Vertebral function during tadpole locomotion

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Abstract

Most anuran larvae show large lateral oscillations at both the tip of the tail and the snout while swimming in a straight line. Although the lateral deflections at the snout have long been considered an inefficient aspect of tadpole locomotion, a recent hydrodynamic model suggests that they may in fact help generate thrust. It is not clear though exactly where this bending takes place. The vertebral column is extremely short and seemingly inflexible in anurans, and any axial flexion that might occur there is hidden within the globose body of the tadpole. Here we test the hypothesis that lateral deflections of the snout correlate with bending of the vertebral column within the torso of tadpoles. To quantify vertebral curvature, three sonomicrometry crystals were surgically implanted along the dorsal midline in locations corresponding to the anterior, middle, and posterior region of the presacral vertebral column. Swimming trials were conducted in a flume where synchronized video recordings were collected in dorsal view. Our results confirm that cyclic lateral bending occurs along the vertebral column during swimming and indicate that vertebral curvature is temporally in phase with lateral oscillation of the snout. Lateral oscillation of the snout increased significantly with increasing vertebral curvature. Similarly, tail beat amplitude also increases significantly with increasing vertebral curvature. Our results suggest that cyclic lateral flexion of the vertebral column, activated by the axial muscle within the torso of tadpoles contributes to snout oscillations and the generation of thrust during undulatory swimming in anuran larvae.
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Introduction

Tadpoles wobble when they swim. Not only do their tail tips make large lateral excursions with each tail beat, but their snouts oscillate as well. These lateral deflections of the snout can be as much as a quarter of the maximum amplitude at the tip of the tail (Wassersug and Hoff, 1985). Such movements are extreme enough to have given tadpoles their vernacular name "polliwogs," meaning "wiggling heads" (from Middle English "polwigle" = "pol" for head + "wog" from wiglen, to wiggle).

Lateral oscillations at the snout for any vertebrate swimming on a straight path look fundamentally inefficient. During rectilinear locomotion, lateral deflections of the snout do not appear to contribute to thrust, yet require energy. *Prima facie*, the greater the yaw for any elongated vertebrate swimming otherwise in a straight line, the greater the surface area of the animal

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that is perpendicular to the path of motion. In steady flow this increase in frontal area would add to pressure drag.

It is not surprising then that tadpoles have long been presumed to be inefficient swimmers, at least compared to most teleost fishes; in fact, they have been the reference organisms for poor vertebrate swimmers. In discussing Paleozoic ostracoderms, for example, Romer (1966) declared "… the locomotion of the oldest vertebrates must have been of the relatively ineffective and uncontrolled type seen in a frog tadpole."

Wassersug and Hoff (1985) suggest that, given their generally globose bodies, the increase in frontal area with snout oscillations may not be that substantial. Also, given the relatively low Reynolds numbers at which tadpoles swim ($Re \sim 10^3$–10^4; Liu et al., 1996), small changes in pressure drag may not be especially costly (cf. Aleyev, 1977, p. 10).

In trying to formulate an adaptive argument for why lateral deflections at the snout may actually be advantageous rather than detrimental for tadpoles, Wassersug (1989) suggested that most tadpoles, as suspension feeders and grazers, more often swim to escape predators rather than to chase active prey. As such, they do not need to keep their snouts on a straight path or target as they swim. Instead, constant yawing motions of their snouts means that they initiate a new turn with each half tail beat, which is ideal for evading an attacking predator.

A more recent three-dimensional computational model of the unsteady flow around a swimming tadpole by Liu et al. (1997) challenges the presumption that yawing of the head is fundamentally inefficient. Liu et al. showed, to the contrary, that the lateral oscillations of a tadpole's snout produce strong girthwise (i.e., crosswise) flow that shifts from side to side fast enough to produce leading-edge suction at the snout. This region of alternating suction corresponds to an alternating high-pressure region on the opposite side of the snout with each half tail beat. Thus, provided that the snout is deflected actively and forcefully, the leading edge suction produced by this motion could actually contribute (modestly at least) to thrust.

