

THE KINEMATICS OF SWIMMING IN LARVAE OF THE CLAWED FROG, *XENOPUS LAEVIS*

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SUMMARY

The kinematics of swimming in larval *Xenopus laevis* has been studied using computer-assisted analysis of high-speed (200 frames s^{-1}) ciné records. The major findings are as follows.

1. At speeds below 6 body lengths (L) per second, tail beat frequency is approximately 10 Hz and, unlike for most aquatic vertebrates, is not correlated with specific swimming speed. At higher speeds, tail beat frequency and speed are positively correlated.

2. *Xenopus* tadpoles show an increase in the maximum amplitude of the tail beat with increasing velocity up to approximately $6 L s^{-1}$. Above that speed amplitude approaches an asymptote at 20% of body length.

3. Anterior yaw is absent at velocities below $6 L s^{-1}$, unlike for other anuran larvae, but is present at higher speeds.

4. At speeds below $6 L s^{-1}$ there is a positive linear relationship between length of the propulsive wave (λ) and specific swimming speed. At higher speeds wavelength is constant at approximately 0.8 L.

5. There is a shift in the modulation of wavelength and tail beat frequency with swimming speed around $5\text{--}6 L s^{-1}$, suggesting two different swimming modes. The slower mode is used during open water cruising and suspension feeding. The faster, sprinting mode may be used to avoid predators.

6. Froude efficiencies are similar to those reported for fishes and other anuran larvae.

7. Unlike *Rana* and *Bufo* larvae, the axial muscle mass of *Xenopus* increases dramatically with size from less than 10% of total mass for the smallest animals to more than 45% of total mass for the largest animals. This increase is consistent with maintaining high locomotor performance throughout development.

INTRODUCTION

Recent studies on the locomotion of the typical anuran larvae, *Rana* and *Bufo* (Hoff & Wassersug, 1985; Wassersug & Hoff, 1985) have emphasized that the kinematics of their locomotion is similar to that of many fishes, despite gross differences in morphology. Indeed, although anuran larvae characteristically have

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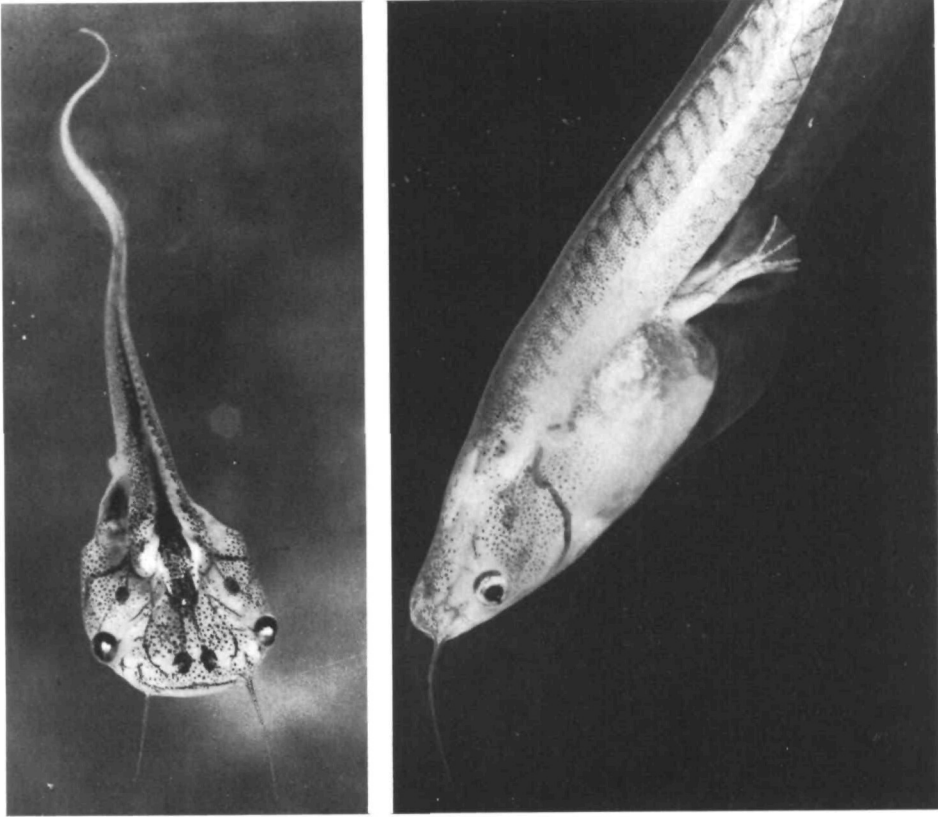


