of forward motion (angle of incidence, θ), and the lateral velocity for the tip of the tail and midtail of an *R. catesbeiana* larva swimming at a forward velocity of $2 \, L \, s^{-1}$. The midtail here is defined as the highest point of the tail fin, which for *R. catesbeiana* larvae is approximately 65 % of the distance from snout to tail tip. Vertical lines have been drawn in Fig. 10 to facilitate comparison between the parameters.

The results presented in Fig. 10 indicate that the mid-portion of the tadpole tail has its highest lateral velocity as it crosses the midline. Also as it crosses the midline it is oriented posteriorly in line with the axis of forward motion. The kinematics of this portion of the tail is identical to those proposed for the end of the tail of fish, the major propulsor, in Lighthill's slender body model for fish locomotion (Lighthill, 1971). In contrast, the terminal portion of the tadpole tail crosses the axis of forward motion at an angle closer to, and, in fact, occasionally exceeding 90 °. As the tail tip crosses the midline its velocity is near maximum but often decelerating. With such an angle of incidence and velocity, the tail tip could not produce thrust efficiently and appears instead to be passively oscillated, much as a wave travels down a whip or a flag flaps in a breeze. These plots suggest that the tail tip contributes little to the generation of thrust.

Fig. 10. Traces comparing the kinematics of the terminal segment of the tail (where the tail is shallowest) with the midtail segment (where the tail fin is highest), for a representative *Rana catesbeiana* larva swimming at $2 \, L \, s^{-1}$. For both tail segments the top trace, labelled 'Position', indicates the path of motion for that segment with respect to the mean path of forward motion indicated by the x-axis. The middle trace, labelled 'Angle of incidence', indicates the angle of orientation from the path of forward motion made by that body segment as it crosses the path of forward motion. When the angle of incidence is zero that body segment is oriented in line with the path of motion. When the angle is 90 ° (indicated by dashed line) that body segment is crossing the path of forward motion at a right angle. The bottom trace, labelled 'Lateral velocity', indicates the velocity of that body segment perpendicular to the path of forward motion (x-axis). Several vertical lines have been drawn in to facilitate comparison between the three variables. Note that the tail tip often crosses the path of forward motion at an angle in excess of 90 °. Note also that the kinematics of the terminal portion of the tail tip are more irregular than the midtail segment. The midtail, but not the tail tip, has a kinematic pattern most consistent with the generation of thrust. The traces suggest that the terminal segment of the tail moves passively, in a whip-like fashion (see text). Fig. 14 shows an idealized summary diagram from data of this form.
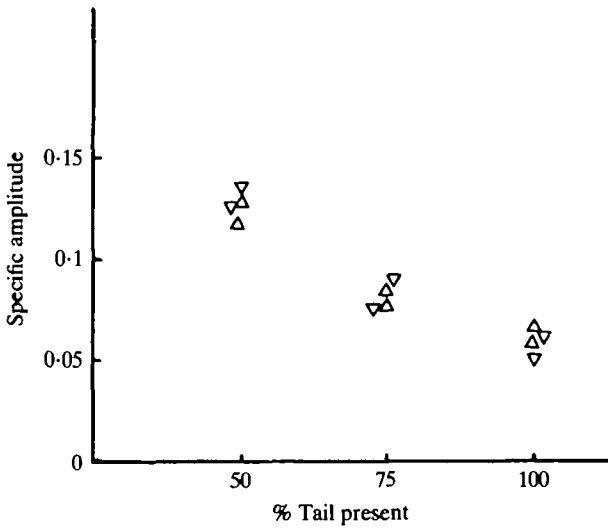
Fig. 11. Plots to illustrate the effect of various amounts of amputation of the terminal end of the tadpole tail on specific amplitude measured at midtail, where the tail fin is highest. Data are for four anaesthetized and curarized *Rana clamitans* ($N = 2$) and *R. septentrionalis* ($N = 2$) larvae mounted to the oscillator in Fig. 1. Symbols are as in Fig. 2. The amplitude and frequency of the oscillations at the base of the tail, where the driving pin was located, were matched to amplitude and frequencies of free-swimming tadpoles of the same size. Note the dampening effect that the terminal portion of the tadpole tail has on the amplitude of the tail anteriorly.

To confirm that the posterior portion of the tadpole tail is moved passively during normal, forward swimming, we passively oscillated freshly killed (anaesthetized and curarized) tadpoles on the apparatus shown in Fig. 1. Tadpoles on this apparatus were oscillated about a mounting pin placed between the otic capsules. This position was selected for mounting because it is the point of least lateral movement during normal swimming (see above). The driving pin (Fig. 1) was placed at the base of the tail, which (as indicated above) is at the centre of the axial muscle mass for tadpoles (Fig. 8). Tadpoles were then oscillated at frequencies and amplitudes matched to the frequency and amplitude at the tail base for free-swimming tadpoles of identical size. The kinematics for all points more posterior on the tadpole's tail in these oscillator preparations is indistinguishable from the kinematics of freely swimming tadpoles.

Dye injected into the water at the snout of these oscillator-mounted tadpoles became entrained around the mounted tadpoles and streamed posteriorly. Vortices were shed behind these tadpoles in the normal alternating pattern (see Fig. 11 in Lighthill, 1975; p. 137). All of these observations strongly suggest that during normal swimming the terminal portion of the tadpole tail is oscillated passively rather than by rostral to caudal waves of active muscle contraction. Since these experiments challenged the role of the terminus of the tail in providing thrust, additional experiments were performed to examine other roles for the tail tip in tadpole locomotion.