While this is the antithesis of the view that the oscillations at the snout of a swimming tadpole are costly and inefficient, what is left unexplained is where along the axis of the body these yawing motions are produced. If Liu et al. (1997) are correct that the rostral oscillations help to generate thrust, we would expect them to be actively produced and not simply the result of passive recoil from oscillations generated in the tail. In fact, the amplitudes of the lateral movements at the snout tip and the base of the tail compared to the point of least lateral extension (which lies between the ears) suggest that some bending must be taking place within the common head-body of the anuran larvae. However, because of the rotund nature of the head-body of tadpoles, deformations within the trunk have not been reported nor are they visible on high-speed videos of swimming tadpoles [see, for example, Fig. 9 in Wassersug and Hoff (1985), which depicts a *Rana catesbeiana* (bullfrog) tadpole swimming at approximately 8 bodylengths/s, recorded at 200 frames/s].

In fact it is not obvious where or how tadpoles might produce lateral bending within their common head-body. Both adult and larval anurans share an extremely short torso and an exceptionally short vertebral column (Handrigan and Wassersug, 2007). Other than the larvae of some megophryid toad-frogs, tadpoles typically have less than a dozen vertebrae overall and <10 presacral vertebrae (Haas et al., 2006; Handrigan et al., 2006). This short stiff torso is thought to facilitate jumping in adult frogs, but may also restrict lateral bending of the trunk in tadpoles (most recently reviewed in Handrigan and Wassersug, 2007). In theory, the movement could take place between the occipital region of the cranium and the first vertebrae. However, both tadpoles and frogs characteristically lack the cervical specializations that permit a large range of motion between the cranium and the torso in most tetrapods – i.e., anurans lack an anatomical neck. The only known exception is in the genus *Leptobrachella*, which has an actively burrowing tadpole and an atlas–occipital complex that permits a large range of motion at this joint (Haas et al., 2006).

In this paper we use sonomicrometry to test the hypothesis that tadpoles in fact bend their whole vertebral column within their globose bodies. We examine whether the kinematics of this bending are consistent with it being the mechanism for lateral deflections of the snout during rectilinear swimming in tadpoles. Lastly we assess whether the axial musculature within the torso is adequate for actuating this movement.

Materials and methods

Study animals

Four *R. catesbeiana* tadpoles ranging in total length from 10.1 to 11.5 cm were used in this study (Table 1). Tadpoles were housed in glass aquaria and maintained on a diet of Reptomin© sticks (Tetra Terrafauna Inc., Melle, Germany) provided *ad libitum*. Developmental stages of the tadpoles ranged from 33 to 35 (Gosner, 1960). All animal care and experimental protocols used in this study were approved by the University of Massachusetts Institutional Animal Care and Use Committee.

Table 1. Kinematic data from five steady swimming trials per individual

Ind.	Total length (cm)	Tail beat amplitude (cm)	Tail beat freq. (hz)	k (cm^{-1})	Snout deflection (cm)	V (cm/s)	Froude efficiency
1	10.8	0.17 ± 0.02	4.05 ± 0.50	0.07 ± 0.01	0.038 ± 0.005	43.58 ± 5.36	0.73 ± 0.02
2	10.5	0.22 ± 0.14	4.49 ± 0.39	0.10 ± 0.01	0.066 ± 0.009	47.16 ± 4.17	0.82 ± 0.02
3	11.5	0.21 ± 0.01	3.95 ± 0.32	0.14 ± 0.02	0.074 ± 0.006	45.38 ± 3.68	0.83 ± 0.02
4	10.1	0.17 ± 0.02	3.96 ± 0.15	0.10 ± 0.01	0.056 ± 0.004	39.97 ± 1.53	0.76 ± 0.03

k is vertebral curvature; V is wavespeed; means $\pm$ S.E.M. are presented.

Morphology

Morphological measurements were collected following the swimming experiments described below. Tadpoles were euthanized with an overdose of tricaine methanosulfonate (MS222). Total length and snout–vent length were measured externally with a ruler. Tadpoles were then fixed in formalin and sectioned (thick sections) at 20 intervals corresponding to 5% of total length. Sections were photographed with a Nikon Coolpix 990 digital camera (Nikon Corp., Melville, NY, USA). Digital images were uploaded to a Macintosh computer and analyzed using Image-J (v. 1.32) software (http://rsb.info.nih.gov/ij/). Each image was calibrated using a small ruler placed in the field of view of the digital images (Standard error <0.001 cm; ~ 400 pixels/cm). For all 19 sections the area of the image corresponding to axial muscle was quantified. The percentage of axial muscle present at each body position was calculated as the area present in each section divided by the total area of axial muscle summed over all 19 sections. Data from all four individuals were pooled and used to generate a single curve describing the relative axial muscle mass present at each body position.