Fig. 1. Two views of *Xenopus laevis* larvae swimming in the normal, head downward posture. The anterior view (left) shows the wave form in the tail during normal, slow speed swimming. Note that the propulsive wave has low amplitude and is confined to the end of the tail. The lateral view (right) shows the enlarged ventral fin that extends forward onto the tadpole's body. Magnification approximately $2\times$ (left) and $2.5\times$ (right).

globose bodies, no pectoral or pelvic fins and little axial muscle, they move through water as efficiently as most other aquatic vertebrates of similar size.

The present study investigates whether differences in the ecology and morphology of tadpoles can affect swimming performance. Data are obtained for the larva of the African clawed frog, *Xenopus laevis* (family Pipidae), which is distinguishable from the tadpoles of *Rana* and *Bufo* in that it is an obligate, midwater, microphagous suspension feeder. It is positively buoyant and hovers midwater in large schools in a head-down position (Fig. 1) by sculling with the terminal portion of a long filamentous tail (Van Dijk, 1972; Passmore & Carruthers, 1979). Both *Rana* and *Bufo* are negatively buoyant and are frequently found resting on the bottom. They do not hover midwater and do not have long filamentous tails.

We examine swimming performance by quantifying standard kinematic parameters using high-speed cinematography and computer-assisted frame-by-frame analysis. We use the kinematic parameters most commonly used in studies of aquatic undulatory locomotion in other vertebrates. These include the amplitude, frequency

and length of the propulsive wave, as well as Froude efficiency – a derived measure of kinematic efficiency based on swimming speed of the animal and the speed of the propulsive wave.

We show that the swimming of *Xenopus* larvae differs markedly from *Rana* and *Bufo* in several ways that relate to differences in life history. We also suggest that the distinctive morphologies and modes of swimming reflect major differences in the neuronal mechanisms for regulating locomotion.

MATERIALS AND METHODS

Xenopus laevis larvae were raised in the laboratory and maintained at room temperature ($21 \pm 1^\circ\text{C}$). Four medium-sized larvae (total body length, L, 3.5–4.6 cm) were used to film 21 sequences of normal swimming.

Axial muscle mass was determined by gross dissection of 20 tadpoles ranging from 10 to 90 mm in total length. The masses recorded include notochord and connective tissue. For calculations of centre of mass, tadpoles were cut into 10% L sections and the mass of each section was assumed to be at its geometric centre. All animals used in this study were at free-swimming, pre-metamorphic developmental stages (Nieuwkoop & Faber, 1956).

All other materials and methods were as described by Wassersug & Hoff (1985).

All results are presented in comparison with published data for more typical tadpoles of the families Ranidae and Bufonidae (Wassersug & Hoff, 1985). To facilitate those comparisons, data from *Rana* and *Bufo* are most often pooled. However, where there are major differences among the previously studied species they are treated individually.

RESULTS

In *Xenopus* there is no correlation between swimming speed (U) and tail beat frequency (f) at velocities below 6 L s^{-1} ($r = 0.20$, $P > 0.5$; see Fig. 2). Below 6 L s^{-1} the mean tail beat frequency is 9.75 s^{-1} (s.e. = 1.37). At higher velocities, however, the tail beat frequencies of *Xenopus* tadpoles fall on the regression line for *Rana* and *Bufo* larvae. The lowest swimming speed recorded for *Xenopus* was 2.1 cm s^{-1} or 0.46 L s^{-1} for a 4.6-cm individual. The highest speed was 49.7 cm s^{-1} or 14.2 L s^{-1} for a 3.5-cm individual. Tail beat frequency ranged from a low of 7 s^{-1} to a high of 22 s^{-1} .