One of these experiments looked at the effect of partial tail amputation on the kinematics of the remaining, anterior portion of the tail. Fig. 11 presents the results of oscillator-mounted preparations where 0 %, 25 % and 50 % of the tail was removed from long-tailed larvae and the specific amplitude then measured anteriorly at the
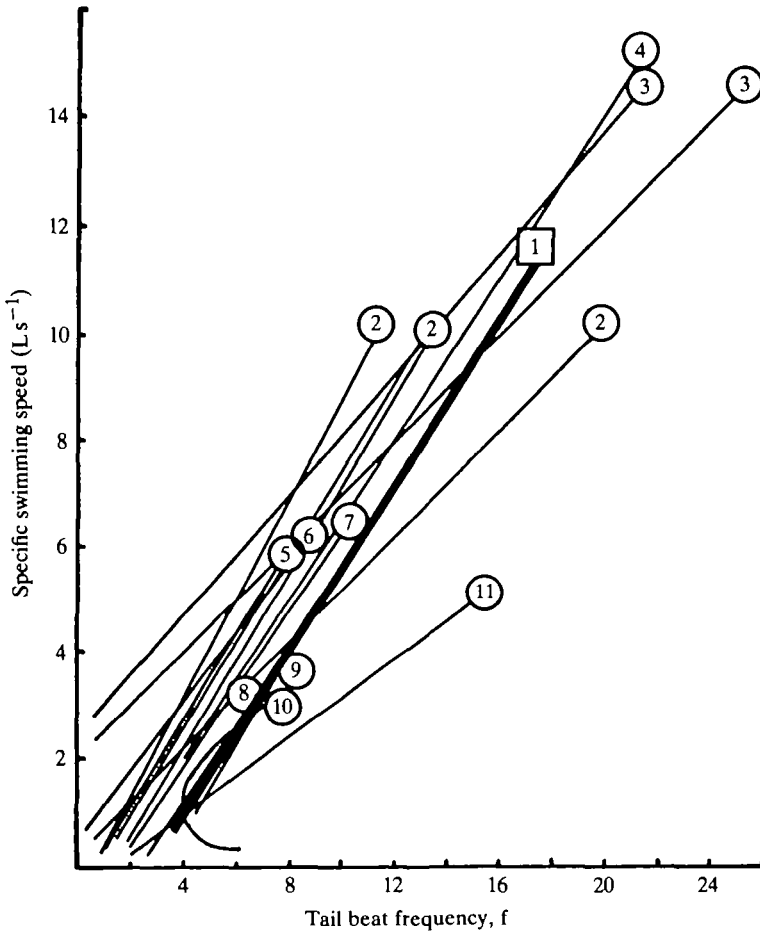
Fig. 12. A comparison of regression lines describing the relationship between tail beat frequencies and specific swimming speed for tadpoles and fishes. The heavy line for tadpoles (no. 1) is reproduced from Fig. 2; all other lines are taken from the literature: no. 2–chub mackerel, *Scomber japonicus*, Pacific sardine, *Sardinops sagax* and jack mackeral, *Trachurus symmetricus*, Hunter & Zweifel (1971); no. 3–tuna, *Thunnus albacares* and *Euthynnus pelamis*, Yuen (1966); no. 4–dace, *Leuciscus leuciscus*, trout, *Salmo gairdneri* (*Salmo irideus*) and goldfish, *Carassius auratus*, Bainbridge (1958); no. 5–mullet, *Mugil cephalus*, bluefish, *Pomatomus saltratrix* and Atlantic bonito, *Sarda* (= *Pelamys*) *sarda*, Pyatetsky (1970); no. 6–Pacific bonito, *Sarda chiliensis*, Magnuson & Prescott (1966); no. 7– trout, *Salmo gairdneri*, Webb, Kostecki & Stevens (1984); no. 8– trout, *Salmo gairdneri*, Webb (1971); no. 9–goldfish, *Carassius auratus*, Smit, Amelink-Koutsaal, Vijrerberg & von Vaupel-Klein (1971); no. 10–mandarin fish, *Synchropus picturatus*, Blake (1979); no. 11–knifefish, *Xenomystis nigri*, Blake (1983). In this relationship tadpoles closely resemble subcarangiform fishes.

highest point of the tail fin. Ablation of 25 % of the tail increased the specific amplitude at midtail by an average of 23 %, while removal of half the tail increased midtail amplitude by a full 50 %.

When dye was injected into the water during these experiments and the animals photographed, the detrimental effect of these ablations on turbulence around the larvae was clear. Removal of a mere 5 mm of the tail from a 33-mm *R. septentrionalis* larva increased the width of the turbulent zone at the high point of the tail fin from

17 to 36 mm. Ablation of a further 6·5 mm increased the width of the turbulence to 78 mm.

We conclude from these experiments that: (1) the mid-portion of the tadpole tail, where the fin is highest, is primarily responsible for generation of thrust; (2) the tapered terminal portion of the tail contributes little to the generation of thrust; but (3) this terminal portion is important for inertial damping of oscillation in the tail anterior to it and; lastly, (4) this damping role is crucial in reducing turbulence and thus drag on the tadpole.

DISCUSSION

Basic kinematics

The relationship of tail beat frequency to specific swimming speed for tadpoles is the same positive, linear relationship commonly reported for carangiform and sub-carangiform fishes (Fig. 12). In fact, of the many studies with teleost fishes in which the equation for this relationship is published, half report slopes higher and half lower than the one shown for tadpoles (Fig. 12). The intercept, however, for the tadpole line is lower than that for most teleost fishes. In other words, at very low specific swimming speeds tadpoles tend to beat their tails faster than do most bony fishes studied to date. This is not unexpected and may be an artifact of size. Our tadpoles are smaller than most fishes studied to date and, as noted by Hunter & Zweifel (1971), Wu (1977) and Webb, Kostecki & Stevens (1984), there is a negative relationship between tail beat frequency and size for fishes when specific swimming speed is kept constant.

Taking the size difference into consideration, the similarity between tadpoles and teleosts in tail beat frequency is more striking. None of our tadpoles depart more than two tail beats per second at all our recorded swimming speeds from what is predicted for trout of comparable size swimming at comparable speeds (equation no. 10 in Webb *et al.* 1984).

Our data on specific maximum amplitude plotted against specific swimming speed show a relationship similar to that reported by Bainbridge (1958) for fishes; namely, a positive correlation of specific amplitude with swimming speed up to about $4 \, L \, s^{-1}$. More recent workers (e.g. Hunter & Zweifel, 1971; Webb *et al.* 1984) have questioned whether this relationship is really valid for teleosts. Bainbridge performed no regression analysis on his data and there are a variety of factors that could affect specific amplitude at low swimming speeds, most notably subtle changes in acceleration. We, however, took care to control acceleration and the high correlation coefficient that we found for a log fit to the tadpole data argue against artifact here.