Sonomicrometry and videography

In this study sonomicrometry was used to measure length changes along the vertebral column of tadpoles during swimming. Instantaneous length changes were then used to calculate vertebral curvature. Tadpoles were anesthetized using a 1 g/L solution of MS222 buffered with sodium bicarbonate. Once anesthetized, an incision was made in the skin covering the trunk. Three piezoelectric crystals, each 1 mm in diameter, were placed along the dorsal midline of tadpoles. The location of crystals corresponded to the anterior, middle, and posterior regions of the vertebral column (Figs. 1a and b). Each crystal was tightly secured in place using 6-0 silk sutures. The distance between each crystal pair was measured with digital calipers during surgery. While the tadpoles were still anesthetized, the

piezoelectric crystals were connected to a sonic micrometer (TRX-6, Sonometrics Corp., Toronto, ON) and axial bending was imposed on the tadpole to ensure secure placement of the transmitter and confirm signal quality. The resting distances between each pair of crystals were confirmed while anesthetized tadpoles were stretched straight. The skin incision was then closed with 6-0 silk sutures.

Tadpoles were given about 45 min to recover from anesthesia and then placed in a swim flume with a working section of 65 cm $\times$ 20 cm $\times$ 20 cm (Loligo Systems, Hobro, Denmark). Sonomicrometry data were collected at sampling frequency of 496 Hz, with a
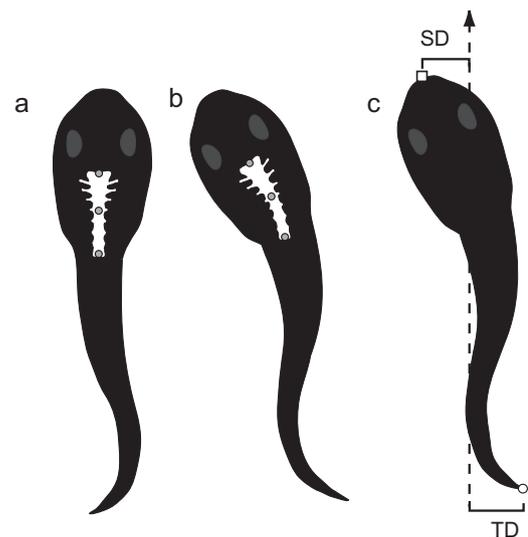

Fig. 1. Sonomicrometry and kinematic measurements during swimming. (a) The location of three sonomicrometry crystals along the vertebral column (grey markers). This crystal arrangement was used to measure three straight-line distances: anterior to middle, middle to posterior and anterior to posterior. Instantaneous changes in these distances were used to calculate vertebral curvature. The tadpole is shown with the trunk held straight and no vertebral curvature (a) and with the snout deflected laterally as a result of increased curvature of the vertebral column (b). The lateral deflections of the snout (SD) and tail (TD) are measured relative to the path of travel (c).

transmit pulse of 535 ns and using 1.54 mm/μs as the speed of sound. Raw data files were then converted to ASCII format and exported to Sonoview (v. 3.1.4) for post-processing. The sonomicrometry data for each swimming sequence were smoothed using a running average algorithm with a five-point window. Filtered data were overlaid onto raw traces to ensure that the peak length changes were not significantly altered as a result of the smoothing protocol. Unsteady and non-linear swimming trials resulted in obvious asymmetries in the sonomicrometry traces and were discarded. Analysis was limited to steady swimming sequences with a minimum of four complete tail beat cycles and five swimming bouts were analyzed per individual.

Swimming bouts were filmed in dorsal view at 30 frames/s (60 fields/s) using a Sony DCR-VX2000 camcorder (Sony Corp., New York, NY, USA). Sonomicrometry traces were superimposed onto video recordings using a TelevEyes/Pro video overlay box (Digital Vision Inc., USA). The synchronized video was captured on a Sony, GV-D900 digital video recorder (Sony Corp., New York, NY, USA). This process allowed us to correlate the swimming kinematics with sonomicrometry measurements.