The specific maximum amplitude (A) for *Xenopus* is generally lower than for *Rana* and *Bufo* throughout the entire range of swimming speed (Fig. 3). Linear regressions of the log-transformed data show a positive correlation between U and A for both *Xenopus* ($r = 0.40$, $P < 0.05$) and *Rana* and *Bufo* ($r = 0.50$, $P < 0.05$). These two lines differ in both slope ($F = 2302$, $P < 0.05$) and elevation ($F = 594$, $P < 0.05$). The non-*Xenopus* data form two distinct clusters on either side of the common *Rana/Bufo* line. The line, in fact, divides the *Rana/Bufo* group into two by relative tail length; species in the upper group (*Rana catesbeiana* and *Bufo*

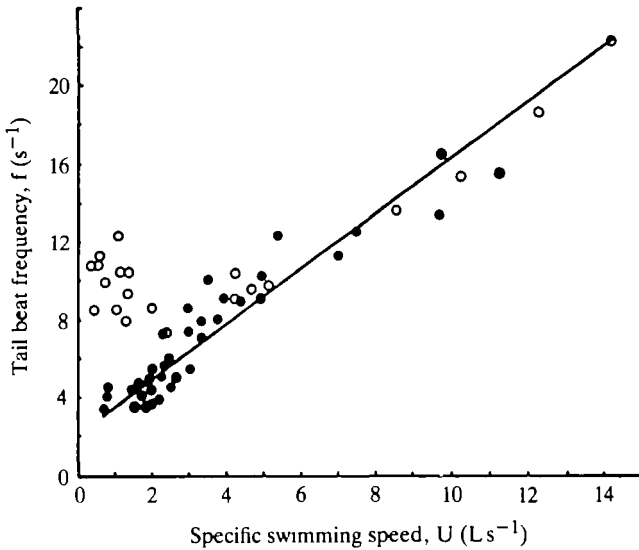


Fig. 2. Tail beat frequency, f , as a function of specific swimming speed, U , for *Xenopus* (○) and *Rana* and *Bufo* (●). All data for *Rana* and *Bufo* shown in this and other figures are taken from Wassersug & Hoff (1985). For *Rana* and *Bufo*, swimming speed increases linearly with tail beat frequency (least-squares linear regression shows $U = 0.67f - 1.25$, $r = 0.95$, $P < 0.01$), while for *Xenopus*, tail beat frequency remains fairly constant at approximately 10 Hz during slow and moderate swimming (up to 6 L s^{-1} ; L = body length), then follows the *Rana* and *Bufo* line.

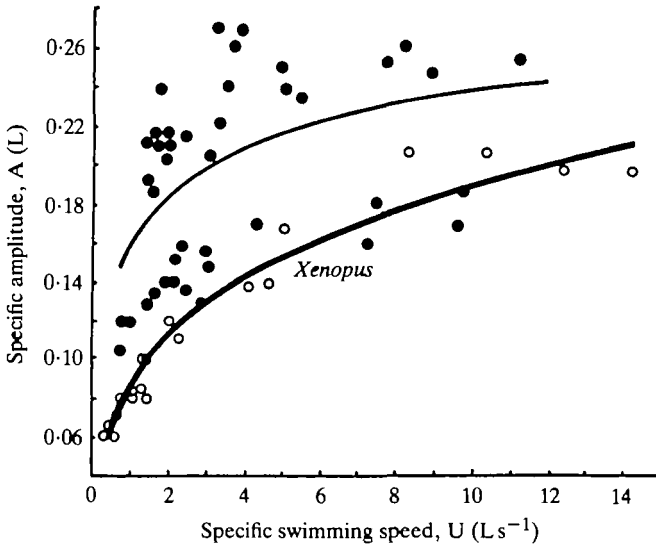


Fig. 3. Specific maximum amplitude (A) for *Xenopus* (○, heavy line), is generally lower than for *Rana* and *Bufo* (●, light line) throughout the entire range of swimming speed, U . Linear regressions of the log-transformed data show a positive correlation between U and A for both *Xenopus* ($r = 0.40$, $P < 0.05$) and the *Rana/Bufo* group. These lines differ in both slope ($F = 2302$, $P < 0.05$) and elevation ($F = 594$, $P < 0.05$). The non-*Xenopus* data form two distinct clusters on either side of the *Rana/Bufo* line which reflect tail length (see text). The upper group (*Rana catesbeiana* and *Bufo americanus*) has relatively shorter tails (60% L , L = body length) and the lower group (*Rana clamitans* and *Rana septentrionalis*) has relatively longer tails (67% L). *Xenopus* has the same relative tail length as the lower group and clusters with those animals (at least at moderate speeds of $3\text{--}9 \text{ L s}^{-1}$).