Webb *et al.* (1984) recognized that there may be substantial interspecific variation in specific amplitude among fishes. In fact, in sharks the relationship of specific maximum amplitude to specific swimming speed appears to be negative (Webb & Keyes, 1982). The tadpole tail is clearly more flexible than that of most, if not all, cartilaginous and non-anguilliform bony fishes (compare, for example, figures for amphibian larvae making abrupt turns in Blight, 1977, with figures for fish turning in Weihs, 1972; Webb, 1983 and other papers cited therein). This greater flexibility may be related to the amplitude modulation at low swimming speed that we record (see below).
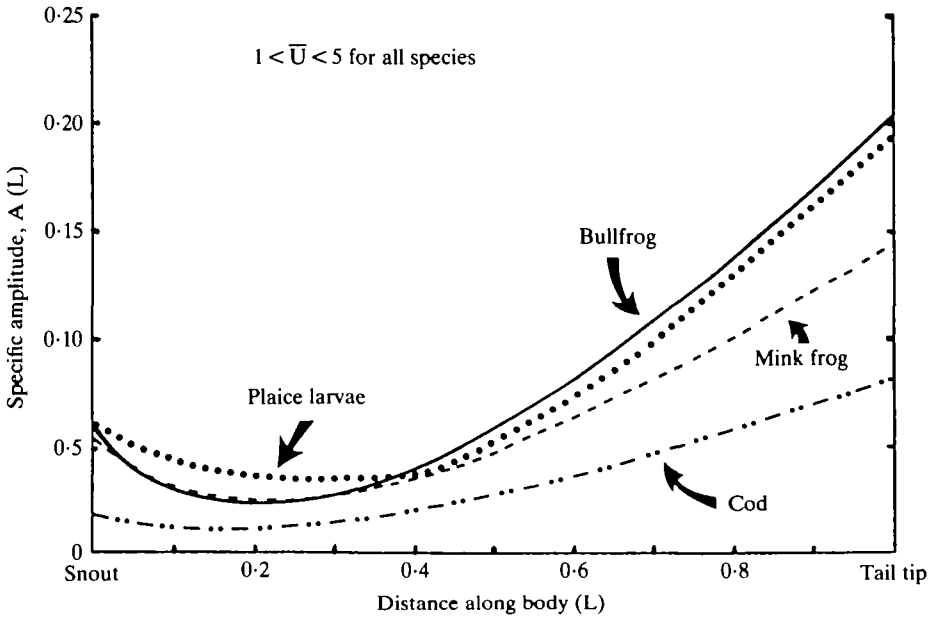
Fig. 13. Plots of the specific amplitude at all points along the body for long- and short-tailed *Rana* tadpoles compared to larval and adult fishes. Data on fishes are taken from Batty (1981) for the plaice, *Pleuronectes platessa*, and Videler & Wardle (1978) for the cod, *Gadus morhua*. All organisms were swimming at approximately the same specific swimming speed, U, measured in L s^{-1}. Note the excessive amount of yaw at the snout in the larval forms.

At swimming speeds above 4 L s^{-1} we find little correlation of specific amplitude with swimming speed. This is consistent with what has been reported in all teleost studies (see Webb, 1975; Webb *et al*. 1984 and older references cited therein). For teleosts swimming at > 4 L s^{-1} the average amplitude at the tip of the tail ranges from 20 to 23 % of the total body length and rarely exceeds 25 % of total length. Our short-tailed tadpoles regularly swam with specific amplitude this high, but our long-tailed forms never approached this value (Fig. 3). As indicated in Bainbridge's original plots, there is enormous variation about this presumed upper limit for specific amplitude. As a result, although our two groups differ significantly from each other in mean specific amplitude, neither differs significantly from values reported for teleost fishes.

Webb (1977) and Webb *et al*. (1984) discuss the fact that specific amplitude generally decreases with increasing absolute size in fishes. Our tadpoles do not differ from fishes in this regard (analysis limited to tadpoles that swam over 3 L s^{-1}). Part, but not all, of the difference between the short-tailed and long-tailed tadpoles is the result of this absolute difference in size. In several sequences where we have animals of comparable size and speed, but different body proportions, there remains a clear difference in specific amplitude.

A distinctive feature of anuran larval locomotion compared to that of fishes is the great amount of lateral movement that occurs at the snout (Fig. 4). In Fig. 13 we have plotted the specific amplitude at all points along the body from the tip of the snout to the tip of the tail for representative long-tailed and short-tailed *Rana* larvae. We have

transposed onto this two similar plots from the fish literature for comparison (i.e. plaice larva, *Pleuronectes platessa*, from Batty, 1981, and cod, *Gadus morhua*, from Videler & Wardle, 1978). This figure confirms that the amount of lateral movement seen at the snout of tadpoles is proportionately larger than for the adult cod; however, the larval plaice shows an equal amount of lateral movement anteriorly. All other adult fishes for which we have been able to find comparable data show proportionately less lateral displacement anteriorly, whether they are anguilliform, carangiform or ostraciform (data taken from Gray, 1968; Grillner & Kashin, 1976; Videler & Hess, 1984; Hess & Videler, 1984).

Excessive yaw, or wobble, anteriorly may be a typical feature of aquatic vertebrate larvae and embryos. Blight (1976) states that the 'chief difference between the swimming of the newt embryo and that of the typical adult fish is that the amplitude of lateral oscillation of the head is much reduced in the latter'. The excessive anterior lateral movement in tadpoles is probably the cause of the subjective and somewhat erroneous impression that larval anurans have little steering ability (cf. Romer, 1966, p. 17) and swim inefficiently (see also quote from Romer in Introduction).

Blight (1976, 1977) has discussed in some detail the muscular activity patterns in fishes that serve to reduce excessive yaw at the snout. He sees (Blight, 1976) 'a behavioural significance in stabilising the cephalic sensory receptors during locomotion, particularly in animals which hunt active prey'. Most tadpoles do not hunt active prey but are indiscriminate suspension feeders and grazers (Wassersug, 1975, 1980; Seale, Hoff & Wassersug, 1982; Seale & Wassersug, 1979). They do most of their feeding while relatively stationary. Thus, excessive wobble anteriorly during swimming should not be a handicap during feeding. On the other hand, the few tadpoles which do hunt active prey in the open water, for example *Hymenochirus* larvae (Sokol, 1966; Ueck, 1967), use only the most posterior portion of the tail for locomotion during hunting. Their eyes are directed anteriorly and, consistent with Blight's behavioural expectation, they can glide through the water towards prey without any perceptible lateral movement of their heads (personal observation).