Data analysis

Instantaneous distances between crystal pairs were converted to vertebral curvature using geometric calculations. First, an instantaneous radius of curvature (R) was calculated in centimeters for the vertebral column using the following equation:

$$R = D_{ap}/(2 \cos(\sin^{-1}(D_{ap}/(D_{am} + D_{mp})))), \qquad (1)$$

where D_{am} is the straight line distance between the anterior and middle crystals, D_{mp} the the straight line distance between the middle and posterior crystals, and D_{ap} the straight line distance between the anterior and posterior sonomicrometry crystals. Although the length changes measured along the vertebral column were relatively small, they were at least an order of magnitude above the maximum resolution of the sonometrics system (24 μm). The radius of curvature was used to calculate curvature, κ (cm^{-1}), using the following equation:

$$\kappa = 1/R. \qquad (2)$$

When the vertebral column is straight, D_{ap} equals $D_{am} + D_{mp}$ (Fig. 1a); therefore, the radius of curvature becomes infinitely large and κ approaches zero. As the vertebral column bends the sum of D_{am} and D_{mp} become larger than D_{ap}, the radius of curvature decreases and κ increases (Eq. (1)). For each swimming bout, the maximum curvature value for each tail beat was used to calculate a mean maximum curvature for that bout.

Videos of swimming bouts were used to measure the lateral oscillation of the snout, tail beat frequency, tail beat amplitude, and Froude efficiency (Table 1). The video analysis was performed using Image-J (v. 1.32) software. Snout oscillations were measured by tracking the position of a digitized point on the tip of the snout throughout the swimming sequence. For each tail beat, the maximum lateral deflection of the snout was quantified relative to the path of travel (Fig. 1c). Mean snout deflections were then quantified for each swimming bout. Tail beat amplitude was similarly measured by tracking the position of a digitized point on the tip of the tail throughout the swimming sequence. For each tail beat, the maximum lateral deflection of the tail tip was quantified relative to the path of travel (Fig. 1c). Mean tail beat amplitudes were then quantified for each swimming trial. Tail beat frequency was quantified as the number of tail beats in a swimming bout divided by the duration of that bout. Froude efficiency (FE) (Webb, 1975) is described by the following equation:

$$FE = 1 - 0.5(1 - U/V), \qquad (3)$$

where U is the swimming speed and V (wavespeed) the rearward speed of the propulsive wave in the tadpole's tail. For each swimming trial, U was based on the calibrated speed of the swim flume and ranged between 1 and 4 bodylengths/s. Wavespeed was measured by tracking and quantifying the average velocity of a digitized landmark on the crest of each undulatory wave. Mean wavespeed for all tail beats in a swimming bout was used in the above equation to quantify Froude efficiency.

To examine how each kinematic variable is correlated with vertebral curvature, a major axis regression (orthogonal regression) was performed on vertebral curvature and each of the four kinematic variables for each individual. Since no significant difference ($p > 0.05$) was detected between the regression lines of individuals, data from four individuals were pooled and used in a single major axis (MA) regression analysis. MA regressions were performed with JMP v. 5.0 (SAS, Cary, NC, USA) assuming equal variance. Pearson product–moment correlation coefficients and p-values ($\alpha = 0.05$) were calculated for each regression.

Results

Trunk morphology

The eight vertebrae that make up the entire vertebral column of the R. catesbeiana larvae are all contained within the tadpole's globose body (Fig. 1). The trunk makes up about 33% of the total length of the tadpole. The vertebral column makes up approximately 20% of

the total length of the tadpole. The remaining portion of the common head-body contains the cranium.