americanus) have relatively shorter tails (60% L), while those in the lower group (*Rana clamitans* and *Rana septentrionalis*) have relatively longer tails (67% L). *Xenopus* has the same relative tail length as the lower group and clusters with those animals at least at moderate speeds of $3\text{--}9\text{ L s}^{-1}$. A comparison of the regression for *Xenopus* with one for just the longer-tailed ranids ($r = 0.77$, $P < 0.01$) shows that the lines still differ in slope ($F = 445$, $P < 0.05$), but not in elevation ($F = 53$, $0.1 > P > 0.05$). This difference reflects the fact that *Xenopus* can swim more slowly and with much lower tail beat amplitude than any of the other tadpoles. [See Wassersug & Hoff (1985) for further discussion of the kinematic consequences of tail length for the *Rana/Bufo* group.]

The amplitude of the travelling wave all along the body in *Xenopus* is similar to that for *Rana* at high swimming speeds, but at lower velocities *Xenopus* shows lower amplitudes at all points along the body than any of the *Rana* and *Bufo* we have examined (Fig. 4). At all speeds there is considerable yaw at the snout in *Rana* and *Bufo*. *Xenopus*, however, shows no measurable lateral movement of the anterior two-thirds of its body at low speed. At higher swimming speeds *Xenopus*, much like *Rana*, swims with higher amplitudes all along the body and considerable yaw at the snout.

In *Xenopus*, as well as in *Rana* and *Bufo*, there is approximately one full wave on the body at all swimming speeds. For *Rana* and *Bufo* there is no correlation between wavelength and specific swimming speed, but *Xenopus* shows a strong positive correlation between these parameters at lower speeds (Fig. 5). At higher speeds ($>6\text{ L s}^{-1}$) wavelength is relatively constant ($\bar{\lambda} = 0.85\text{ L}$, s.e. = 0.02), following the

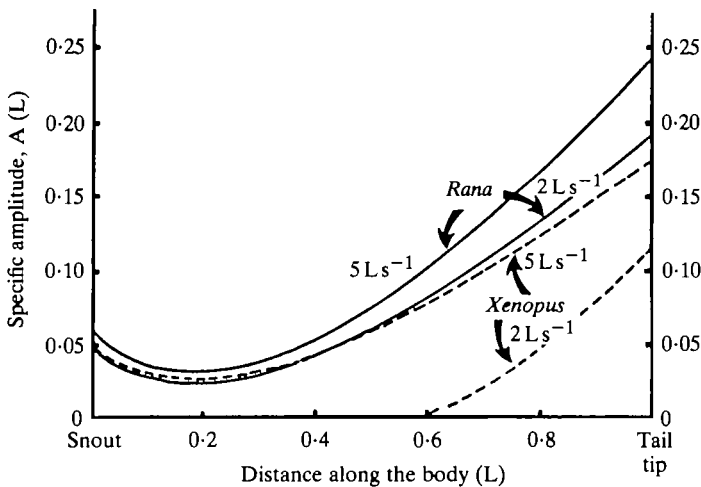


Fig. 4. Specific amplitude as a function of the distance along the body for *Xenopus* and *Rana* tadpoles at low and moderate swimming speeds. *Xenopus* shows no detectable anterior yaw (amplitude = 0) at low swimming speeds, while at higher speeds the snout wobbles back and forth much like *Rana*. For both *Xenopus* and *Rana* the point of minimum specific amplitude is in the region of the otic capsule (0.16 L for *Xenopus* and 0.20 L for *Rana*). L = body length.

pattern of the other tadpoles, although wavelength in the other larvae is considerably greater ($\lambda = 0.96$, S.E. = 0.09).

Froude efficiency [$\eta = 1 - 0.5(1 - U/V)$] (where V is the speed of the propulsive wave) values for *Xenopus* follow the line plotted for the other tadpoles (Fig. 6). However, *Xenopus* will swim readily both slower and faster than other tadpoles. At swimming velocities below those recorded for other tadpoles Froude efficiency is lower and at the highest velocities Froude efficiency is higher for *Xenopus* than for the other larvae.