The fact that the point of least lateral displacement during forward swimming in tadpoles is exactly at the level of the semi-circular canals supports an often cited hypothesis on the evolution of the vertebrate ear. In his classic paper on this subject van Bergeijk (1967, p. 15) states that the reason vertebrates evolved their accelerometers (i.e. their semi-circular canals) where they did in their body is that 'the most accurate and noise free information about tangential motion is . . . provided by those organs that have the least lateral motion' and that 'these organs [the semi-circular canals] are situated near the base of the skull which remains relatively stable, while the rest of the body (including the nose) moves laterally'. Whereas van Bergeijk boldly asserts this, we believe that our data are the first to confirm that the point of least lateral movement for aquatic vertebrates is, indeed, at the level of the semi-circular canals.

It is worth pointing out that anterior yaw in swimming animals is generally seen as energetically disadvantageous because yaw increases frontal area and thereby also pressure drag. But, as pointed out by Aleyev (1977, p. 10) and many hydromechanical engineers before him, 'at low Reynolds numbers the total drag on a body moving in water or air depends very little on shape, . . . and only at relatively high Reynolds

numbers does the difference between poorly and well streamlined bodies become significant . . .'. Aleyev considers $Re > 5 \cdot 0 \times 10^3$ the approximate cut-off point where the drag on a sphere (with relatively larger frontal area) *versus* a well streamlined body of revolution would noticeably differ. This is in the middle of the Re range for swimming tadpoles. Thus most tadpoles, and certainly our smaller and slower ones, may be little handicapped by their rotund shape and anterior yaw. Furthermore, the anterior wobble of the anuran larva is, to a certain extent, an illusion. The tadpole head is not laterally displaced during swimming so much as it is rotated or rocked back and forth about the point of minimum amplitude. For the species and swimming speeds we examined, the body is sufficiently round that this action results in little increase in frontal area, and therefore little increase in pressure drag.

Webb *et al.* (1984) reviewed many of the problems of accurately measuring propulsive wavelength. Because the wavelength for our tadpoles was typically less than the body length, it was relatively easy to measure wavelength here. Except for the weak correlation of wavelength with swimming speed for the long-tailed tadpoles, the overall flat relationship that we observed (Fig. 5) between wavelength and speed fits that of subcarangiform fishes, such as trout (Webb *et al.* 1984). Our tadpoles differ from fishes, however, in the relationship of wavelength to body length. While we obtain the same exponent of $0 \cdot 83$ in the power function fit that Webb *et al.* (1984) reported for their trout, the tadpole curve is displaced noticeably downwards. In other words, tadpoles have a shorter wavelength than trout of the same size. These differences range from 18 to 22 % of specific amplitude for individuals of 5–10 cm, respectively. The shorter wavelength in tadpoles supports the idea that they have a more flexible tail than most teleosts of comparable size.

The shortest wavelengths we observed were at the lowest speeds in the long-tailed tadpoles. It should be obvious that, since amplitude and wavelength are necessarily linked (i.e. the further lateral the tail moves the less length available in it for extra bends), these are the same tadpoles which exhibit the least specific amplitude.

Webb *et al.* (1984) suggest that larval fishes, which have smaller specific wavelength than adult fishes, may be better designed for cruising. The lowest specific wavelength that we observed, however, occurred only at low speeds and only during intermittent swimming. The low specific wavelength of larval amphibians compared to adult fishes may reflect unavoidable differences in the stiffness of biological materials rather than an adaptation to a specific swimming mode. Virtually all materials are more flexible when their cross-sectional areas are small, including the materials that make up the tails of tadpoles and fishes. As discussed below, tadpoles lack the skeletal supports that additionally stiffen the body and fins of fishes (cf. Videler, 1975; Wainwright, 1983). All our tadpoles were capable of bending the tail more than $180°$ so that the side of the tail touched the body. No carangiform or subcarangiform fishes of similar size are evidently as flexible (see Aleyev, 1977; Chapter 4).

We have fitted our Froude efficiency data to the theoretical efficiency curve Lighthill (1960) proposed for fishes. Tadpoles have the same pattern of increasing efficiency with increasing velocity. As pointed out by Webb *et al.* (1984, p. 90) from energetic and evolutionary considerations, speed sprints are important in predator avoidance so that 'higher Froude efficiencies at higher speeds would contribute to maximizing performance where this is most important'.
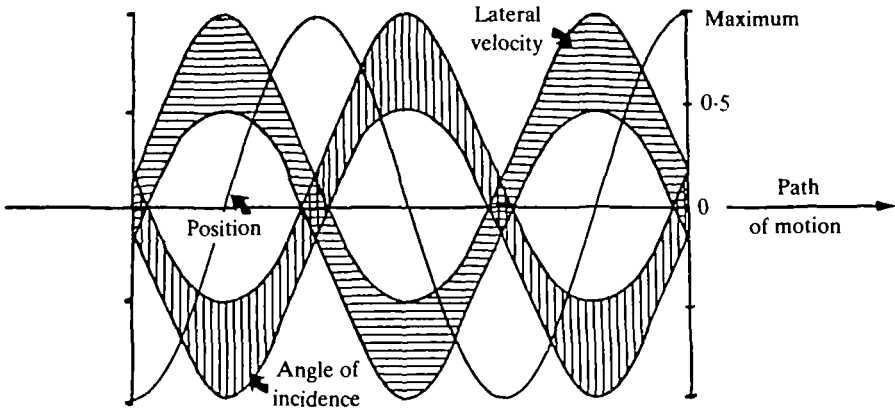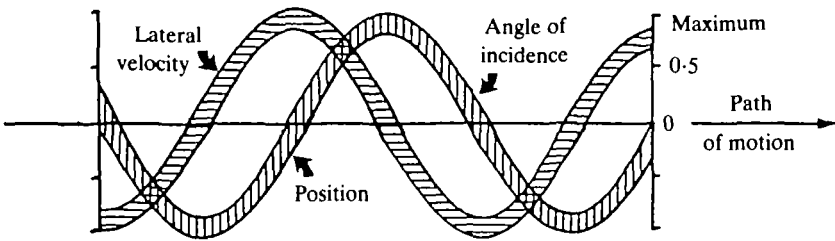
Fig. 14. Idealized summary diagram comparing the kinematics of a tadpole's midtail, where its tail fin is highest, with that of its tapered terminal portion. The data for this diagram were compiled from traces of the form shown in Fig. 10. The traces for the three variables – position, angle of incidence and lateral velocity – are as defined in Fig. 10, but are here overlain to emphasize kinematic features that are in or out of phase. The vertical axis is in units of 'percentage of maximum' for both angle of incidence and lateral velocity. The band width indicates the range of variation seen in the raw data for the kinematic variables. Note that, for the midtail, lateral velocity is near maximum and angle of incidence near zero as it crosses the path of forward motion. In contrast, the terminal portion of the tail crosses the path of forward motion at an angle of incidence closer to 90° and with much greater variation in lateral velocity.