The trunk musculature of tadpoles is segmented, with myosepta forming clear boundaries between subsequent segments. A total of eight myomeres are present in the trunk, each corresponding to one vertebral segment. All eight segments attach directly to the vertebral column and increase in size from anterior to posterior (Fig. 2a). Our results show that 39% of the total axial musculature is held within the globose bodies of tadpoles while the remaining 61% is in the tail (Fig. 2). The substantial amount of axial muscle within the torso of tadpoles suggests that the trunk portion of this musculature plays an important role in tadpole locomotion.
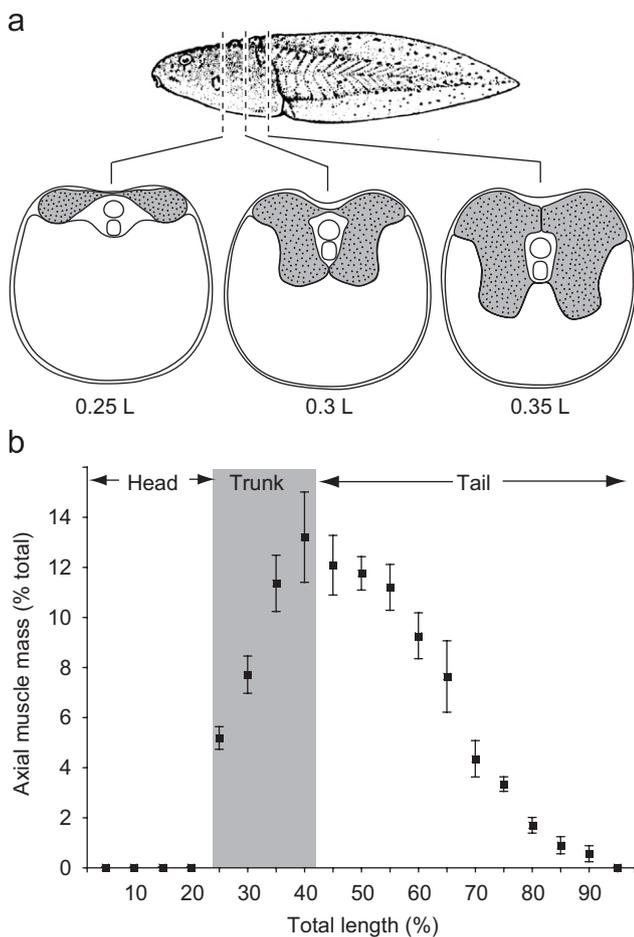

Fig. 2. Distribution of trunk musculature in bullfrog tadpoles. (a) Transverse sections of the trunk highlight the musculature (in grey) hidden within the globose body of anuran larvae. The trunk musculature attaches directly onto the vertebral column. (b) The distribution of axial muscle mass along the length of the tadpole. Sections at 5% intervals of total length were used to quantify the percentage of the total amount of axial muscle present at each point along the body. On average 39% of the axial musculature is located in the trunk. Means $\pm$ SD are shown for four individuals. Tadpole image is modified from Hoff and Wassersug, 2000.

Vertebral curvature during swimming

Instantaneous curvatures of the vertebral column calculated using sonomicrometry are shown alongside movements at the tail and snout in Fig. 3. We find that vertebral curvature changes during swimming and that such changes are in phase with lateral oscillation of the snout (Fig. 3). Movements at the tip of the tail were out of phase with vertebral bending. This phase shift results from the time required for an undulatory wave to propagate down the tail. Instantaneous changes in curvature suggest that vertebral bending is closely associated with snout oscillation.

To assess the function of vertebral bending, the average maximum vertebral curvature for each swimming trial was plotted against four kinematic variables and MA regressions were performed. The results show that the magnitude of vertebral curvature correlated significantly with the magnitude of snout oscillations ($R = 0.84$, $p < 0.001$; Fig. 4a); i.e., increased vertebral curvature corresponds with increased lateral deflection of the snout. We also found that vertebral curvature is significantly correlated with tail beat amplitude ($R = 0.59$, $p = 0.009$; Fig. 4b) such that larger lateral movements anteriorly correspond to larger undulatory waves at the tail tip. We found no significant correlation between vertebral curvature and tail beat frequency (Fig. 4c). Our results also show that Froude efficiency is significantly correlated with vertebral curvature ($R = 0.73$, $p = 0.003$; Fig. 4d) suggesting that swimming trials with greater vertebral curvature are more efficient at transferring propulsive forces to the water.

Discussion

Our data demonstrate that alternating left–right lateral bending of the trunk in tadpoles occurs during normal straightforward swimming. This axial bending correlates nicely with both oscillations of the tail tip and of the snout as tadpoles swim in a straight line: the higher the curvature of the vertebral column, the greater the amplitude of the lateral deflection at either the rostral or the caudal end of the tadpole.