Xenopus shows a dramatic increase in the relative amount of axial muscle with size ($r = 0.96$, $P < 0.01$; slope = 9.7; see Fig. 7). The smallest *Xenopus* have less than 10% of their mass as axial muscle, while the largest are 45% axial muscle. *Rana* has more axial muscle than does *Bufo* (19–26% compared to 8–14%), but both genera show a fairly constant percentage of axial muscle throughout the entire size range. For these two genera only *Rana catesbeiana* shows a significant increase of muscle mass with size, but the slope is very low ($r = 0.64$, $P < 0.05$; slope = 0.38) compared with *Xenopus*.

Total body mass is also arranged differently in *Xenopus* than in other tadpoles. The centre of mass in *Xenopus* is more anterior (at 17–20% L; $N = 8$) than in *Rana catesbeiana* (at 30–35% L; $N = 6$).

DISCUSSION

Xenopus tadpoles differ from *Rana* and *Bufo* tadpoles in that *Xenopus* swim continuously. This swimming is normally downward against their own buoyancy with little apparent forward movement. At these very low speeds *Xenopus* move only the posterior portion of the tail. This portion of the tail undulates at a near constant frequency (approximately 10 Hz) independent of swimming velocity in the range of slow to moderately fast cruising speeds ($< 6 \text{ L s}^{-1}$). At these speeds *Xenopus* has a relatively novel way of regulating velocity. Instead of increasing tail beat frequency as it increases speed (like most fishes and other tadpoles), *Xenopus* recruits more of the tail, thereby increasing wavelength and propulsive surface area. In contrast, *Rana* and *Bufo* tadpoles swimming at comparable low to moderate speeds use the whole tail. It should be pointed out that although the whole tail undulates in these forms, bends in the posterior portion of the tail may be strictly passive (Wassersug & Hoff, 1985).

These kinematic differences alone suggest that neuromuscular regulation of locomotion is fundamentally different in these two genera. This suggestion is supported by the observation that the spinal cord of *Rana* larvae is dramatically reduced posteriorly compared to that of *Xenopus* larvae of the same size and developmental stage (Nishikawa, Hoff & Wassersug, 1985). Spinal nerves in the posterior portion of the tail of *Xenopus* may thus arise from the spinal cord more caudally than in *Rana*. Furthermore, *Xenopus* myotomes in the posterior portion of the tail abut closely and may be electrically coupled, whereas in *Rana* posterior myotomes are separated by large bands of connective tissue and electrical coupling is not possible (Nishikawa *et al.* 1985).

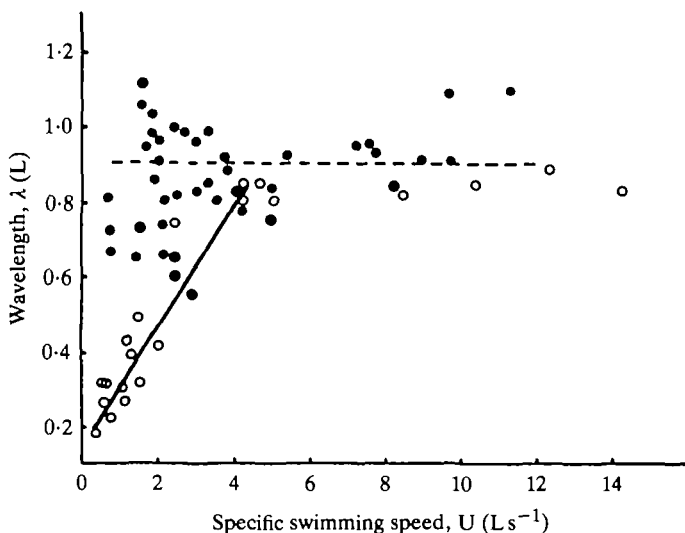


Fig. 5. Length of the wave on the body as a function of specific swimming speed for *Xenopus* (○) and *Rana* and *Bufo* (●) tadpoles. For *Rana* and *Bufo* wavelength (λ) is fairly constant ($\bar{\lambda} = 0.91$, s.e. = 0.09) throughout the entire range of swimming speeds, while in *Xenopus* more of the tail is used as the swimming speed increases from zero up to about 6 L s^{-1} (L = body length). At higher speeds ($>6 \text{ L s}^{-1}$) wavelength in *Xenopus* remains at approximately $0.85L$ (s.e. = 0.02).