The peak value for Froude efficiency that we found, 0·84, is as high or higher than most recorded for a variety of good, subcarangiform teleosts, such as cod, mackerel, trout and saithe (e.g. Webb, 1971, 1984; Webb et al. 1984; Videler & Wardle, 1978 and others cited therein). The scatter of our results about the theoretical efficiency vs swimming speed curve (Lighthill, 1975) is also as tight, if not tighter, than that presented in most fish studies. It should be pointed out that Froude efficiency as calculated by Lighthill makes the simplifying assumptions that variation in amplitude along the body is zero and that thrust is produced along the whole length of the body. These assumptions are not true of tadpoles or most fishes and variation in amplitude may certainly affect efficiency. Tadpoles, in contrast to most fishes, are like prolate spheroids with ribbon-like propellors partially towed in the wake. As such, the conditions of flow around the tadpole's tail may differ from that of fishes. It is, thus,

surprising that these animals are kinematically so similar. Our data should lay to rest any presumptions that tadpole locomotion must be mechanically inefficient compared to that of fishes.

None of the tadpoles studied here had efficiencies as low as the lowest efficiencies reported for fishes, nor were we able to force any of our tadpoles to swim any distance at all at specific swimming speeds much below 1 L s^{-1}, where fishes exhibit the lowest Froude efficiencies. Fishes that are designed to swim at such low velocities, for example, knifefish (*Gymnarchus niloticus*) and seahorses (*Hippocampus hudsonia*), use non-caudal propulsors to maintain mechanical efficiency at low speed (Blake, 1983; Webb, 1984). Except near metamorphosis, tadpoles do not have mature enough lateral appendages to aid in locomotion. They also lack supporting rays in their fins, which might allow them to scull like the seahorse or knifefish. Thus, since they lack the structures that fishes use for sustained swimming at low speeds, it is not surprising that we have not observed tadpoles swimming at speeds much below 1 L s^{-1}, nor with very low Froude efficiencies.

Bufo larvae have a lower propeller efficiency than *Rana* tadpoles over most of the speed range that we tested. They also have relatively higher tail beat frequencies for comparable swimming speeds. Furthermore, they have the least amount of axial muscle mass – approximately half that of *Rana* tadpoles of comparable length. Given these results it is not surprising that *Bufo* larvae have been reported to have lower maximum sprint speeds than other tadpoles (Santiago, 1982). *Bufo* larvae may depend on defences other than speed and manoeuvrability to escape predation. They are, for example, known to be unpalatable to a variety of potential predators (Wassersug, 1973).

The kinematics of the mid-portion of the tail (Figs 10, 14) indicate that the portion of the tail where the fin is highest moves in a way that is most advantageous for the generation of thrust. As one moves more posteriorly from that point the tail kinematics becomes progressively less optimal for the generation of thrust and more likely to generate drag (Fig. 14). This may be a reason why the tadpole tail fins taper to a point.

The posterior portion of the tail, however, serves a major role in reducing excessive amplitude anteriorly. The ablation experiments confirm this, but the fact that the longer-tailed tadpoles had lower specific amplitude already demonstrates that it is true for naturally swimming tadpoles.