We can be confident that the majority of lateral bending that we observed is not taking place at the articulation of the cranium with the atlas for two reasons. First, movement at this joint is restricted in *Rana* by the arrangement of the condyles between the first vertebra and the occipital region of the skull. These condyles in *R. catesbeiana* are bilateral and widely separated with a midline rostral projection (as illustrated and described for *R. esculenta* in Ecker, 1971). This configuration may permit some dorso-ventral flexion, but little lateral flexion.
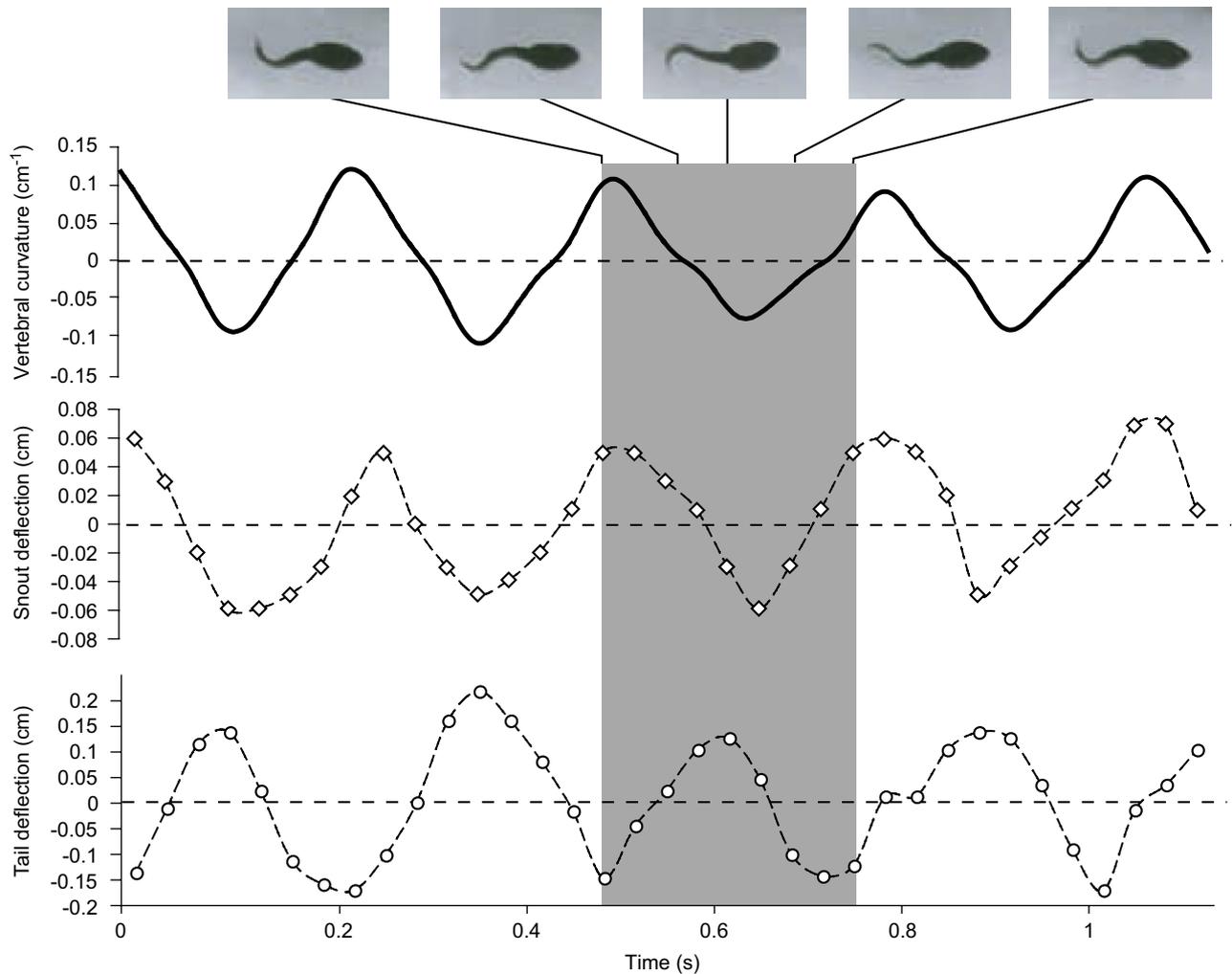
Fig. 3. Time-series traces of vertebral curvature and swimming kinematics. Vertebral curvature (calculated from sonomicrometry data) is shown (solid black) above the lateral deflection at the tip of the snout and the tail. Movements to the tadpole's left are measured as negative and movements to the right as positive values. Video frames for a single tail beat are shown at 0.06 s intervals (highlighted region). Note that changes in vertebral curvature are in phase with snout oscillations.