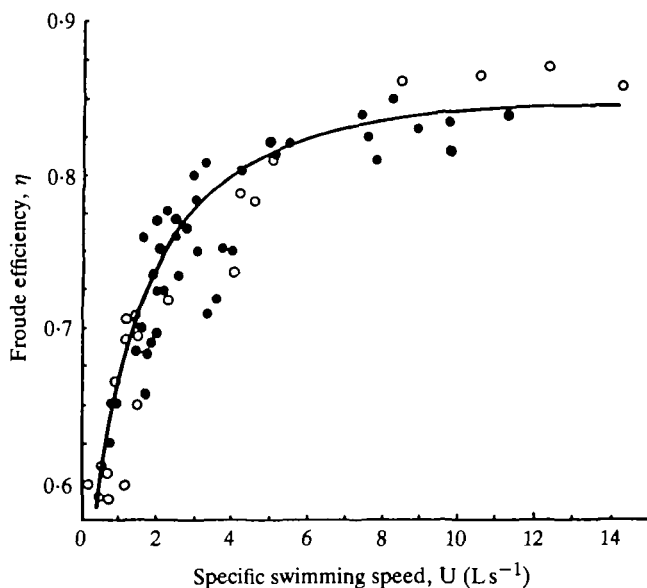


Fig. 6. Froude efficiency, η [$=1-0.5(1-U/V)$], as a function of specific swimming speed. The data are fitted to a rotated rectangular hyperbola. *Xenopus* as well as *Rana* and *Bufo* values follow closely the single, common curve with asymptotes at 0 and 0.84 . This curve closely matches curves for these variables in subcarangiform fishes (Webb, 1984). *Xenopus*, however, is both more efficient at higher swimming speeds and less efficient at lower speeds than tadpoles of the other species.

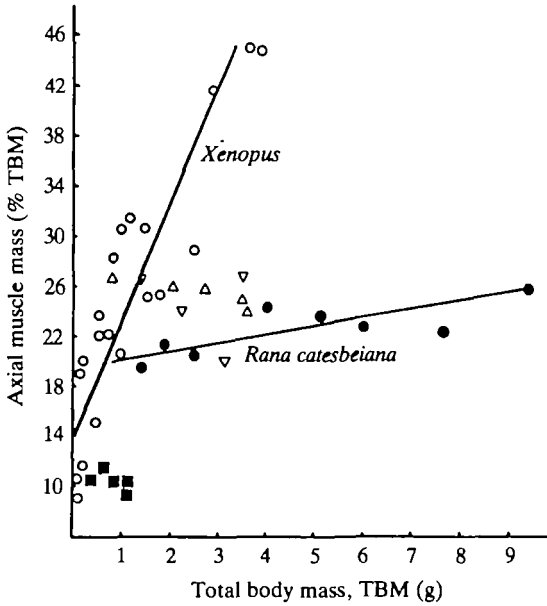


Fig. 7. Axial muscle mass versus total body mass (TBM) for *Xenopus* (○), *Rana catesbeiana* (●), *R. septentrionalis* (△), *R. clamitans* (▽) and *Bufo americanus* (■). Axial muscle mass does not vary with size in *Bufo* and increases only slightly with size in *Rana*. In *Xenopus*, the relative proportion of axial muscle mass increases greatly with size up until metamorphosis.

These structural differences in the nervous system and musculature lead us to suggest that in *Xenopus* reflex loops in the posterior portion of the tail may be much shorter and tail movements may be initiated more caudally than in *Rana*. Also a wave of muscle contraction initiated in the posterior portion of the tail could be transmitted myogenically in *Xenopus* but not in *Rana*. The caudal initiation of movement in *Xenopus* is documented in this study, but myogenic transmission of movement has yet to be demonstrated.