Passive oscillation experiments similar to the ones performed here have been performed on salamander embryos (*Ambystoma mexicanum*) by Blight (1977, Fig. 14). Although Blight was impressed by the kinematic match between the embryos in his oscillating manipulation and free-swimming individuals, no quantitative data are provided for assessing the preparation. (Deviation from the natural kinematics may be the result of the fact that Blight placed his mounting pin through the centre of the embryo's body and the driving pin through the head.) Nevertheless, the major conclusion of Blight's study is affirmed by our own research. For *Rana* and *Bufo* tadpoles, at least, normal kinematics do not require a travelling wave of muscle contraction for forward locomotion. Synchronous contraction of the musculature on one side, then the other, in the anterior portion of the tadpole tail can produce normal kinematics. While Blight's model has not been accepted by all workers studying the neuronal regulation of swimming in amphibian larvae (e.g. Stehouwer & Farel, 1980), recent independent
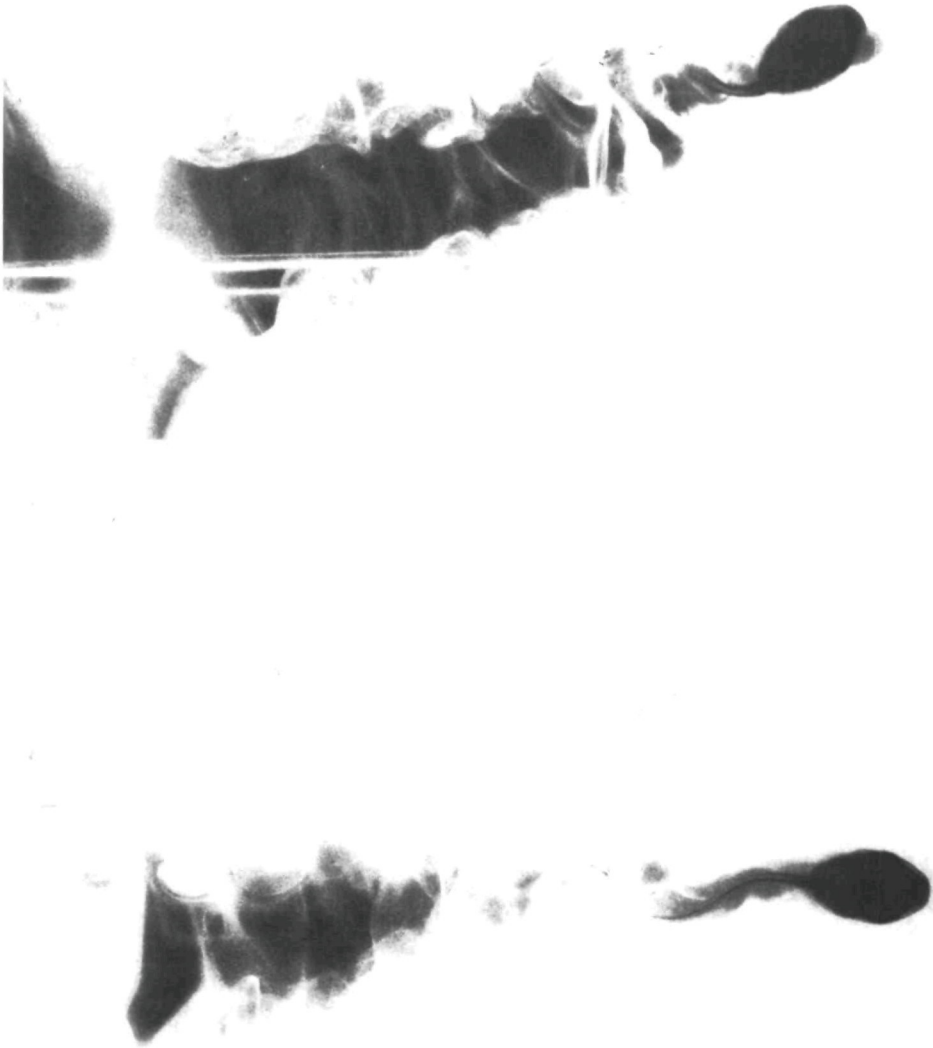
Fig. 15. Two photographs of a *Rana pipiens* larva swimming through a shallow layer of milk (following the procedure of Rosen, 1959) in order to visualize the wake. In both photographs the larva is swimming at approximately $2 \, L \, s^{-1}$. In the top photograph, however, the tapered terminal portion ($= 15 \% \, L$) of the tadpole's tail has been amputated. Note that the tadpole produces a wider and more turbulent wake when the tail tip is absent.

work on the saithe suggests that it applies during fast forward swimming in subcarangiform teleosts as well (Hess & Videler, 1984).

There are both energetic and evolutionary implications to the role of the posterior portion of the tail as a 'splitter' plate. Hoerner (1965; Chapter 3, Fig. 8) shows that the presence of a simple, straight tail along the edge of a cylinder can reduce the drag coefficient by from 15 % to over 40 % of that on the cylinder alone, in the *Re* range of 10^4 to 10^5. The wider wake seen in Fig. 15 for a tadpole with only 15 % of its tail removed means that much more work is performed in moving water laterally by a tadpole with a truncated tail than one with a normal tail. This increased turbulence may increase susceptibility to attack by predators. By maintaining an orderly wake well posterior to the trunk and head of a tadpole, the tail lessens water movements that could stimulate the mechanoreceptors of potential tadpole predators. Some tadpoles additionally have conspicuously pigmented tail tips, which have been found to lure predators visually towards the tail and away from the head of a moving tadpole (Caldwell, 1982).

The adaptive significance of tadpole locomotor behaviour and tail morphology

In a recent major synthesis of vertebrate functional morphology, Webb (1984) relates the locomotor morphology of aquatic vertebrates to their foraging habits. In his Fig. 3, Webb pictorially presents a great diversity of aquatic vertebrates ordered along two axes: the first covers the spectrum from 'microphages' to 'macrophages', and the second runs from 'food widely distributed' to 'food locally abundant'. In the corner of Webb's figure allotted to microphagous vertebrates that feed on locally abundant food, there is only a question mark. Although Webb does not include tadpoles in his analysis, there is now a wealth of information to indicate that tadpoles are aquatic vertebrates truly specialized for microphagous feeding on locally abundant food (Wassersug, 1972, 1980; Seale, 1980; Seale & Wassersug, 1979; Seale & Beckvar, 1980). Tadpoles are essentially suspension feeding machines; their globose head-body is largely mouth and intestines. The mouth of a typical frog or toad tadpole contains massive gill filters, special branchial food traps, and batteries of papillae, all used to capture fine particles from the water (Wassersug, 1980). To testify to the fact that what these animals strain from the water may be locally abundant, one notes that up to half of the mass of field-collected tadpoles may be stomach contents (Calef, 1973). However, Slade & Wassersug (1975; also Wassersug, 1974, 1975) have pointed out that local abundances of microphagous food are likely to be ephemeral and that the organisms that are adapted to foraging on them, such as tadpoles, are themselves likely to be ephemeral; i.e. all tadpoles are committed to metamorphosis. Although a few tadpoles occur in the shallow margins of large permanent lakes, anuran larvae are generally restricted to small temporary pools and vernal ponds. These habitats can have explosive rises of phytoplankton (Seale, 1980). Tadpoles feed on this rich temporary resource until it is depleted or until the pond itself dries up. They are then obliged to metamorphose.