Secondly, the musculature running from the torso to the cranium is slight in *R. catesbeiana* and makes up less than 5% of the total trunk musculature (Fig. 1). In some burrowing and stream-associated tadpoles, such as those of *Otophryne* (Wassersug and Pyburn, 1987), a substantial amount of both paraxial muscle and ventral musculature (i.e., a rostral extension of the m. rectus abdominis) continues far forward onto the head. These rostral attachments improve mechanical advantage of these muscles for cranial flexion and extension. In *R. catesbeiana*, however, there is no forward extension of the dorsal musculature and the longitudinal abdominal muscle is slight. Whatever lateral bending takes place between the atlas and the skull during normal undulatory swimming in these tadpoles must be of the same order of magnitude of that seen between subsequent vertebrae, if not less.

The magnitude of axial bending within the vertebral column is not correlated with tail beat frequency. This suggests that tail beat frequency is controlled largely within the tail proper and not obligatorily linked to the amplitude of cranial movement. Indeed the lack of a correlation between tail beat frequency and vertebral bending is most evident when tadpoles swim at slow speeds (Hoff and Wassersug, 2000). At the slowest swimming speeds ($\sim$1 L/s) tadpoles use a relatively high tail beat frequency but limit the recruitment of the axial musculature to the posterior third of the tail (electromyographic data in Hoff and Wassersug, 2000).

Vertebral curvature is correlated with Froude efficiency in swimming tadpoles. This correlation provides further support for the hypothesis generated from a computational fluid dynamic model, which showed that "fish-like" swimming kinematics (with no snout oscillations) imposed on a tadpole body results in decreased
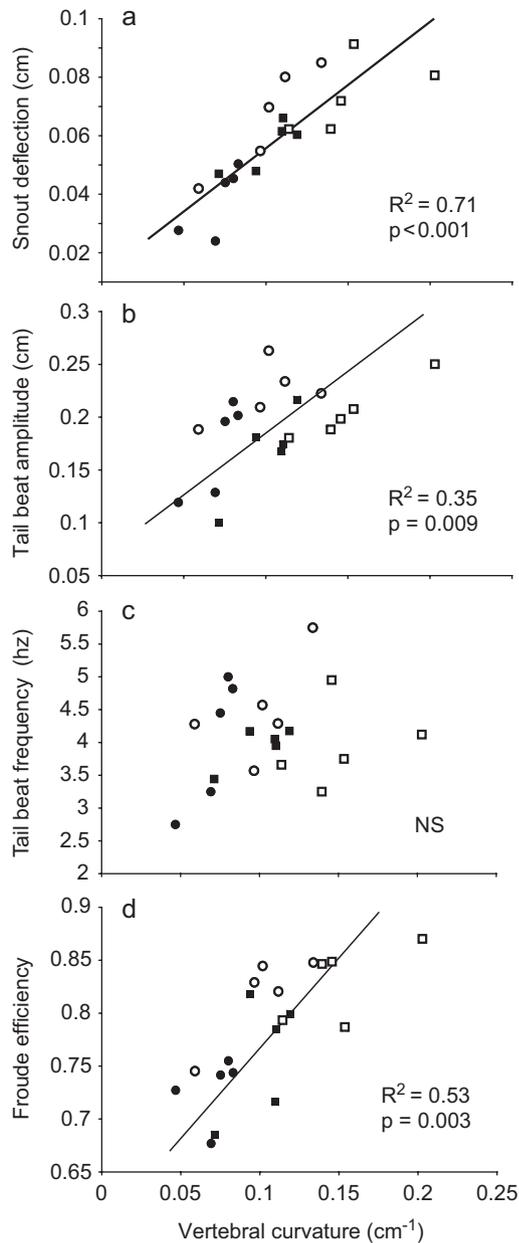
Fig. 4. Relationships between the magnitude of maximum vertebral curvature and swimming kinematics. Average values are calculated for each swimming trial and each individual is represented by a different symbol (five trials per individual). Data from all individuals are pooled and a major axis regression is used to assess the correlation between variables. These results show that the average maximum lateral oscillations of the snout (a), tail beat amplitude (b), tail beat frequency (c), and Froude efficiency (d) are significantly correlated with vertebral curvature. Froude efficiency is calculated as $1 - 0.5 [(V-U)/V]$, where U is the swimming speed and V the speed of the propulsive wave.

efficiency (Liu et al., 1997). Our results highlight the potential mechanism by which the bending of the axial skeleton rostral to the tail aids locomotor efficiency in tadpoles.