Body morphology and swimming styles have recently been put in the context of feeding strategies for fishes (Webb, 1984) and the same type of analysis is possible for anuran larvae. Although the tadpoles of the three genera studied to date are all suspension feeders, *Rana* and *Bufo* are not obligated to midwater microphagy; the tadpoles of these genera have hard mouth parts that they use to graze on vegetation or other substrates. They are negatively buoyant and are most often found resting on the bottom or in vegetation. They swim only sporadically, either to avoid predation (Huey, 1980; Feder, 1983) or to move between patches of food. When they do swim, they are kinematically similar to fishes like cod and trout (see Hoff & Wassersug, 1985, and references to fish swimming cited therein). However, they usually do not maintain constant velocity for more than a few seconds and even when they are forced to swim in a constant velocity flow chamber their swimming at all flow speeds is often sporadic (Wassersug & Feder, 1983). They swim in short bursts and then allow themselves to drift backwards with the current.

In contrast, the *Xenopus* tadpole has no hard mouth parts and cannot graze on substrates. Rather, it hovers continuously in midwater. In a flow chamber, *Xenopus* maintains its position in the current as the water velocity increases. The anterior portion of the body shows no lateral displacement during slow swimming, but at higher speed there is considerable yaw, much as in *Rana* and *Bufo*. We have little data in the range $2\text{--}5\text{ L s}^{-1}$ so we cannot yet determine whether the shift in swimming mode is achieved by a gradual transition from tail tip to whole body propulsion or whether there is a discrete switch from the slow to fast mode. In Figs 2 and 5 we have tentatively indicated that this shift in swimming mode takes place abruptly at about 6 L s^{-1} , but it may begin at speeds as low as 2 L s^{-1} .

Anterior stability in *Xenopus* at low swimming speeds may be important in maintaining feeding currents for tadpoles in schools (Katz, Potel & Wassersug, 1981). *Xenopus* larvae tend to orient parallel to neighbours in a school (Wassersug, Lum & Potel, 1981), and it is clear from observations of undisturbed tadpoles in schools in large aquaria that the individual tail filament entrains water currents around the body of each tadpole and its neighbours. Large tail amplitude during schooling and lateral displacement of the anterior portion of the body would add turbulence to these otherwise relatively laminar currents and could disrupt feeding. Increased turbulence would also increase the rate of mixing of filtered water with unfiltered water and could lower individual feeding efficiencies (cf. Seale, Hoff & Wassersug, 1982). It may be noteworthy that at higher swimming speeds, when the snout of a *Xenopus* larva wobbles back and forth like that of *Rana* and *Bufo*, *Xenopus* reduces its buccal pumping rates (Wassersug & Feder, 1983). This necessarily reduces buccal irrigation for both respiration and feeding (Seale & Wassersug, 1979; Feder *et al.* 1984).

The mechanism for reducing lateral displacement at the snout is not fully understood. We would expect that any lateral displacement at one end of the body would be accompanied by recoil at the other, but in *Xenopus* no recoil is observed. Because *Xenopus* maintains a full wave in the tail at all swimming speeds, lateral forces would be balanced on either side of the body, and yaw would be reduced. The fact that the propulsive wave has low amplitude (Fig. 3) and is confined to the posterior portion of the tail (Fig. 1) may further reduce lateral displacement at the snout. In addition, Lighthill (1970) suggested that anterior yaw can be reduced in aquatic vertebrates by expanding the forward portion of the body dorsoventrally and moving the centre of mass forward. Indeed, *Xenopus* has a ventral fin that extends forwards onto the body and may serve as a keel to reduce anterior yaw (Fig. 1). Such a fin fold is unknown in bottom-dwelling tadpoles. The centre of mass is also significantly further forward in *Xenopus* than in *Rana*.

The lowest swimming speeds recorded for *Xenopus* are half the lowest speeds recorded for *Rana* and *Bufo* (see region near origin in Fig. 6). We believe that this difference is not due to biased sampling; after many weeks of observing tadpoles swimming in laboratory and field situations we conclude that *Rana* and *Bufo* larvae simply are not capable of sustained swimming at speeds much below 1.0 L s^{-1} .