How then does the locomotor morphology of tadpoles relate to their feeding ecology and their preference for small, temporary bodies of water? Let us first compare and contrast tadpoles with other types of aquatic vertebrates using Webb's (1984, Table 1) classification. Here all aquatic vertebrates are sorted into four classes depending on whether they: (A) use body and caudal fin for periodic propulsion; (B) use body and caudal fin for transient propulsion; (C) use median (non-caudal) and paired fins for propulsion; or (D) simply do not swim, except in very rare situations.
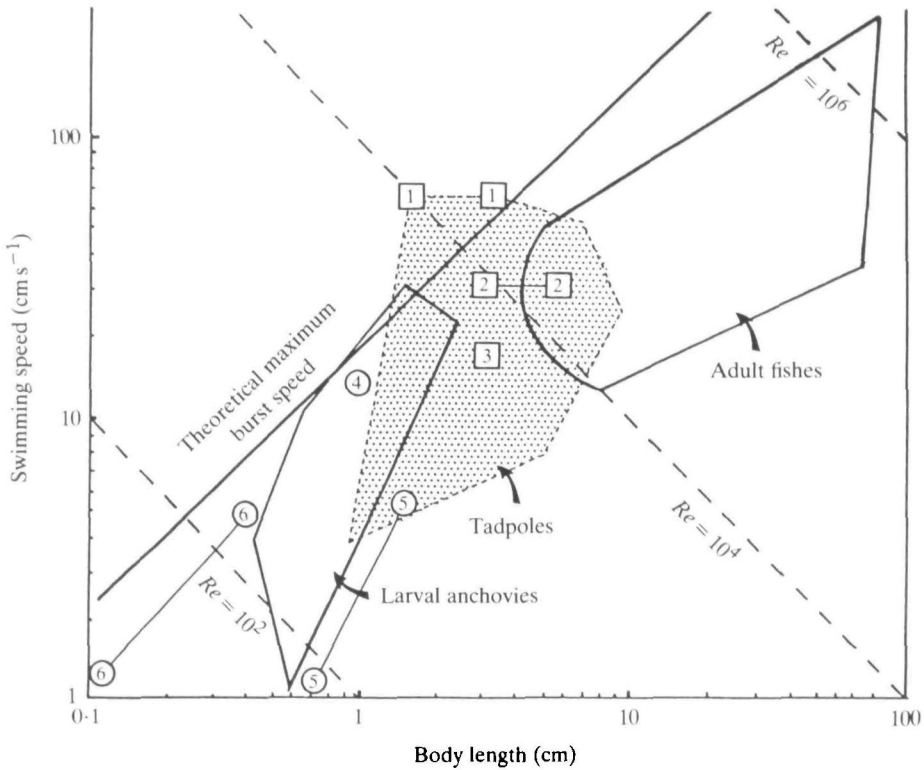
Fig. 16. Variation of swimming speed with body length; basic diagram modified from Wu (1977, Fig. 10) and Yates (1983, Fig. 6-2). Data for tadpoles are taken from the present study (stippled area) plus: no. 1–the cricket frog, *Pseudacris triseriata*, raw (unpublished) data from Wassersug & Sperry (1977); no. 2–the leopard frog, *Rana berlandieri*, Feder (1983b); and no. 3–the boreal toad, *Bufo boreas*, Huey (1980). Data on adult fishes (upper bounded area) are from sources cited in Wu (1977) and Yates (1983). Data for larval fishes are from Hunter (1972) for larval anchovies, *Engraulis mordax* (lower bounded area) plus: no. 4–plaice larva, *Pleuronectes platessa* L., Batty (1981); no. 5–walleye larvae, *Stizostedion vitreum vitreum*, Houde (1969); and no. 6–herring larvae, *Clupea harengus*, Rosenthal (1968). The heavy line for 'theoretical maximum burst speed' is for fishes (taken from Wu, 1977). Dashed lines indicate boundaries of constant Reynolds number.

The common ranid and bufonid tadpoles that we have studied can be readily excluded from three of these classes. The easiest one to deal with is class 'D', which Webb presents as benthic organisms, such as deep sea fishes that live in nutrient-poor environments. Given velocities reported here and elsewhere (see Fig. 16), the stamina reported in Wassersug & Feder (1983) and the high activity of tadpoles exposed to mild hypoxia (Wassersug & Seibert, 1975; West & Burggren, 1982; Feder, 1983a), it is clear that anuran larvae are typically not sessile, benthic, class 'D' creatures. (Some exceptions, however, may occur among fossorial, arboreal and gastromyzophorous tadpoles; cf. Wassersug, Frogner & Inger, 1981; Wassersug & Heyer, 1983).

Class 'A' vertebrates are organisms considered best adapted for sustained swimming at relatively high velocities; e.g. carangiform fishes with high aspect ratio lunate tails, narrow caudal peduncles and relatively stiff, streamlined bodies. This is an energy conserving design (see Weihs & Webb, 1983 and many other papers cited therein) most appropriate for organisms that must travel great distances to feed on widely

distributed food (Webb's Fig. 3; 1984). Organisms, including tadpoles, that live in small bodies of water where food is not widely dispersed, rarely, if ever, have this 'A' morphology. Tadpoles (and fish larvae – cf. Batty, 1981, 1984; Webb *et al*. 1984) are far more flexible than class 'A' vertebrates. They lack the skeleton that stiffens the fins in class 'A' vertebrates and that is the key to energetically efficient swimming at higher *Re* values (e.g. $Re > 10^4$) (Lighthill, 1975; Webb, 1977).

Webb's class 'C' vertebrates are specialized for slow swimming and precise manoeuvring. These organisms, in contrast to tadpoles, are all viewed as macrophages by Webb (1984). Many also differ from the tadpoles of the present study in having high Froude efficiencies at low swimming speeds. This is accomplished in type 'C' fishes, such as the Notopteridae, Gymnotidae and Molidae, by intricate movements of the median body fins not possible in tadpoles. A few tadpoles can scull with the terminal portion of their tail (e.g. *Xenopus* and *Hymenochirus*) and are capable of the slow movements that characterize some fishes that swim in this mode. Chaetodontiform fishes, however, which Webb identifies as archetypal class 'C' vertebrates, primarily use their paired fins for locomotion. Webb, citing studies by Blake (1976, 1977, 1978), states that these fishes 'can turn about the vertical axis near the centre of mass, without the body translocation necessary in BCF [body and caudal fin propulsors, i.e. locomotion modes A and B] turns'. In contrast, tadpoles lack paired appendages for locomotion until just before metamorphosis and when they first appear they generally hinder rather than help locomotion (Wassersug & Sperry, 1977).