Although this study focused on the steady swimming behavior of tadpoles, the actions of the trunk will likely play an even more significant role during turning and escape maneuvers. In fact, tadpoles rarely swim steadily along a straight path for more than a few seconds (Wassersug, 1989) but rather have the propensity to swim along curvilinear paths and initiate tight turns to evade predators. Since the lateral movements of the head are relatively large during turns and escapes (Eidietis, 2006), the magnitude of vertebral curvature may far exceed that observed during steady rectilinear swimming. Therefore, bending of the vertebral column is likely to also play a crucial role in directional changes associated with these non-steady behaviors.

Our data on the distribution of axial muscle in a bullfrog tadpole closely match data in Wassersug and Hoff (1985). Approximately 40% of the axial musculature is found within the torso. This is such a large proportion of the total body mass of an anuran that it would be unlikely to be either vestigial or purely embryonic. However, since deformation of the body is not conspicuous when tadpoles swim, it was not a foregone conclusion that this musculature contributed to tadpole locomotion. Indeed, as with most of the limb musculature in a developing tadpole, axial muscles could have a function in the post-metamorphic anuran without being active in the tadpole stage.

The data presented here, in conjunction with electromyographic data in Hoff and Wassersug (2000), support the idea that the axial musculature actively bends the torso during swimming in the premetamorphic anuran, even if that bending is not externally visible. The maximum amount of bending for the whole vertebral column is approximately 25° during steady swimming. This is a large enough range of motion that it could not occur at just one or two intervertebral joints without anatomical specializations. Such specializations have not been observed in *Rana* tadpoles. It appears instead that the lateral bending of the torso is distributed along the length of the presacral vertebral column. In that case this would only amount to 3–4° of bending at each intervertebral joint. Examination of cleared and stained specimens suggests that the ossified vertebral centra of tadpoles are separated far enough from each other to permit this amount of bending. A comparison of the trunk and tail curvatures suggests that the presence of ossified centra within the trunk does not constrain the magnitude of bending but rather directs it to the intervertebral joints.

Our study only examined yawing motions and did not explore how tadpoles accomplish pitching movements, which, as pure actions, are minimal for tadpoles. Because tadpoles typically live in shallow water, most of their movements are in the horizontal plane. Even when bullfrog tadpoles surface to breathe air, they descend not by pitching over, but by sharply turning to their side (Wassersug et al., 1999).

Some tadpoles can be forced to swim in a vertical plane in unique situations, such as in microgravity (see figures in Wassersug, 1992). *Xenopus laevis* larvae in this situation executed repetitive outside loops. Those tadpoles pitch downward by bending their tails in the vertical plane. Although we have not been able to collect data on *R. catesbeiana* tadpoles making pitching motions, there is no evidence that they have any more dorso-ventral flexibility in their axial skeleton than they do for lateral bending.

One hypothesis that follows from our data is that the anuran genera with the fewest vertebrae should also have the least amount of rostral yaw during swimming. Anurans of the family Pipidae have the fewest presacral vertebrae (5–8, Trueb, 1973) and, consistent with our hypothesis, they do not oscillate their snouts during normal locomotion. Whether mid-water suspension feeders (e.g., *Xenopus*; Hoff and Wassersug, 1986) or predators that slowly stalk active prey (e.g., *Hymenochirus*; Deban and Olson, 2002), pipid larvae scull with their tail tips and do not incorporate any lateral flexion of their torso when swimming at normal speed.

In conclusion, the axial musculature of non-pipid tadpoles is adequate to contribute significantly to both rostral and caudal lateral oscillations during rectilinear locomotion. Although their vertebral skeleton is short, anurans such as *Rana* have enough vertebrae and range of motion at each intervertebral joint to collectively account for the observed lateral deflections at their snout during normal swimming. As suggested by Liu et al. (1997), left–right oscillations at the snout may contribute to the generation of thrust rather than cause drag during tadpole locomotion.

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