At these low swimming speeds *Xenopus* swims with a mechanical efficiency more than 50% below the lowest efficiency recorded for *Rana* or *Bufo* (Fig. 6). However, because *Xenopus* uses only the posterior filamentous portion of the tail, little muscle mass is involved in very slow swimming or hovering. Thus, the low mechanical efficiency in *Xenopus* does not reflect low metabolic efficiencies (see Feder & Wassersug, 1984, for metabolic data on hovering *Xenopus* larvae and references cited therein for comparative data on other species).

While *Xenopus* shows the lowest swimming speed and the lowest mechanical efficiency of any tadpole studied to date (Fig. 6), it also has the highest mechanical efficiency and the highest swimming speed. *Xenopus* adults are aquatic and inhabit large, more or less permanent bodies of water. In these large bodies of water the pelagic *Xenopus* larvae occur in open water (Passmore & Carruthers, 1979) and presumably far from cover compared to bottom-feeding tadpoles living in smaller ponds or pools. The greater speed and greater efficiency at high speed of *Xenopus* larvae may reflect the need for longer flights to escape predation.

The positive allometry of muscle mass with body size shown strongly in *Xenopus*, but much less so in *Rana* and not in *Bufo* (Fig. 7), is consistent with this difference in maximum velocity and efficiency at high speed. Both *Rana* and *Bufo* maintain approximately the same proportion of their body mass as muscle throughout their larval lives, while in *Xenopus* relative muscle mass increases dramatically with size.

Gray (1953) states that because the rate of output of energy per weight of muscle does not vary with the size of an animal one would expect maximum velocity to vary as the cube root of body length (if the relative amount of muscle remains the same). Indeed, Fry & Cox (1970) and Wardle (1977) report decreases in maximum specific velocity with increases in length from approximately 25 L s^{-1} for a 20-cm fish to 6 L s^{-1} for a 100-cm fish. In some fishes, muscle mass (as a percentage of total body mass), also decreases with increasing size (47.4% at 20 cm to 37.8% at 100 cm for cod; Bainbridge, 1960), and this may also contribute to the decline in maximum specific velocity. Because *Xenopus* shows the opposite trend (namely the larger individuals have relatively more muscle), we would expect *Xenopus* to show less decline in maximum specific velocity with increasing size than tadpoles of other species.

One reason why other anurans do not increase relative axial muscle mass with increasing size may be that they breed in small bodies of water where the most common predators are relatively small invertebrates. Neither high mechanical efficiency during sustained swimming nor maximum swimming speed may be the critical factor in escaping such predators in these confined habitats. Rather, as Brodie & Formanowicz (1983) and Crump (1984) have suggested, in these situations tadpoles may escape predation simply by growing rapidly and becoming too large to be attacked successfully.

A further reason may be that the overwhelming majority of frogs have terrestrial adults whereas *Xenopus* is totally aquatic. Wassersug & Sperry (1977) have pointed out that during the transition from an aquatic to a terrestrial way of life the anuran is more vulnerable to predation. Therefore, it is reasonable to invest minimally in the

ephemeral tadpole locomotor morphology; principally axial musculature and associated caudal structures. Both *Rana* and *Bufo* have relatively little axial musculature at the onset of metamorphosis and tail resorption is fast. In *Xenopus laevis*, the metamorphic transition is comparatively slow (26 % of larval life compared to a mean of 14 % for 11 other species studied; from data in Wassersug & Sperry, 1977) and metamorphosing *Xenopus* swim relatively effectively using both a long muscular tail and well-developed hind limbs. Thus *Xenopus* does not face the trade-off between high performance in the aquatic environment and the transience of the tadpole body form to the same extent as terrestrial frogs.

Based on adult characteristics, *Xenopus* and other members of its family, the Pipidae, are usually considered to be generalized frogs compared to the ranids and bufonids (e.g. Dowling & Duellman, 1978; Laurent, 1979). The more protracted metamorphosis in pipids, which is here associated with an increase in axial muscle mass in *Xenopus* during larval development, has been independently interpreted as evidence for the more generalized or archaic nature of pipid frogs (Wassersug & Hoff, 1982). Alternatively, it may only reflect continuous occupation of the aquatic environment.

As a final point, our locomotor analysis to date deals strictly with constant velocity swimming in a straight path. It remains to be determined what effects the unusual morphology of the *Xenopus* larva has on swimming performance during acceleration and turning.

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