Fast starts and turns characterize the last of Webb's locomotor propulsion modes, class 'B'. Aquatic vertebrates of this type are capable of large linear and angular acceleration. Their bodies are flexible compared to members of the other classes. The typical class 'B' vertebrate has a deep body with a large surface area, especially caudally. Webb (1984) gives the pike, *Esox*, as an example of this locomotor type, but several key anatomical components of class 'B' swimmers, such as the deep body posteriorly and flexible tail, also characterize tadpoles. Like the pike, bouts of intense swimming are transient for tadpoles.

There are, of course, many ways that a tadpole differs from the pike. The pike, like other teleost fishes, has erectile fins. In order to keep its mouth on target when it strikes at prey, the pike commonly starts a strike from an 'S'-posture (Webb & Skadsen, 1980). This is more efficient for a fast start than the 'C'-posture because it reduces yaw anteriorly due to recoil. Tadpoles, which swim to escape predators, lack erectile fins, and cannot form an 'S'-posture quite like that of a class 'B' swimmer. As stated above, they exhibit much lateral movement anteriorly during swimming. Some of this lateral movement, however, may be adaptive for it means that the tadpole can make large, rapid changes in direction with every tail beat when fleeing predators (including even, occasionally, the pike).

We have preliminary evidence that tadpoles can, in fact, turn rapidly, through more than 180° with zero radius of curvature. They essentially accomplish the same rotatory feat as the chaetodontiform fishes discussed above, but by a totally different mechanism. On videotapes of *Rana pipiens* tadpoles we have observed turns of 180° with no body translocation (K. Hoff & R. J. Wassersug, unpublished). These turns, which can take place in well under 50 ms, require folding the body and tail right up against each other. Such turns would be mechanically impossible if the tail were

stiffened by fin rays, ribs, scales or even hydrostatically. Experiments of Feder (1983b), on the escape behaviour of tadpoles, indicate that such high manoeuvrability is crucial to the survival of tadpoles in the wild.

Rapid acceleration, high velocity and abrupt turns are essential for tadpole survival, but swimming rarely has to be sustained. Feder (1983b) reports that chases by turtles on tadpoles in large open enclosures averaged only 11.5 ± 1 s ($\bar{X} \pm$ s.e.) whether or not the tadpole escaped. In the small bodies of water where tadpoles occur, sustained swimming may, in fact, be disadvantageous, since casual movements of tadpoles attract natural predators, such as turtles. Feder (1983b), for example, has shown that the painted turtle (*Chrysemys picta*) will attack moving leopard frog larvae (*Rana berlandieri*) from as far away as 175 cm, but will attack non-moving tadpoles from only 30 cm or less.

We come to the conclusion that tadpoles represent an example of an aquatic vertebrate that uses body and caudal fins for transient propulsion, but is capable of extremely abrupt turns more often seen among fishes that rely on median and paired fin propulsion. One advantage to the tadpole in having an exceptionally flexible tail is that it can turn abruptly. As shown by Feder (1983b), this turning ability is crucial for tadpoles to escape natural predators. By using an extremely flexible tail, rather than lateral paired appendages, for turning, the tadpole reduces drag during high-speed swimming. However, the extremely flexible tail introduces a lot of lateral movement at the snout. This yaw is, in part, controlled passively by the dampening effect of the tapered terminal portion of the tail. It is a functional alternative to the stiffened tail and body fins of fishes, but it is not without some cost associated with drag on the terminal portion of the tail. Tadpoles may swim with *mechanical* efficiencies comparable to those of teleost fishes, but this does not mean that tadpoles are *energetically* as efficient. It is already known that at high speeds tadpoles have little stamina (Wassersug & Feder, 1983).

Certain features give fishes an advantage over tadpoles when both speed and endurance are simultaneously called for. Those skeletal components that tadpoles lack store potential energy in fishes (Wainwright, 1983). The anteriorly-directed mouths of most teleosts mean that they can use ram ventilation (Roberts, 1975), while most tadpoles, like those of *Rana* and *Bufo*, have ventrally-directed mouths which precludes this energy-saving, respiratory mechanism. Together these differences give fishes some advantages in open lacustrine situations. As already noted, tadpoles rarely occur in bodies of water large enough to be permanent and to maintain fishes. Predation by fishes may, in fact, be the limiting factor which keeps tadpoles out of large, open water habitats.

Why has nature not evolved a tadpole built like a lake-dwelling teleost? We suspect that there may be developmental constraints that limit this possibility. Anuran metamorphosis involves complete resorption of the tail. While the tail is largely made up of axial musculature, a tadpole's tail is distinctly thinner than the tadpole's body and the total amount of muscle is relatively small (Fig. 8). The axial muscle mass for tadpoles is, on average, less than half that of carangiform or subcarangiform fishes (cf. Wardle & Reid, 1977 and references therein). This reduction in mass may allow for more rapid resorption during metamorphosis. Similarly, as spectacular as anuran metamorphosis is, the process involves little or no remodelling of bone or post-cranial

cartilage (Goette, 1875). If tadpoles had the fin rays and other skeletal elaborations of teleost fishes, the absolute time necessary to resorb these elements would probably lengthen the transformational process. However, anurans in the middle of metamorphosis – with forelimbs exposed and tail still in tow – are neither efficient at the undulatory locomotion of tadpoles nor at the saltatory locomotion of the transformed frogs (Wassersug & Sperry, 1977). Because of the cumbersome morphology of frogs at metamorphosis, natural selection acts to keep this transformational period as short as possible (Arnold & Wassersug, 1978). In sum, even if there were ecological and energetic advantages in having a tadpole built like a teleost, there appear to be developmental constraints limiting the evolution of such an animal.

As a final reminder, our conclusion, that the terminal portion of the tadpole's tail does not serve a primary role in thrust generation, has so far applied only to the situation of constant velocity swimming in a straight line. We have not, for example, examined the role of the tail tip in turning. Although the portion of tail in *Rana* larvae posterior to the highest point of the fin, contains only 5 % of their total mass, if that musculature were never used we would expect it to atrophy. This does not occur. We believe that this 5 % of the mass may be very important to tadpoles in certain limited situations. We have on a few occasions observed tadpoles in the laboratory swimming backwards as they pulled on food items with their mouths. In this situation all of the motion was in that posterior portion of the tail.

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